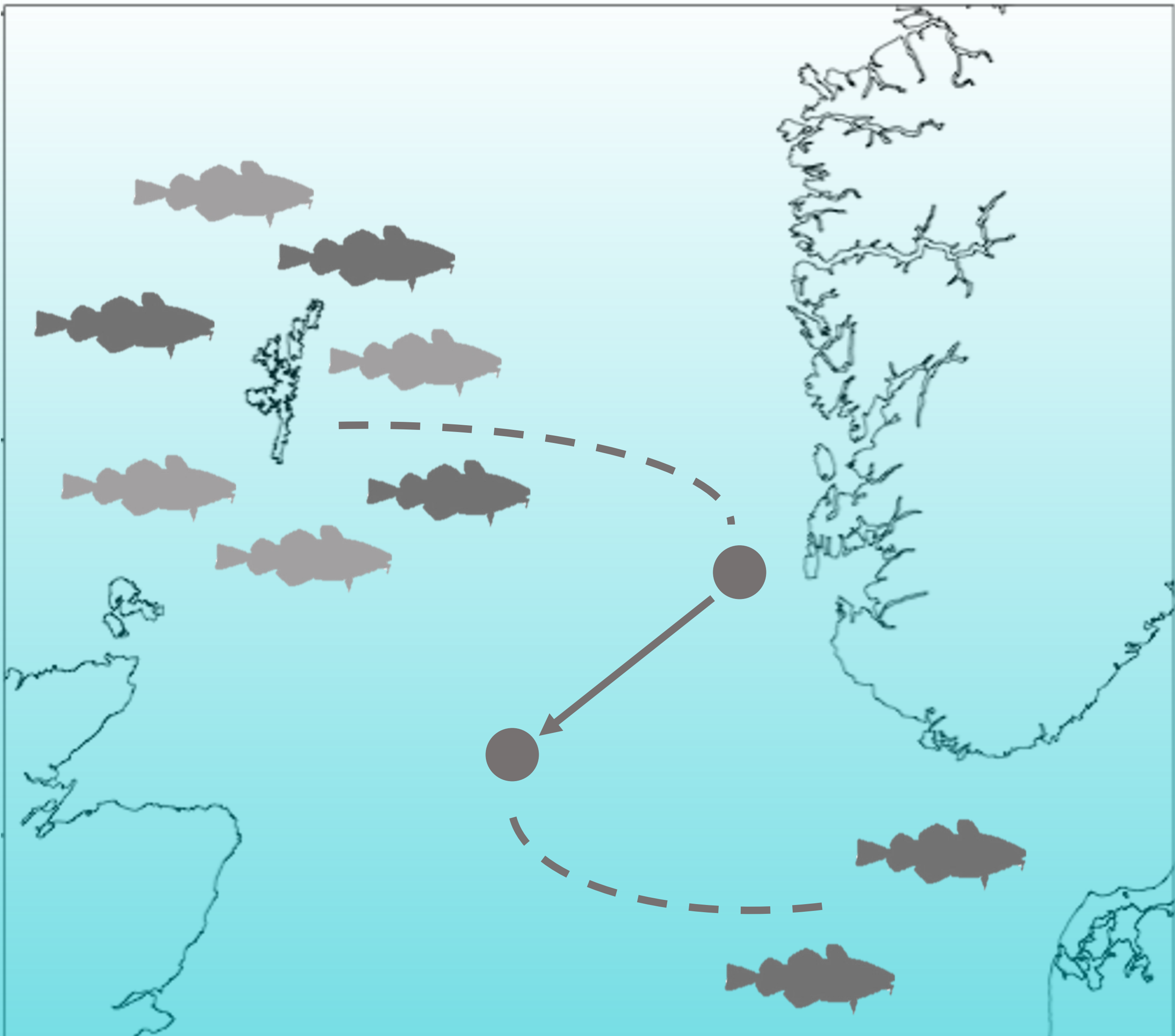

Regime shifts in perspective

The North Sea and Atlantic cod (*Gadus morhua*) as paradigmatic examples

Alexandra M. Blöcker

"*A day without laughter is a day wasted*"
Charlie Chaplin

I dedicate this thesis to my always beloved

Mutti Marion,

who always believed in me, supported all my crazy ideas,

and always ensured me to be on the right track.

Thank you Mom.

You may be out of my sight, but you will always be with me.

Regime shifts in perspective

- The North Sea and Atlantic cod (*Gadus morhua)* as paradigmatic examples -

DISSERTATION
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ABSTRACT

Marine ecosystems are heavily impacted by anthropogenic stressors, in particular fish stocks worldwide are overexploited. Policies were implemented to reduce fishing pressure and to aim for fish stock recovery to sustain impacted socio-ecological systems, with limited success. Recovery can be hindered by so-called regime shifts, where a system can no longer withstand the pressure of certain drivers, loses stability in structure and functioning, and abruptly shifts to another system state. Transforming back to a former state can be hampered by hysteresis and irreversibility.

The North Sea and Atlantic cod (*Gadus morhua*) are paradigmatic examples for regime shifts. Both have been affected by regime shifts, with North Sea cod remaining in a depleted state. A common understanding among stakeholders about the regime shift concept, underlying driving forces, and consequences of these shifts are of high importance, as a foundation for sustainable management measures to avoid marine resource depletion.

This thesis focuses on the framing of the regime shift concept among stakeholders involved with Atlantic cod and regime shifts in the North Sea, as well as the detection of regime shifts in the North Sea fish community, with a particular focus on Atlantic cod. I used qualitative and quantitative methods to analyze the perception of different stakeholders on regime shifts and to determine underlying regime shift drivers as well as recovery potential of fish stocks.

We first studied stakeholders' conceptual framing around the regime shift concept using semi-structured interviews (Chapter I). We found that, based on different perceptions of the details of a regime shift, knowledges vary from non-knowledge (no knowledge) and general knowledge (abrupt changes) to detailed knowledge (multiple states). Furthermore, the application of the concept is diverse, depending on differences in reference states, and temporality and time, featuring different outcomes of whether and how a regime shift has occurred.

Knowing that regime shift dynamics can diminish successful fisheries management, we further analyzed if the implementation of the Common Fisheries Policy was successful to reduce fishing pressure and to enhance fish stock recovery (Chapters II, III). We found that fishing reduction can be a success through positive tipping if populations, such as plaice (*Pleuronectes platessa*) and hake (*Merluccius merluccius*), are not strongly influenced by regime shift dynamics and not critically affected by increased sea temperatures (Chapter II). However, regime shift dynamics can prevent fish stock recovery through negative tipping, as for saithe (*Pollachius virens*) and Atlantic cod, if non-linear stock dynamics and hysteresis, caused by the interplay of long-term high fishing pressure and increased temperatures, occur. Cod in particular transitioned to a collapsed state and recovery potential is low (Chapter III). Low recruitment and spawning stock biomass, fishing pressure above sustainable reference levels, changes in phytoplankton and zooplankton abundances, and temperature increase trap cod in a depleted state. Lastly, we investigated if a system can be transformed back to former levels or remains in an irreversible state (Chapter IV). We found that the North Sea fish community underwent an irreversible regime shift from a gadoid to a demersal dominated state.

Due to changes in structures and functioning, regime shifts have strong implications for the socio-ecological system. The findings in this thesis highlight that an adaptive ecosystem-based management approach is required to successfully manage fish stocks in the North Sea. A common understanding of the regime shift concept among stakeholders is essential to support communication and enhance the acceptance of management measures. Including stakeholders in decision-making and incorporating regime shift dynamics in fisheries management can help decision-makers to grasp regime shift states and resulting consequences, thereby enabling them to apply adjustable management measures for realizing a sustainable socio-ecological system

ZUSAMMENFASSUNG

Marine Ökosysteme werden durch anthropogene Treiber stark beeinflusst und gerade Fischbestände sind weltweit überfischt. Um den Fischereidruck zu senken und hiermit die Fischbestände wiederherzustellen, wurden umfassende Richtlinien eingeführt. Diese waren jedoch nur teilweise erfolgsversprechend. Die Erholung von Fischbeständen kann durch sogenannte Regime Shifts verhindert werden: Ein System kann dem Druck durch bestimmte Einflüsse nicht mehr widerstehen, verliert hierdurch seine Stabilität in Struktur und Funktionalität, und transformiert abrupt zu einem neuen Zustand. Diesen neuen Zustand in den alten Zustand umzukehren, kann durch Hysteresis und Irreversibilität verhindert werden.

Die Nordsee und der Atlantische Kabeljau (*Gadus morhua*) sind exemplarisch für Regime Shifts. Beide wurden durch Regime Shifts beeinflusst, wodurch der Nordsee Kabeljau sich noch stets in einem erschöpften Zustand befindet. Ein gemeinsames Verständnis des Regime Shift Konzepts zwischen Interessenvertretern, sowie der zugrundeliegenden Treiber und der Konsequenzen eines Regime Shifts ist daher für eine nachhaltige Bewirtschaftung erschöpfter mariner Ressourcen enorm wichtig.

Die vorliegende Doktorarbeit beschäftigt sich mit der Rahmung des Regime Shift Konzepts zwischen Interessenvertretern die sich mit dem Kabeljau und Regime Shifts beschäftigen, sowie mit der Erkennung von Regime Shifts in der Nordseefischgemeinschaft, mit einem Augenmerk auf dem Kabeljau. Ich habe qualitative und quantitative Analysen genutzt, um die Wahrnehmung von Regime Shifts bei unterschiedlichen Interessenvertretern, zugrundeliegende Treiber und das Erholungspotential von Fischbeständen zu analysieren.

Zunächst führten wir semi-strukturierte Interviews durch, um die konzeptionelle Rahmung des Regime Shift Konzepts durch Interessenvertreter festzustellen (Kapitel 1). Wir fanden heraus, dass auf Grund unterschiedlicher Wahrnehmungen der Details eines Regime Shifts, Wissen von kein (gar kein Wissen) und generellem Wissen (Abrupte Veränderungen) zu detailliertem Wissen (Mehrere Systemzustände) variiert. Ebenfalls ist die Anwendung des Konzepts divers und bestimmt, in Abhängigkeit von unterschiedlichen Referenzzuständen, Temporalität und Zeit, ob und wie ein Regime Shift stattgefunden hat.

Wissend, dass Regime Shift Dynamiken den Erfolg einer Bewirtschaftungsmaßnahme verringern können, haben wir ebenfalls den Erfolg der Gemeinsamen Fischereipolititk (GFP) zu der Reduzierung des Fischereidrucks und der Erholung von Fischbeständen analysiert (Kapitel 2, 3). Wir stellten fest, dass eine Fischereidrucksenkung durch positive Kipppunkte Erfolg haben kann, wie bei der Scholle (*Pleuronectes platessa*) und dem Seehecht (*Merluccius merluccius*), wenn Bestände nicht stark durch Regime Shift Dynamiken und Temperaturanstiege beeinflusst werden (Kapitel 2). Dennoch können Regime Shift Dynamiken die Erholung von Fischbeständen durch negative Kippeffekte verhindern, wie bei Seelachs (*Pollachius virens*) und Kabeljau, wenn eine nichtlineare Bestandsdynamik und Hysterese auftreten, die durch das Zusammenspiel von langfristig hohem Fischereidruck und erhöhten Temperaturen verursacht werden. Vor allem Kabeljau ist zu einem kollabierten Zustand mit einem nur geringen Erholungspotential übergegangen (Kapitel 3). Geringe Rekruten und Laicherbiomasse, ein Fischereidruck über den nachhaltigen Referenzwerten, Veränderungen der Phytoplankton- und Zooplanktonabundanzen und ein Temperaturanstieg halten den Kabeljau in einem dezimierten Zustand. Zuletzt haben wir ermittelt, ob ein System in seinen alten Zustand zurückgehen kann oder der neue Zustand irreversibel ist (Kapitel 4). Wir haben festgestellt, dass in der Nordseefischgemeinschaft ein irreversibler Regime Shift von einem gadiden- zu einem demersal-dominierten Zustand stattgefunden hat.

Auf Grund tiefgreifender Veränderungen von Strukturen und Funktionalität, haben Regime Shifts starke Folgen für das Sozial-Ökologische System. Die Resultate dieser Doktorarbeiten zeigen die Notwendigkeit eines adaptiven ökosystem-basierten Managements für eine erfolgreiche Bewirtschaftung der Nordseefischbestände auf. Ein gemeinsames Verständnis des Regime Shifts Konzepts zwischen Interessenvertretern ist wichtig, um die Kommunikation und die Akzeptanz von Bewirtschaftungsmaßnahmen zu stärken. Durch das Einbeziehen von Interessenvertretern, sowie von Regime Shift Dynamiken, in das Fischereimanagement können Entscheidungsträger Regime Shift Zustände und deren Konsequenzen erfassen und anpassungsfähige Bewirtschaftungsmaßnahmen zur Verwirklichung eines nachhaltigen sozio-ökologischen Systems umsetzen.

CONTENTS

PREFACE

"Science is a curious trade,
because scientists thrive by giving away the results of their work.
A fisherman who did that would be bankrupt in a season."
Alan Christopher Finlayson

Science encompasses gaining and teaching knowledge of our natural and physical world, structure and behavior, using valid methods and publishing the results. In a continuously and rapidly changing world, scientists are expected to look for facts that can be proven, and to put guesses, likes and dislikes aside to perform objective research. Qualitative methods such as interviews, as well as quantitative statistical analyses are combined to understand which drivers change the world that fast, and what these changes imply for the natural and human sphere.

Given a rising world population and increasing anthropogenic pressures, the world's oceans are undergoing alterations. Marine resources are exploited at high levels and experience strong depletions. Among the world oceans, the North Sea is considered highly affected by fishing exploitation and a climate change hot spot area. Due to these drivers, the North Sea fish community underwent several abrupt changes, so-called regime shifts. Here, the Atlantic cod (*Gadus morhua*) is a paradigmatic example in representing an abrupt collapse due to fishing without any signs of recovery.

There is an urgent need to understand the presence of regime shifts and their consequences for the North Sea marine and human communities to incorporate suitable and sustainable management measures preventing marine resource depletion. My thesis contributes to this need by considering the framing of the regime shift concept, understanding why and how the North Sea fish community - with a focus on Atlantic cod - underwent abrupt changes, and by determining the potential for fish stock recovery.

1. INTRODUCTION

The marine environment under stress

The globe consists of 29% land and 71% water (Visbeck 2018; Volkov 2018). The estimated number of species inhabiting Earth varies widely from 8.7 million (Mora et al. 2011) to at least 1 billion (Larsen et al. 2017). From the 8.7 million, only 14% species on Earth and 9% marine species have been described in a data base yet, most of them belonging to the higher taxa (Mora et al. 2011). Terrestrial species inhabit areas that range from hot deserts to cold ice, varying between extreme arid and humid climatic conditions (Jung et al. 2020). Living on land ourselves, the terrestrial part of the Earth and even of other planets appear more tangible to the human perception, whereas the wideness of the oceans is elusive (Hoving 2020). As on land, the marine environment is strongly divers and brings along extreme living conditions, including nutrient rich upwelling systems (Kämpf & Chapman 2016), the widely unexplored deep sea (Michael & Etter 2010), or warming surface waters (Bindoff et al. 2019).

The heterogeneity of the oceans provides us humans with benefits from the ecosystem through ecosystem services (Barbier 2017). These services include regulating, provisioning, cultural and supporting services and connect the human with the natural world (Barbier 2017; IPBES 2019). Humans strongly depend on these services and, hence, on the oceans' resources for their livelihoods. Therefore, they should be treated sustainably without harming and degrading these services to enable an indefinite use for future generations (Palmer et al. 2004). Still, exploitation of ocean resources increased strongly over the past 50 years, directly and indirectly affecting marine biodiversity and ecosystem functioning (Gissi et al. 2021; Jouffray et al. 2020). Currently, around 65% of the world's ocean surface is increasingly affected by cumulative impacts (Halpern et al. 2015) and solely 13.2.% is considered to be 'marine wilderness' (Jones et al. 2018).

The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) and the Millennium Ecosystem Assessment (MEA) identified five main categories of human-induced stressors which directly affect marine ecosystem processes: i) direct exploitation of fish and seafood (e.g., fishing), ii) sea use and coastal land changes, iii) human-driven climate change, iv) pollution, and v) introduction of invasive species (Arneth et al. 2020; IPBES 2019).

Fishing represented the main impact on the oceans and increased strongly for the past 50 years (Nelson 2005). Starting locally as food provisioning for families, commercial fishing quickly provided proteins for humans worldwide (Sahrhage & Lundbeck 1992). Whereas many gear types like hooks and lines, traps or baskets are still based on traditional gear, the efficiency of fishing increased enormously (Sahrhage & Lundbeck 1992; Steneck & Pauly 2019). With the industrial revolution, fishing vessels became bigger and could operate in a broader fishing range, increasing the formerly local variety of fish at markets. Given these rapid developments, nearly all world fish stocks reached a profoundly depleted state and some even collapsed (Steneck & Pauly 2019). Only 65.8% were fished within the biological sustainable levels in 2017 (FAO 2020).

Nowadays, the other four stressors are gaining importance with high chances of becoming the main drivers in the future (Arneth et al. 2020; IPBES 2019). Especially climate change is expected to outpace the others in causing severe biodiversity losses (Arneth et al. 2020; IPBES 2019; Pecl et al. 2017). Climatic drivers can strongly affect the marine ecosystem on different trophic levels, from phytoplankton to zooplankton, and up to the top predators (Alheit et al. 2005; Beaugrand et al. 2002; Beaugrand & Reid 2003; Reid et al. 2016). Temperature increase and acidification play an important role in particular, causing redistribution of species (Beare et al. 2004; Engelhard et al. 2014; Pecl et al. 2017; Petitgas et al. 2012) and losses of unique habitats, e.g., coral reefs (Anthony et al. 2011; Hoegh-Guldberg et al. 2017). Hence, climatic drivers combined with the effects of overfishing, including changes in fish age or size structures and reduced genetic variability, increase the chances for marine resources to become depleted (Rijnsdorp et al. 2009).

Strong species depletions, or even collapses, due to (prior) overfishing are known in particular for fish stocks (Kurlansky 1997; Möllmann et al. 2021; Rice 2018; Sguotti et al. 2019, 2020; Steneck & Pauly 2019). A prime example is the collapse of the Atlantic cod (*Gadus morhua*) stock in Newfoundland, Canada, in the 1990s, causing unemployment of many fishers (Kurlansky 1997; Rice 2018). This shows that a collapse in the ecological system (cod stock) can adversely affect the social system (fishers employment), since both, human and nature, are components linked within one socio-ecological system (SES) (Ostrom 2007). Besides one system component affecting the other, positive feedbacks between the components can cause system changes as well. Thus one social driver like a growing population and its direct effects on the value of a marine resource can force the ecological system towards depletion through further interactions and feedbacks between the components (Scheffer et al. 2009; Sterk et al. 2017).

Prevention of marine resource depletion is high on global policy agendas. The United Nations' Sustainable Development Goals (SDG), in particular SDG14, demand to "conserve and sustainably use the oceans, seas and marine resources for sustainable development" (UN 2021: 21). Further, the post-2020 global biodiversity framework calls for a "halt [of] biodiversity loss by 2030 and achieve recovery and restoration by 2050" (IUCN 2022: 1). Moreover, the United Nations Decade for Sustainable Development 2021-2030 has recently been set in place to find common ground between different countries for an ocean science framework to ensure the understanding of oceanic responses to stressors and management measures, building a science-policy interface (UN 2020).

Considering the developments highlighted above, there is an urgent need to understand the depletions of marine resources that occur, and the underlying stressors and their consequences, especially for fish stocks as the main provisioning ecosystem service that we as humans benefit from. Their changes and collapses need to be fully understood and incorporated into fisheries management if global sustainability goals shall be met.

Regime shifts

Depletion of marine resources and even collapses in marine populations occurred and still occur worldwide due to anthropogenic pressures and sometimes came as a surprise (Steneck & Pauly 2019). This surprise effect can be explained by the regime shift concept, which describes a system (e.g., ecosystem, population) that abruptly changes from one state to another through internal (e.g. stock-recruitment relationship) and external stressors like fishing or temperature change (Scheffer et al. 2001). Such regime shifts can result in stock depletions or changes in food webs and community structures (Möllmann et al. 2021; Sguotti et al. 2019; Woodward et al. 2010). External and internal pressures can cause an ecosystem to respond in three different ways, resulting in a change of state: a) linear, b) non-linear but continuous, or c) non-linear and discontinuous (Fig. 1). Whereas the linear and continuous responses are rather a gradual transition, discontinuous dynamics imply an abrupt change between two states, which are distinguished by an unstable equilibrium (Möllmann & Diekmann 2012; Scheffer et al. 2001; Sguotti & Cormon 2018).

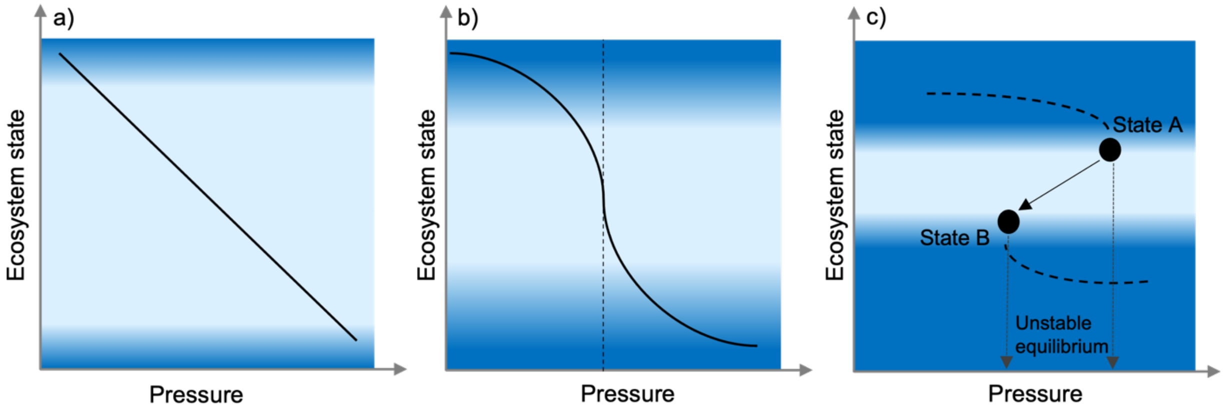

Figure 1. Ecosystem responses to external pressures. a) linear response, b) non-linear and continuous response; vertical line indicates threshold for the abrupt change, c) non-linear and discontinuous response; arrows show unstable equilibrium area. Dark blue indicates different system states, white indicates transition phase (Scheffer et al. 2001, modified).

There is no single definition of the regime shift concept within the scientific community, and it is unclear if all three response types fall under this definition or only the latter one (discontinuous) (Steele 2004). It encompasses abrupt changes in structures of communities (Conversi et al. 2015) up to shifts at multiple trophic levels due to changing oceanic conditions (Collie et al. 2004).

Throughout this thesis, I use the term regime shift to refer to abrupt changes in a system that result in discontinuity (response type c).

Within this concept, a stressor causes the system to reach a certain point, the tipping point, at which the system can no longer withstand the pressure and shifts to a new state (Scheffer et al. 2001; Sguotti & Cormon 2018). Due to altered system functioning and feedback mechanisms, the system is kept in the new state and a return to the old state is hindered; this phenomenon is called hysteresis (Möllmann & Diekmann 2012; Scheffer et al. 2001; Sguotti & Cormon 2018). Hysteresis is limiting the possibility of a system to recover to the previous state (Sguotti & Cormon 2018), referring to the restoration of underlying ecosystem processes and functions (Ingeman et al. 2019).

Marine ecosystems are never completely stable and fluctuations are continuously caused by stressors (Scheffer et al. 2001). Whether a system can withstand the strength of stressors or crosses a tipping point not only depends on the stressor's intensity, but also on the system's resilience. Resilience, first introduced by Holling 1973, is defined as a system's persistence to absorb disturbances and withstand changes while maintaining its existing structure and characteristics, hence, remaining in its current state (Beisner et al. 2003; Holling 1973). Continuous cumulative stressors can reduce a system's resilience and cause the shift towards a new, resilient state potentially experiencing hysteresis (Scheffer et al. 2001).

Quantitative methods to determine the occurrence of a regime shift vary from time series analyses, testing statistically for abrupt changes (Möllmann & Diekmann 2012), to stochastic modelling approaches including the effects of multiple stressors (Grasman et al. 2009). Among the former are for example change point analyses, which are based on changes of mean and variance in the time series (Erdman & Emerson 2007; Killick & Eckley 2014). More complexity is included in the stochastic approaches such as the stochastic cusp model (Fig. 2). Originating in catastrophe theory, the cusp model tests for discontinuous dynamics in a state variable, like the spawning stock biomass of a fish species (Sguotti et al. 2019; Zeeman 1979). In addition, the cumulative and interacting effect of two stressors (one manageable stressor, e.g., fishing pressure; and one stressor affecting the relationship between the state variable and the manageable stressor, e.g., temperature) is used to determine if a regime shift has appeared and, if so, which response path has occurred (Diks & Wang 2016; Sguotti et al. 2019; Zeeman 1979). In case the response reflects a discontinuous path, the system shows a regime shift with two alternative stable states and hysteresis (Diks & Wang 2016; Petraitis & Dudgeon 2016).

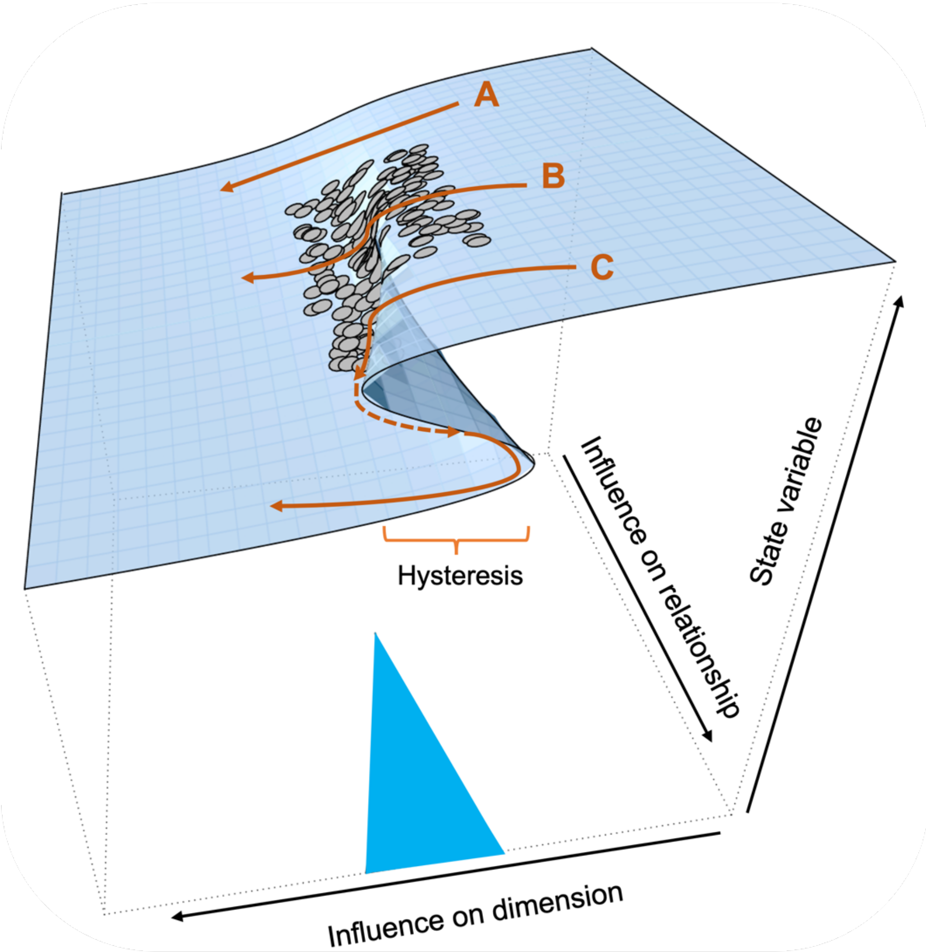

Figure 2. CUSP model. 3D illustration of a cusp model outcome. A - linear response, B - non-linear, but continuous response, C - discontinuous response with hysteresis; grey dots - data points of state variable (Grasman et al. 2009).

The role of stakeholders in understanding regime shifts

Since there is no common agreement on the definition of a regime shift (Steele 2004), qualitative methods such as interviews can help to overcome this problem. They can be applied to understand how the concept is framed and perceived by different stakeholders (Bhattacherjee 2012). This way, one can determine if a system transition is indeed seen as a regime shift by all stakeholders. If so, one can investigate what exactly happened based on which drivers, which possible sustainable management measures can support the current system state, and if the new state is desirable or not.

Understanding regime shifts is crucial because of their wide ranging impacts not only on one system component like fish stocks, but also due to their cascading effects within the systems like lower and higher trophic levels or even across SES components (Conversi et al. 2015; Kurlansky 1997; Rice 2018; Sguotti et al. 2019). Due to their discontinuous dynamics, regime shifts are often perceived as a surprise and are only detected when the shift has already taken place (Kurlansky 1997; Rice 2018). Regime shifts in marine resources are mostly related to an undesired state of depletion caused by a negative tipping point, asking for rapid management action. Still, management efforts aimed at recovery to former levels often do not succeed due to hysteresis (Möllmann et al. 2021; Sguotti et al. 2019, 2020). In contrast, also positive tipping points causing, for instance, a drastic increase of marine resources require management such as the regulation of their usage by different parties (Lenton 2020). Therefore, analyses of how regime shifts are conceptually framed by stakeholders are needed to understand system changes and the effect of cumulative stressors on a system to prevent and prepare for negative or positive surprises.

The North Sea

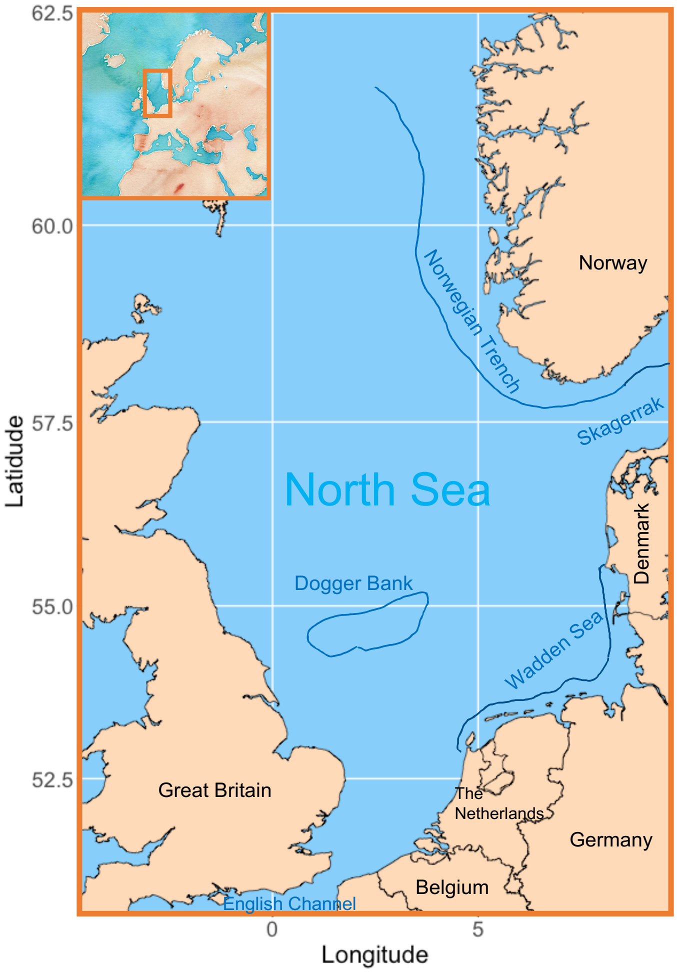

Figure 3. The North Sea.

The North Sea is a highly variable semi-enclosed marine ecosystem located in the north-east Atlantic (Fig. 3) (Ducrotoy et al. 2000). It is located on the European continental shelf and has a mean depth of around 90 meters, but consists of several bottom formations building exceptions. The Norwegian Trench with its width of 20 to 30 kilometers is the extreme in depth, reaching around 700 meters (Ducrotoy et al. 2000). In contrast, the Dogger Bank, a vast moraine, is on average only 25 meters deep (Veenstra 1965). A worldwide unique area of the North Sea is the shallow Wadden Sea located between the coasts of the

Netherlands, Germany and Denmark and the countries' islands. About 1% of the North Sea is covered by the Wadden Sea, half of which consists of tidal flats (Ducrotoy et al. 2000).

The North Sea is characterized by inflows of colder Atlantic water at its wider opening in the north and of warmer water at the narrower English Channel in the south. After floating counter-clockwise through the North Sea basin, outflow of water back into the Atlantic Ocean occurs along the Norwegian coast (Hjøllo et al. 2009). Further exchange with brackish water takes place with the Baltic Sea in the Skagerrak and Kattegat area, whereas rivers such as the Elbe or the Rhine provide an inflow of freshwater (Winther & Johannessen 2006). Despite seasonal fluctuations, these currents strongly determine sea temperature, causing an almost constant water temperature of around 10 °C in the deeper northern parts (Mathis et al. 2015).

These physical circumstances support a variety of marine species across all trophic levels. Here, only key species within the complex food web are mentioned (Lynam et al. 2017). At the lowest trophic level, phytoplankton production is more present in the shallow coastal zone than in the open sea, driven by salinity and temperature (Ducrotoy et al. 2000). In particular dinoflagellate and diatom species make up a big share of the phytoplankton community. Their relative abundance is strongly determined by changes in temperature (Hinder et al. 2012): dinoflagellates favor colder and diatoms prefer warmer temperatures (Bedford et al. 2020). The abundance of phytoplankton is crucial for the occurrence of zooplankton like small (<2 mm) and large (>2 mm) copepods (Capuzzo et al. 2018; Nohe et al. 2020). The North Sea copepod community is dominated by two important prey species for fish: *Calanus finmarchicus* which favors colder waters and *Calanus helgolandicus* which prefers warmer water (Beaugrand et al. 2002; Beaugrand & Reid 2003). On a higher trophic level, fish species prey on different copepods. Atlantic cod (*Gadus morhua*), for instance, preys on *C. finmarchicus* (Beaugrand et al. 2003), sprat (*Sprattus sprattus*) profits from high abundances of *C. helgolandicus*, and Atlantic herring (*Clupea harengus*) from small copepods (Lynam et al. 2017). The food web further includes top predator species like sea birds and mammals, but also Atlantic cod, whiting (*Merlangius merlangus*), haddock (*Melangogrammus aeglefinus*), and saithe (*Pollachius virens*) which prey on fish like the lesser sandeel (*Ammodytes marinus*) in their adult live stages (Frederiksen et al. 2006; Lynam et al. 2017).

The North Sea and Human Activities

The North Sea provides ecosystem services (provisioning, regulating, cultural, supporting) to more than 500 inhabitants per km^2 along its coasts (IPBES 2018). Compared to other areas in the world, anthropogenic impacts are increasing even stronger, which is why it is considered a high impacted area (Emeis et al. 2015; Stock et al. 2018). The five main stressors direct exploitation of fish and seafood (e.g., fishing), sea use and coastal land changes, human-driven climate change, pollution, and invasive species can all be found and partially reinforce each other (Arneth et al. 2020; IPBES 2019). Sea use and coastal land changes include, e.g., different shipping types like cargo, operations or passenger (Robbins et al. 2022); constructions of wind farms to meet the 2050 renewable energy goals (Gusatu et al. 2020); and oil platforms, which increase pollution due to oily substances having negative impacts on the marine environment (Carpenter 2019). In contrast, pollution decrease in terms of declining eutrophication caused a change in the blooming pattern of dinoflagellates and diatoms. An earlier and longer growing season as well as seasonally homogenized communities structures are the result (Nohe et al. 2020).

The main direct impact of human activities on the key North Sea fish species is fishing, which increased steadily given industrial innovations. The switch from sailing boats to steamships made the use of passive gear, e.g. longlines, redundant. Targeted hunting by trawlers using otter boards became possible and increased the fishing capacity strongly. First signs of stock exploitation were already visible in the 1890s, but instead of implementing management measures the fleet continued fishing in not yet depleted areas close to Iceland. Overall, fish species suffered from strong fishing pressure for decades, causing many stocks to be depleted or even collapsed (Jackson et al. 2001; Kurlansky 1997; Sguotti et al. 2019). To prevent further declines, the EU's fisheries management introduced the Common Fisheries Policy (CFP) in 1983 (latest revision in 2014). The CFP aims for an economically, environmentally and socially sustainable fishery (EU 2013). The policy includes the concept of a Maximum Sustainable Yield (MSY), which defines the highest yield of a stock that can be extracted without harming its reproductive success (EU 2013). Therefore, fishing pressure was reduced and some stocks like plaice (*Pleuronectes platessa*) recovered abruptly to unprecedented levels (ICES 2021). However, others like Atlantic cod experienced a regime shift towards a collapse and remained in a depleted state (Sguotti et al. 2019, 2020).

Besides fishing, climatic and hydroclimatic changes have a key impact on fish stocks by alternating the species community. The North Sea is considered a hot spot of climatic-induced water temperature warming (Emeis et al. 2015), hence, temperature-related regime shifts are well-studied in this region across several trophic levels (Kenny et al. 2009; Weijerman et al. 2005). In particular increasing temperature led to a major regime shift in the 1980s and caused strong increases of phytoplankton (Beaugrand & Reid 2003; Lynam et al. 2017) and diatoms (Hinder et al. 2012), and decreases of copepods (Kenny et al. 2009; Lynam et al. 2017). These changes on lower trophic levels affect the fish level, increasing stress for depleted stocks (Edwards et al. 2020). Climatic warming not only causes changes within the community's existing links, but the whole community is affected and changed, too. Cold water preferring species are nowadays rather found in the north, whereas warm water preferring and invasive species enter the North Sea from the south (Baudron et al. 2020; Beare et al. 2004; Ducrotoy et al. 2000; Petitgas et al. 2012).

Overall, the North Sea experiences stressors affecting species through top-down (e.g., fishing) or bottom-up (e.g., water warming) interactions, influencing the entire system. To fully understand abrupt system changes and to relate these to the regime shift concept, the full system needs to be considered to incorporate all fundamental mechanisms.

Atlantic cod – the paradigm of shifts

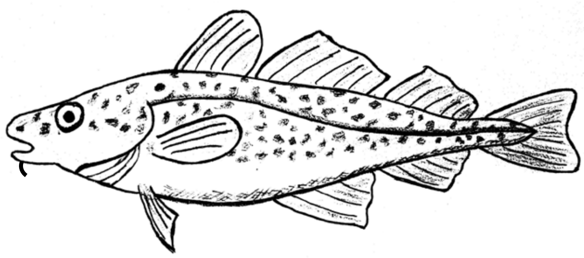

Figure 4. Atlantic cod (*Gadus morhua*).

Atlantic cod is, as Kurlansky 1997 said,

"*The fish that changed the world*" (Fig. 4) (Kurlansky 1997).

Not many fish species can claim to have caused humans to travel across the oceans, to have caused them to search for new settling places, to have triggered wars between countries, to have lost but survived against fishing pressure, to be greatly distributed across the northern Atlantic ocean, ranging from the Canadian coast all the way up to the North-East Arctic, and to be called many names in different or even the same languages. In short: being economically, ecologically and socially highly important (Kurlansky 1997; Rose 2019; Sguotti et al. 2020).

Records of the Atlantic cod fisheries go back to the Basques in the Middle Ages. During these times, the Europeans ate great amounts of whale meat and the Basques became a major supplier. They could sail far distances for whale hunting because of their discovery of large cod schools used for travel provisions. Cod was caught and preserved with salt providing fishers with nutrition during their hunting journeys. In 1497, these cod fishing grounds off Newfoundland were found coincidentally by Giovanni Caboto, who searched for a sailing route from Bristol to Asia. This discovery induced fast colonization of the Newfoundland coasts by the Europeans, developing the world market for cod (Kurlansky 1997). Due to increased fishing pressure over centuries and innovative fishing technologies, the stock collapsed in the late 1980s/early 1990s and is nowadays recognized as one of the most famous “fishery failures” (Rice 2018: 144). In the 1850s and 1870s cod already disappeared from common fishing grounds due to altered migration routes given temperature fluctuations (Kurlansky 1997). More than a century later, the Canadian government assumed that the cod disappearance was related to a similar phenomenon. In 1992, the fisheries minister declared the closure (moratorium) of the cod fishery in the northern Atlantic, leading to around 30.000 unemployed fishers (Kurlansky 1997). The collapse caught the fishery by surprise. Until the 2010s, the major cause for the collapse was still under discussion. Regardless of the cause, recovery is only taking place slowly despite the moratorium (Rice 2018).

In European waters, cod fishing on a large scale was first executed by Scandinavians, who fished for local or subsistence needs (Nielssen 2009). Through the discovery of air-dried preserved cod, the so-called ‘stock fish’, the Vikings could set out to long travels to Iceland, Greenland, Labrador and Newfoundland in the early Middle Ages. Therefore, the expansion of the Viking territory aligns closely with the geographical distribution of cod at the time (Kurlansky 1997). In the 12th century, Bergen in Norway became a growing fishing town with farmers switching to cod fishing. The increased desire to export cod and the expanded trade routes by the Vikings put cod into commercialization (Christensen & Nielssen 1996; Rose 2019). Therefore, Iceland's main export product in the 14th century was dried cod (Kurlansky 1997). To maintain the high export rates, fishing areas were expanded into Greenland's waters. This development caused the first 'cod war' with primarily Iceland and Great Britain fighting over fishing rights (Kurlansky 1997; Rose 2019). Between 1958 and 1976, three more cod wars took place between these countries, each ending with a victory for Iceland (Kurlansky 1997).

Similar to the situation off Newfoundland's coast, cod suffered from the high exploitation in European waters. Especially cod in the North Sea experienced an abrupt decline in the 1990s (Sguotti et al. 2019). An increase of gadoid species (e.g., saithe, haddock, cod) due to favorable feeding conditions in the 1960s, the so-called 'gadoid outburst', led to intense fishing above sustainable levels (Cushing 1980). The cod stock decreased gradually and despite a recovery plan in the 1990s to reduce fishing activities, the stock does not show any signs of recovery (ICES 2012, 2020). The abrupt decline is caused by discontinuous system dynamics, and is therefore identified as a regime shift (Sguotti et al. 2019). In addition to fishing pressure, which strongly reduced the stock's biomass, climate change induced environmental changes affecting young cod production and a decreased distribution caused hysteresis. As a result, recovery potential is diminished (Blanchard et al. 2005; O'Brien et al. 2000; Rindorf & Andersen 2008; Sguotti et al. 2019).

Not only does the collapse of cod have consequences for the economic and social systems connected with it (Kurlansky 1997; Rice 2018), it affects the ecological system as well. Atlantic cod is a key top predator species in the North Sea food web. Being a demersal, omnivorous hunter, it feeds on zooplankton in early life stages and on crustaceans and forage fish in the adult life stage (Link & Sherwood 2019; Lynam et al. 2017). The cold water loving species exists in different marine ecosystems, standing depths of <500m, with a maximum of 600m, and bottom temperatures between 0-11°C (Righton & Metcalfe 2019). Despite these low temperatures, the cod's thermal range is much broader and optimal growth takes place at 11-16°C (Chabot & Claireaux 2019). Sizes of cod depend on their habitat (Fig. 5); an adult cod in the North Sea can reach 126 cm, but individuals in other regions can become even larger than 1.6 m (Gulf of Maine) (Wang et al. 2014).

Figure 5. Agúst Ólafsson holding an Atlantic cod (*Gadus morhua*), deckhand aboard the Ver, around 1925. (National Museum of Iceland, Reykjavik)

The length is related to life history traits aiming at a high fecundity, a high maternal investment with increasing age, and a long life span for reproduction. Cod assemble in aggregations for spawning, where females release millions of eggs into the pelagic water column, which are dispersed by currents (Wright & Roew 2019). Spawning grounds changed over time, with the area of Scottish coastal waters, for instance, being lost due to the collapse of the sub-population in the 1980s (Holmes et al. 2008; Wright & Roew 2019).

Despite its strength in life history traits with high reproduction and the capacity of withstanding great varieties in the physical environment, the stock in the North Sea underwent a regime shift (Blanchard et al. 2005; O'Brien et al. 2000; Rindorf & Andersen 2008; Sguotti et al. 2019). Besides fishing, climatic and atmospheric changes enforced this shift; a prey mismatch of copepods was caused by increased warming during the 1980s North Sea shift, reducing food availability for young cod (Beaugrand et al. 2003). Furthermore, cod distribution is changed due to warming effects, shifting the southern boundary northwards and reducing the thermal habitat to the northern North Sea (Baudron et al. 2020; Engelhard et al. 2014).

Atlantic cod has changed the world, but has also undergone severe changes itself. For North Sea cod, it is still unclear, what fundamental mechanisms despite strong decreases in fishing pressure diminish the recovery potential of the stock, and what mechanisms are necessary to enhance recovery of the once economically, ecologically and socially most important fish species in the world.

Motivation and outline of the thesis

The motivation of this thesis lies in the abrupt changes in the North Sea fish community, identified as regime shifts, leading to either recovery or non-recovery of fish stocks - with a focus on Atlantic cod -, and to changes in the community composition. The understanding of the regime shift concept is controversial, complicating the understanding of whether a shift has taken place or not. This thesis aims at bringing to light different framings of the regime shift concept, supporting common agreement between stakeholders. I furthermore investigated whether and why shifts have taken place in the North Sea fish community, if species show recovery after an adverse state, and how the community has changed in composition. The outcomes can contribute to a better understanding of discontinuous dynamics and their underlying reasons, as well as their consideration in sustainable fisheries management to prevent surprises.

To identify what the regime shift concept is and how the concept is perceived, my co-authors and I performed a comprehensive analysis of qualitative stakeholder interviews (**Chapter I**). We show how the concept was established in fisheries science, and how it is conceptually structured and assessed by stakeholders in the North Sea context with the focus on Atlantic cod. Con- and divergences are elaborated and are brought into context of sustainable management of fish species.

Using quantitative statistical methods, my co-authors and I assessed the effectiveness of fisheries management implying fishing pressure reduction on the recovery of fish species in the North Sea (**Chapter II**). We used stock assessment data from six commercially important fish stocks and determined positive and negative tipping points with break point analyses in internal stock dynamics, as well as the additional effect of climate change induced temperature increase on recovery potential.

In Chapter II, I outline that Atlantic cod is the only species still being at unsustainable levels, despite fishing reduction. Hence, we took a closer look at this species (**Chapter III**). Subsequentially we applied change point analyses, a Principal Component Analysis (PCA), and the stochastic cusp model from catastrophe theory to stock assessment data to understand if Atlantic cod follows discontinuous dynamics. We included abiotic and biotic stressors in addition to fishing to identify possible drivers such as climate change and ecosystem dynamics that hinder recovery.

The previous studies were all performed on individual stock level. Therefore, we continued our analyses on a community level (**Chapter IV**). We first performed a literature review to determine evidence of regime shifts in the North Sea and then used the stochastic cusp model for a comprehensive regime shift analysis implying multiple trophic levels of the ecosystem. Furthermore, the potential of irreversibility of identified shifts is assessed given cumulative impacts like fishing pressure and climate change.

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2. STUDIES OF THIS THESIS

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Chapter I

Framing the Regime Shift Concept. An Epistemological Analysis of a Central Biological Notion in the Context of the North Sea Cod crisis

Framing the Regime Shift Concept. An Epistemological Analysis of a Central Biological Notion in the Context of the North Sea Cod Crisis

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Abstract

The regime shift concept is nowadays scientifically well-established. It analyses stressors causing abrupt changes in marine ecosystems. The North Sea cod (*Gadus morhua*) collapse, caused by overfishing, represents a paradigmatic example for such a change. Although this process is framed as a regime shift among various stakeholders, a common understanding of the concept seems to be scarce. We conducted qualitative interviews with stakeholders, aiming at analyzing the conceptual structure of regime shifts revealing epistemological con- and divergences of regime shifts among various stakeholders with the aim to pave a way towards a shared understanding of regime shifts for sustainable fisheries management.

Keywords: regime shift, tipping points, abrupt changes, framing of scientific concepts, qualitative interview analysis

1. Introduction

Marine ecosystems are changing rapidly, given strong increases in anthropogenic drivers in the past decades, such as climate change and fishing (Gissi et al. 2021; Halpern et al. 2015; Jouffray et al. 2019). Especially, excessive fishing of marine resources causes and caused depletions, in particular for fish stocks, while their restoration or recovery is not always at hand (Sguotti et al. 2019; Steneck & Pauly 2019). Within this context, abrupt changes from an abundant resource towards an overexploitation can be tackled and analyzed with the help of so-called regime shifts. Generally seen, the regime shift concept describes the abrupt change of a system due to natural or social stressors (Scheffer et al. 2001). These regime shifts taking place all over the world can either be perceived as a surprise by resource users or as a logical consequence of an overuse of maritime resources (Möllmann et al. 2015).

Due to its explanatory potential, the regime shift concept continuously gained attention in the scientific discourse over the last decade and represents a well-established scientific concept today (Möllmann & Diekmann 2012; Sguotti & Cormon 2018). Historically seen, it was developed in the 1970s and originates from two distinct scientific contexts: first, observations and statistical analyses detected biological and physical changes between regimes in the North Pacific from 1976-1980 (Steele 2004; Wooster & Zhang 2004) while, second, mathematical modelling conducted by ecologists paved the way towards calculating or quantifying abrupt shifts given gradual transitions in terrestrial community components (May 1977).

Given its origins and widespread application within different disciplinary contexts, there is to date no common agreement on a clear or even mandatory definition of the regime shift concept within the scientific communities using it (Conversi et al. 2015; Möllmann et al. 2015; Steele 2004). Existing definitions semantically range from “dramatic, abrupt changes in the community structure that are persistent in time, encompass multiple variables, and include key structural species” (Conversi et al. 2015) to “low frequency, high-amplitude changes in oceanic conditions that may propagate through several trophic levels and be especially pronounced in biological variables” (Collie et al. 2004). Some, furthermore, include geographical scales such as “persistent radical shift[s] in typical levels of abundance or productivity of multiple important components of marine biological community structure, occurring at multiple trophic levels and on a geographical scale that is at least regional in extent” (Bakun 2005). Hence, the regime shift concept appears to be of a certain explanatory or even practical use while its precise conceptual content is still not clearly defined.

Nonetheless, the concept of regime shifts is widely applied in the context of research on the North Sea, which represents a well-investigated area where several shifts were identified and explored over time (Kenny et al. 2009; Weijerman et al. 2005). A major regime shift took place in the 1980s and was caused by increases in temperature, leading to changes in phyto- and zooplankton (Beaugrand 2004; Capuzzo et al. 2018; Edwards et al. 2020). Since the North Sea is among the most rapidly warming world oceans, and therefore considered as a climate change hot spot, it exhibits changes at multiple trophic levels. The temperature induced changes on lower trophic levels and caused a prey mismatch for young North Sea cod (*Gadus morhua,* Atlantic cod in the North Sea), limiting young cod survival (Beaugrand et al. 2002, 2003).

Structurally seen, North Sea cod represents a paradigmatic and target species for investigating regime shifts as it is experiencing depletion due to overfishing (Rose 2019; Sguotti et al. 2019). In the 1960s, favorable feeding conditions caused the ‘gadoid’ outburst, an increase in gadoid fish species like cod (Cushing 1980). As a result, increased fishing pressure finally resulted in a strong decline and eventually a collapse of the stock in the 1990s (Cook et al. 1997), which was quantitatively framed as a regime shift (Sguotti et al. 2019). Since the 1980s, the cod stock is below scientifically established sustainability levels (ICES 2020) due to a climate change-induced temperature increase limiting young cod survival and bearing an impact on the adult thermal habitat (Blanchard et al. 2005; Rindorf & Andersen 2008). Efforts to enhance recovery, such as the implementation of a cod recovery plan finalized in 2004, did not prove to be successful as the stock remained below sustainable reference levels (EC 2004; ICES 2012). Hence, the example of the North Sea cod not only highlights the practical and urgent need for the detection of regime shifts in general, but it also calls for a more accurate explanation of what a regime shift actually is and how it can be defined. A common understanding among various stakeholders like decision-makers, NGOs and fishers is in this context of vital importance as it informs and determines restoration or recovery policies. Therefore, if the concept itself is not well-defined it holds the danger to lead management efforts into a dead end (Möllmann & Diekmann 2012; Sguotti et al. 2019).

Against this background, we studied the framing of the regime shift concept among stakeholders involved in science, nature protection, management and those harvesting North Sea cod. We conducted interviews and identified con- and divergences in the theoretical framing of the concept to address the above mentioned issues because knowledge about regime shifts within cod varies from non-knowledge to detailed processes such as tipping points and alternative states. We show that the collapse of a marine resource like North Sea cod does not necessarily imply a regime shift but rather depends on the point of view of each stakeholder which predetermines the application of analytical concepts. Our study therefore contributes to the analysis of the various framings of the regime shift concept to understand and explain the apparent biological changes currently materializing in North Sea cod. In brief, the structural and empirical analysis performed here aims at clarifying the meaning of the notion of regime shift and explores its relevance for explaining the changes taking place within the North Sea cod.

Regime shifts and tipping points in science

The regime shift and tipping point concepts used in marine systems are closely related and one seldom appears without the other (Milkoreit et al. 2018; Möllmann et al. 2015; Sguotti & Cormon 2018). However, the terminology of regime shifts and tipping points stems from various disciplinary contexts (May 1977; Wooster & Zhang 2004), and – more importantly though – both appear not to be clearly defined among scientists (Mathias et al. 2020; Milkoreit et al. 2018; Möllmann et al. 2015).

Terminology-wise, regime shifts are linguistically described by using synonyms such as ‘phase transitions’ or ‘alternative stable states’, which generally highlight the processual aspect of a change from state to another (Möllmann et al. 2015). Besides these contemporary meanings, the term regime shift holds a conceptual history which goes back to the 1960s while it was first used in maritime research in the late 1980s. Here, it was conceptually assisted in analyzing changes between fish populations’ dominance, applying it to anchovies (*Engraulis encrasicolus*) and sardines (*Sardina pilchardus*) as first key species of investigation (Lluch-Belda et al. 1989). From then on, the term steadily gained popularity in the 1990s (Milkoreit et al. 2018) while at the turn of the century phrases like ‘critical transitions’, ‘critical point’, ‘threshold, ‘abrupt change' and 'punctuated equilibrium' were synonymously used to convey what 'tipping points' are (Dakos et al. 2015; Milkoreit et al. 2018). Nowadays, the notion of tipping points is conceived as an addition to the already existing terminology and is used in the same semantic field such as 'critical transitions' or 'regime shifts' (Milkoreit et al. 2018). Thus, standing as an analytical notion for themselves, tipping points are semantically embedded in the overarching regime shifts and transformations concepts (Milkoreit et al. 2018). There is, however, a small but important difference: whereas regime shifts imply incremental structural and functional changes of a system (Scheffer et al. 2009), transformations are framed as a fundamental reorganization of whole systems (Gunderson & Holling 2002).

Among the synonymous ways describing regime shifts and tipping points, differences in the perception of the conceptual structures exist as well. 'Skeptics' and 'believers' engage with the clarification of the regime shift concept and nowadays divide the marine community (Scheffer & Carpenter 2003). A first step towards clarification assumed that systems respond gradually and smoothly to drivers in regime shifts while abrupt changes towards another state were only theoretically described by using conceptual models (Holling 1973). Nowadays three conceptual types of response of a system to drivers are widely accepted: i) the linear and continuous, ii) the non-linear and continuous, and iii) the non-linear and discontinuous response (Möllmann & Diekmann 2012; Scheffer et al. 2001). The latter origins from 'catastrophe theory', where the system reaches a certain point, the tipping point, at which it can no longer withstand the stressor and a transition into a new, alternative system state takes place (Scheffer et al. 2001; Scheffer & Carpenter 2003). Foundations for catastrophe theory, and therefore regime shifts, with systems exhibiting multiple alternative states were already laid in 1885 by the French mathematician Henri Poincaré (Barrow-Green 2005). But it was only in the 1960s and 1970s that these mathematics were introduced to physical and ecological applications, when discussing ecosystem stability became popular among scientists (Holling 1973; Lorenz 1963). In the case of non-linear and discontinuous systems, the return to the original state – often framed as recovery – might be hindered due to emerging functions and feedback mechanisms characterizing the new system: this phenomenon is called hysteresis (Möllmann & Diekmann 2012; Scheffer et al. 2001). Given these types of responses, there is scientific uncertainty if all three fall under the conceptual definition of regime shifts or only the latter, discontinuous one (Steele 2004). Still, the need of a significant driver to shift the system across a tipping point towards an alternative state is still widely applied as the context of regime shifts (Möllmann et al. 2015; Möllmann & Diekmann 2012; Scheffer et al. 2001; Sguotti et al. 2019; Steele & Henderson 1984). Alternative states have also been included as the third regime shift indicator, which are i) abrupt changes in time series, ii) multimodality in the state variable (e.g., fish stock size) and iii) alternative stable states indicated by a bi-fold relationship with the driver (Scheffer & Carpenter 2003). In contrast to theory, states in reality are not strictly stable and systems are rather dynamic and fluctuate in reality (Möllmann et al. 2015).

Drivers play – as we have seen – an important role in the regime shift concept, and are conceived as the underlying forces to change a system's state. Based on discussions revolving around their predominance and their effect on a state variable (Möllmann et al. 2015), shifts in climate and ecosystem are distinguished (Möllmann & Diekmann 2012). Following this line of argument, shifts in the climate regime are caused by differences in one or more external climatic drivers which induce bottom-up changes, and are therefore conceptualized as drivers of an overarching ecosystem shift (Bakun 2005; Dakos et al. 2015; Hare & Mantua 2000). These ecosystem shifts are driven by an interaction between external drivers as well as internal system mechanisms, e.g. trophic control (Scheffer et al. 2001; Scheffer & Carpenter 2003). They consider changes in the abundance of marine biological community components, and can occur on big space- and time-scales (Bakun 2005).

Furthermore, there is no common ground for the temporal and spatial scale of regime shifts, which differ accordingly to the system and its structure. On the one hand, time of drivers can either be estimated as slow or fast, distinguishing, for instance, restoration of historical climate data and real-time data at the same time (Milkoreit et al. 2018). On the other hand, the time-related identification of a regime shift differs per definition. The shortest normative period of an alternative new state, scientifically defined for a regime shift process, is five consecutive years (Norström et al. 2009). Spatially seen, regime shifts have no limits in either way: they can on the one hand be defined as shifts on population level (Sguotti et al. 2019) and on a system's internal feedback like trophic functioning (Alheit et al. 2005), or on the other hand on community level, which for instance include a northward shift of cold water preferring species and a higher likelihood of the occurrence of warm water preferring species (Baudron et al. 2020; Beare et al. 2004; Petitgas et al. 2012).

Diversity in the regime shift and tipping point concepts can, furthermore, be found on the methodological level. Initial biological models of regime shifts were used to determine outbreaks of the spruce budworm (Ludwig et al. 1978), while comparable ones were conceptually extended to investigate changes in freshwater (Scheffer et al. 2001), plankton and fisheries (Steele 2004; Steele & Henderson 1981, 1984). Starting off with easier models considering time series of one ecosystem component, e.g., fish stocks, models were in the course of time continuously broadened in complexity assessing alternative system states and biological shifts driven by a multiplicity of drivers (Collie et al. 2004; Möllmann & Diekmann 2012; Sguotti et al. 2020). Furthermore, given steady increases in anthropogenic and climatic pressures, models that include and predict marine regime shifts on this basis were developed by using early warning signals. However, their predictive ability still remains limited because of environmental stochasticity (Dakos et al. 2015). These varieties in methods, data availability and selection bear an impact on the detection of regime shifts. However, since empirical evidence of regime shifts is witnessed seldom or is rare, statistical modelling appears to be the only way for detecting the causes and processes of regime shifts (Möllmann & Diekmann 2012).

Finally, the detection and knowledge about regime shifts and tipping points has also an important and applied impact in terms of sustainable management measures. Alternative stable states, involving hysteresis, ask for expensive and drastic actions to reduce the intensity of drivers for archiving an initial system state (Möllmann & Diekmann 2012). Within this context, the application of the terms regime shift or tipping point to describe various phenomena, which were earlier analyzed using various types of terminology, can ignore significant differences and create the believe of conceptual similarity (Milkoreit et al. 2018). Using both concepts including their great semantic differences might, on the one hand, express the notion of a deep concept understanding by scientists. On the other hand, it could indicate the loss of focus and the lack of a common understanding (Milkoreit et al. 2018). Despite the apparent conceptual imprecisions, the notion of regime shifts, however, seems to hold a certain analytical value for studying changes in marine ecosystems which is indicated by its worldwide application. They could therefore be conceived as a boundary object as they hold enough immutable content while at the same time flexible interpretations and applications across scientific disciplines, contexts and research objects is possible (Star & Griesemer 1989).

Analyzing regime shifts: black boxes and boundary objects as analytical tools

As we have seen in the previous section, the notion of regime shift exhibits a long conceptual history and has generally been used to understand and scientifically study the causes of rapid changes in an environmental system triggered by biological and/or human impacts.

Bearing in mind, that the notion of regime shift has once been borrowed “from describing phenomena such as lacustrine ecology or fire regimes and [has now been] applied to complex socio-ecological phenomena” (Kull et al. 2017: 3), we set out to analyze whether or not conceptions of regime shift and the connected notions such as abrupt changes and tipping points are framed consistently or divergently among mixed group interviewees. For this to be done, we theoretically favor a critical hitherto constructive approach that aims at opening up conceptual gaps with the aim to exhibit the various framings of the concepts among our interview partners while we try, at the same time, to show a way that might lead towards an improved mutual understanding. This translational approach (Schlesinger 2010) is based on the premise that we theoretically take a meta-perspective on the discourses revolving around the concept of regime shifts, abrupt changes and tipping points while also systematizing and analyzing their framings in the interviews conducted. Such a perspective is informed by research undertaken in the area of science and technology studies and on the sociology of scientific knowledge which investigate the development, understanding and application of scientific technologies, infrastructures, practices, methods or theories. One aspect, which we observed in the case of the notion of regime shifts, consists in the fact that theories and their conceptual constituents are “black-boxed” (Latour 1987). The analytical notion of black-boxing (Johnson & Lidström 2018) refers to the fact that a concept can be used in various and sometimes considerably differing contexts without being semantically or pragmatically explained, adapted or fined-tuned to it (Jasanoff 2006). Thus, in our case the black box of the notion of regime shift appears to be closed and wends its way through scientific and public discourse implying that its semantic, analytical and pragmatic content is largely established and agreed upon. This is, however, not the case as our analysis of the interview data will indicate even though some of our interview partners assumed that it can be used and understood without further elaboration. This clearly indicates that notions such as regime shift, abrupt change and, to a lesser extent, tipping points are not used due to their semantic validity or analytical accuracy, but due to the support of peers such as scientists, stakeholders, administrative staff or politicians involved in and devoted to it. In brief, the social use of the notion stands above its actual meaning or general epistemology (Latour 1987).

To analyze this semantic heterogeneity of the regime shift concept, we suggest to circumvent a purely relativist or objectivist research agenda and use a critical realist approach (Sayer 1999) that avoids the theoretical traps of positivist and relativist rationales (Stone-Jovicich 2015). Such a perspective holds the important advantage that we can move back and forth between “empirical realities and the social processes that produce the […] understandings of those realities” (Kull et al. 2017: 6) and their meanings in the course of our analysis. This enables us to productively explore the middle ground between these two theoretical ends while also focusing on the social contingencies nestling in-between them. Consequently, the regime shift concept and its connected notions could be understood as socially produced and semantically multifaceted entities. Such a framing opens-up a perspective that analytically engages with a ‘cohesive heterogeneity’ as outlined in the analytical concept of a boundary object (Star & Griesemer 1989). Boundary objects represent entities that are “plastic enough to adapt to local needs and the constraints of the several parties employing them, yet robust enough to maintain a common [and socially shared] identity across sites” (Star & Griesemer 1989: 393). Hence, they practically hold the potential to cover social and semantic incongruences while at the same time bridging differences or worldviews between scientific disciplines and/or social actors (Kull et al. 2015). In objectified terms, boundary objects could be conceived as concrete objects, abstract notions or concepts that are shared by and are accessible for different social groups who do not or only in part hold overlapping knowledge systems or epistemologies. This means in the present case that the notion of regime shift, as used by our interview partners, must hold a certain degree of semantic and pragmatic consistency which is at the same time characterized by a necessary nonconformity that make it useful, applicable and practicable in a variety of disciplinary and social contexts. It is these specific non-specificities that characterize boundary objects and make them a means to categorize and share knowledge, enable communication and create communities around a certain issue while assisting in developing more or less clear analytical concepts (Bowker & Star 1999). Hence, the regime shift concept and its associated concepts are heuristic devices that ontologically merge biophysical and socio-ecological systems while at the same time they epistemologically aim to analyzing the relation between these two dimensions.

In sum, one can say that the theory of black-boxing and the notion of boundary objects share the conceptual aspects of specific non-specificities. Thus, the social aspect of the black-boxed boundary objects surpasses the actual and precise semantics of what the notion regime shift actually means. In doing so, it opens-up a perspective on the social dimensions and the social sense of meaning and the astonishing fact that sociality gathered around a theory like regime shifts is possible and does not in fact depend on an exact definition every member in a social group shares when talking about it. On the contrary, the processes of black boxing and the entities of boundary objects appear to populate a socio-scientific world in which the regime shift concept represents a communicative tool to articulate the perceptions related to it and assess them. Taking these aspects seriously, we will empirically analyze the various meanings of the three boundary objects of regime shift, abrupt changes and tipping points after the next section. The analysis will exhibit the semantic heterogeneities and knowledge dimensions of these notions, but before we will focus on the methodological aspects of our analysis.

2. Materials and Methods

To investigate the conceptual perception and assessment of the boundary object regime shift in the context of abrupt changes in Atlantic cod, we conducted semi-structured interviews with relevant stakeholders and performed an inductive data analysis (Fig. 1.1) (Dawson 2009; Gläser & Laudel 2010).

2.1. Data collection

First, we started with an in-depth reading of the relevant scientific literature about the current regime shift of Atlantic cod in the North Sea and analyzed the thematic structuration of this scientific discourse (Fig 1.1.1.). Based on this content-oriented contextualization, a thematic interview guide was developed addressing major issues revolving around the subjects of North Sea cod, regime shifts and tipping points (Fig. 1.1.2.). Major topics of the interview-guide considered the regime shift and tipping points concepts, regime shifts in the North Sea, the general framing of Atlantic cod, cod management and policies, and future aspects dealing with cod. These topics were chosen to conceptually tackle the complexity of regime shifts (from linear to discontinuous, from fast to slow) as they developed in the scientific literature (Beaugrand et al. 2003; Kenny et al. 2009; Sguotti et al. 2019) while the issue of regime shifts in cod in the North Sea was used to 'emplace' and 'reify' the concept (Sguotti et al. 2019).

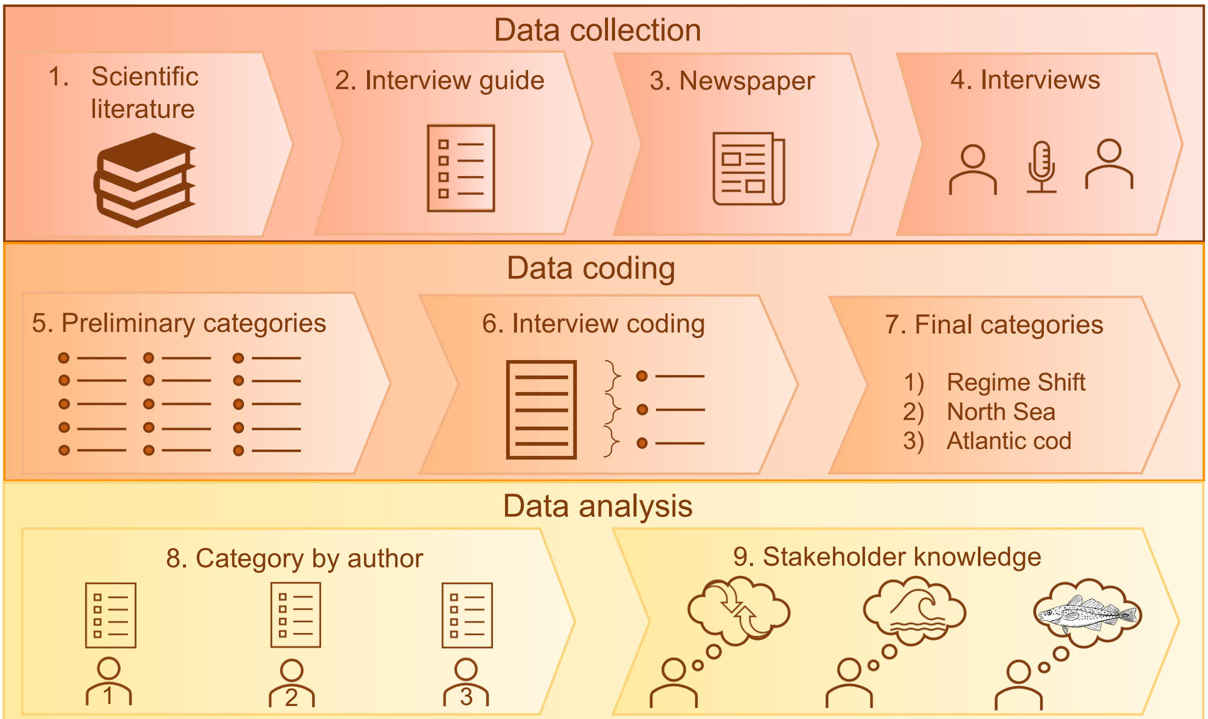

Figure 1.1. Schematic representation of the methodological approach implying data collection, data coding, and data analysis.

To be more precise, the interview guide included questions touching upon what the regime shifts, tipping points and abrupt changes concepts imply. The North Sea, as territorial entity, was used to spatially situate the experience of such changes and assisted in reflecting on its causes and effects of the current state of the Atlantic cod and how it has changed over time. Finally, the questions dealing with the management of Atlantic cod and the future development of the stock aimed at developing a probable assessment of estimated futures against the content discussed in the course of the interview. Each interview ended with the opportunity given to interviewees to address further topics not raised during the interview which were considered for improving the interview guide (See Supplementary Table S1.1).

All interviewees were chosen according to a quota sample, which represents a basic ingredient in the context of the purposive sampling method, and which implies that selected subgroups were chosen based on certain features determined by the authors. Thus, interviewee requirements were defined beforehand and against the background of the scientific literature analyzed to assure a balanced representation of all relevant stakeholder groups (Dawson 2009). More importantly though, a screening of newspaper articles was performed to thematically explore the field and the people associated with the topic of regime shifts in North Sea cod (Fig. 1.1.3.). The search for articles was performed by using the word “Atlantic cod” (in German: “Kabeljau”) in newspaper archives. The publishing outlets considered were the weekly Die Zeit, daily appearing and German-wide newspapers such as the Frankfurter Allgemeine and Süddeutsche Zeitung and more regional newspapers like der Weser Kurier, Cuxhavener Nachrichten and Nordwest Zeitung which all have a regional North Sea focus. The archives dated back to the mid-1940s which ensured historical consistency while also covering the increase of cod in the 1960s, as well as the collapse taking place from thereon. The newspaper screening revealed four major stakeholder types related to Atlantic cod: people involved in fisheries, decision-makers and management on various institutional levels as well as scientists and eNGOs.

Interviewees were selected by i) the first author’s knowledge, ii) the third author’s knowledge, and iii) on the basis of the screening of newspaper articles. Relevant interviewees had to fulfill the following requirements: i) He or she had to be working or are currently working on the topic Atlantic cod or should be associated with North Sea fisheries, ii) interviewees had to be associated with North Sea fisheries for at least 3 years to ensure that they were familiar with the topic and iii) interviewees had to belong to one of the five relevant stakeholder groups identified in the media analysis. Since the collapse of the Atlantic cod took place in the 1990s, retired interviewees who were active during these times were interviewed as well.

In total, we interviewed 18 stakeholders (Fig. 1.1.4., Fig. 1.2). Due to the COVID-19 pandemic, interviews were not conducted on site and therefore held online with the help of the Zoom software. On request, major topics of the interview were provided prior to the interview for preparation purposes. All interviews were performed by the first author from January 2021 – March 2021, lasting between 25 and 60 minutes and were transcribed verbatim.

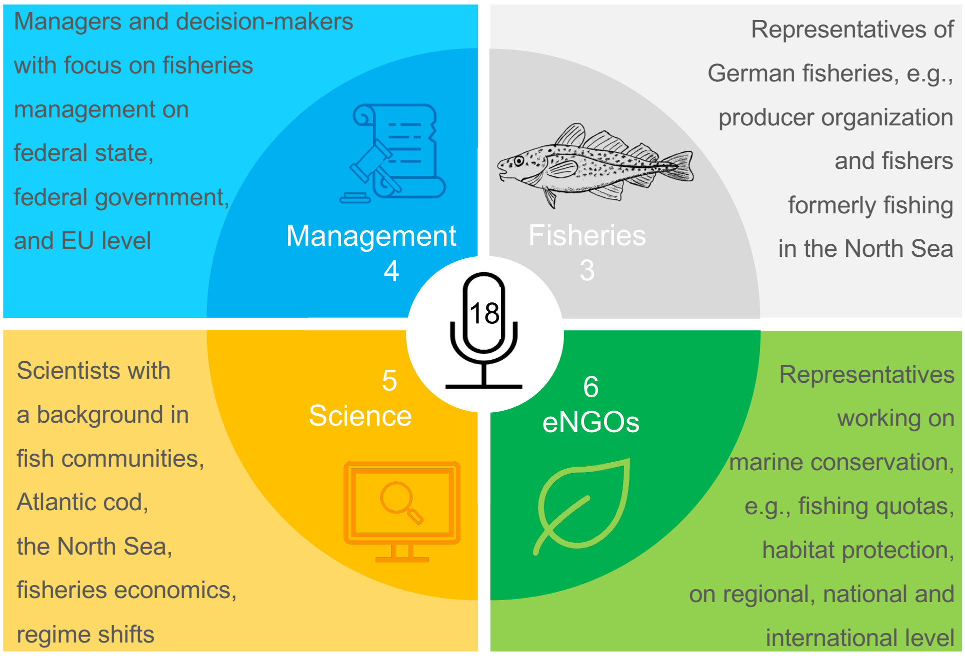

Figure 1.2. Stakeholders interviewed per group. eNGOs = environmental non-governmental organization.

2.2. Data coding and analysis

To understand the regime shift concept, we applied a qualitative approach by screening and coding the data, and by performing a sequential content and thematic analysis (Bhattacherjee 2012; Dawson 2009). This consisted, first, in an iterative and separate reading of four randomly chosen interviews by three authors (AMD, HS, MD) to cooperatively develop preliminary categories for the analysis (Fig. 1.1.5.). Detailed descriptions of each category were carried out upon compliance between the authors (AMD, HS, MD) to create an empirically informed basis for analysis and to secure intercoder-reliability (Saldaña 2015). Furthermore, these categories were critically assessed by expert knowledge of the authors (AB, CM). Out of this iterative process a total of 12 analytical categories developed which can be divided into four main topics:

i) Regime shift, ii) North Sea and related impacts, iii) Atlantic, iv) Atlantic cod – Collapse and Management (Table 1.1). Based on these categories, an analytical guide was prepared for further analyses.

Table 1.1. Four main categories and their sub-categories revealed from the iterative data coding process.

Main category	Sub-category
Regime shift	Regime shift
	Tipping points
	Abrupt changes
North Sea & related impacts	North Sea
	North Sea - Impacts
	Atlantic cod - Impacts
Atlantic cod	Atlantic cod
	Atlantic cod - Development
	Atlantic cod - Development - Recovery
Atlantic cod - Collapse & Management	Atlantic cod - Collapse
	Atlantic cod - Management
	Atlantic cod - Brexit

In a second step, the remaining interviews were evenly distributed among three authors (AMB, HS and MD) implying that each author analyses at least one interview from each stakeholder group (Fig. 1.1.6.). These interviews were coded accordingly using an analytical guide as a coding scheme, assigning the categories within the text (Bhattacherjee 2012; Dawson 2009). Regular feedback rounds were held between the authors to ensure a mutual coding reliability. During a final discussion of this step, the authors decided to focus on the categories Regime shift, North Sea and all impacts, and Atlantic cod as they contributed to the research question (Fig. 1.1.7.). The last topic 'Atlantic cod – Collapse and Management' was removed as it appeared to be out of focus for this study (Supplementary Table S1.2).

In a third step, each author was assigned one main topic, each with three categories, for an in-depth analysis (Fig. 1.1.8.). By re-using the inductive rationale for the detailed analysis, the major categories containing all material were divided into further sub-categories (Dawson 2009; Gläser & Laudel 2010). General groups were created at a first reading and then sub-categories were developed by re-reading them. These sub-categories represent the detailed knowledge of each interviewee and exhibit their understanding of the topics of Regime shift, North Sea and related impacts, and Atlantic cod (Fig. 1.1.9.). At the end, the three sub-categories regime shift, tipping points and abrupt change (Table 1.1) where determined to provide a structured and content-related overview of the regime shift conceptualization and also reveal con- and divergences concerning the depletion of the North Sea cod.

3. Results

The comprehensive analysis of the interviews revealed many topics revolving around i) regime shifts and its related concepts ii) tipping points and iii) abrupt changes. Due to this first result, the three main concepts mentioned form the center of our study in which we analyze their conceptual structuration as articulated in the interviews conducted. Emphasis is put on theoretical con- and divergences explained in terms of consequences for the North Sea cod as a paradigmatic real world example.

Regime shift concept in perspective

Our analyses show that a discourse revolving around the regime shift concept within a wide range of stakeholders exists. Interviewees differ in their ideas about the definition of the concept like what a regime shift actually represents, what it entails, when exactly a regime shift can be determined as such, which timing is needed and what consequences result from it. Given its diversity, interviewees find it difficult to actually accept and use the concept (I14, I12), since it is widely applied due to its importance as a word and not so much due to its conceptual or theoretical content (I12). Hence, a big concern regarding regime shifts lies within the definition of the concept. Interviewees stress that an exact definition is difficult to grasp from the research undertaken as the word “regime shift” is often used without adequate explanation of underlying causes (I12) or causal relationships (I9, 12). The lack of a clear definition hinders the determination of what event qualifies as a regime shift and why (I3, I15). Furthermore, the question arises on which trophic level a regime shift can actually take place. According to two interviewees, a shift on the lowest trophic level, phytoplankton, does not necessarily imply a regime shift on a higher predation level (I12, 13). When looking at the highest trophic level of the food web, an interviewee raised that overfished fish stocks have never been considered as regime shifts in his work (I13). However, once an event is determined as a regime shift, a further discussion arises if irreversibility of the new state is in place (I11) and if a regime shift is mainly considered as a switch towards a depleted state (I14).

Regime shift knowledges

The regime shift concept is widely applied in science nowadays, and still, knowledge about this concept is diversely dispersed across different interview partners and can be classified into three types of knowledges: i) non-knowledge, ii) general knowledge, and iii) detailed knowledge (Fig. 1.3). General knowledge and detailed knowledge both can further be described by differences in conceptual structuration of processes and the time span of the regime shifts. Non-knowledge is expressed as simply not knowing anything about the concept, never having heard about it before, or not knowing anything in detail (Fig. 1.3a, I1, I3, I7). These interviewees were given a quick regime shift example by the interviewee (i.e., the swop from an oligotrophic to eutrophic lake) as input. Based on this example one interviewee revised the former non-knowledge by comparing the newly gained knowledge about a social regime shift to the abrupt occurrence of the COVID-19 pandemic and the rapidly occurring home office situation (I7).

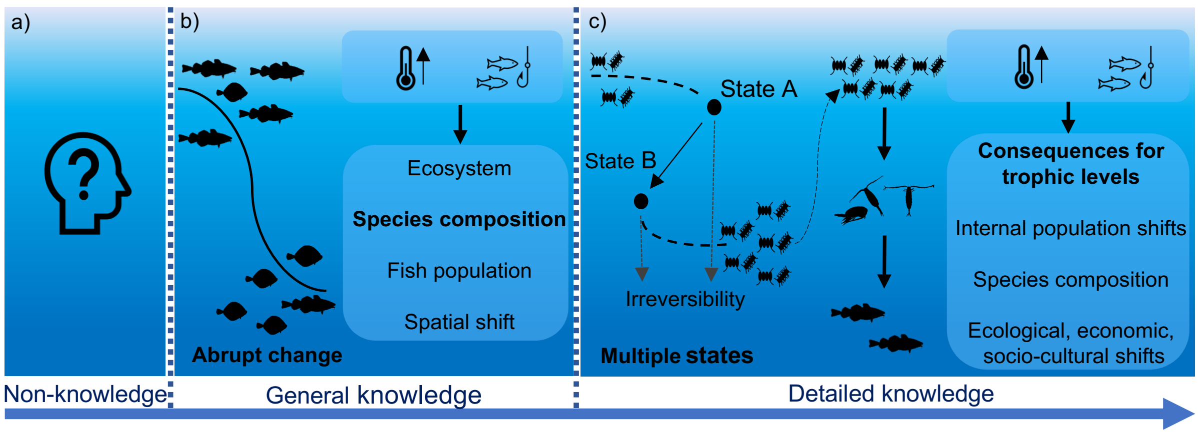

Figure 1.3. Types of knowledges about the regime shift concept. a) non-knowledge b) general knowledge c); in bold the most mentioned affected systems are highlighted.

General knowledge was expressed by six interviewees (Fig. 1.3b). Here, the regime shift concept is known and often described in terms of an abrupt change (I2, I4, I5, I9, I13, I14). The main drivers associated by interviewees with causing a regime shift are external factors: the warming temperature effect induced by climate change and fishing pressure. These drivers can cause shifts on various levels, which all bear an impact on processes on the ecological state. In this context, changes in species composition (change in dominance of species) was the major effect of a regime shift mentioned (I2, I5, I9, I13). This was followed by changes happening in the whole ecosystem (I2, I9), on the fish population level (I4, I14) or in terms of a spatial shift northwards in the North Sea (I5, I16). For fish populations, both, an increase as well as a decrease in the stock size were considered as a regime shift (I5, I14) while two interviewees raised regime shift processes on an economic level. First, the COVID-19 pandemic is mentioned as a regime shift, having an effect on the fishery companies (I13) while, secondly, management measures like fishing bans, discard bans and strong changes in fishing quotas are seen as abrupt measures, influencing fishers negatively by limiting their predictability (I4, I16).

Detailed knowledge was represented by 4 interviewees (Fig. 1.3c). Regime shifts are here associated with a shift of the system from one state towards another indicating that the existence of multiple stable states is known (I10, I11, I12, I15). Whereas tipping points are also associated in this context, determining the point at which a system actually undergoes change (I11). Moreover, steadiness of the different states is described by one interviewee, highlighting that a system transforms from a steady state through a non-steady state to a new steady system state (I10). More detailed knowledge is expressed by describing these transformations between states with the use of words such as “discontinuity” and “catastrophic type” (I12), both used by the interviewee to depict a transformation to be called a regime shift. Two other interviewees raise the aspect of “irreversibility” (I11, I15) which describes the limited possibility for a system in a new state to return to its former conditions state. The two main drivers mentioned causing a regime shift are, as for general knowledge, climate change induced warming and fishing pressure (I10, I11, I12). In addition, interviewees explain that in early stages of the development of the concept, only systemic dynamics were considered to cause a regime shift. The forces and influences of external drivers were included at a later stage of the development of the concept: hence, a shift is not exclusively caused by one or the other but by connected causes (I12, I15).

In the context of detailed knowledge, regime shifts can take place on and across multiple levels. Interviewees mentioned the biological process of a regime shift across multiple trophic levels the most. Thus, a shift from low to high abundances of phytoplankton causes changes in the food web, and therefore leads in the end to the abundance of predator fish (I11, I12). Also changes on population level and in species composition are quite often articulated (I15). In the context of a of a cross-disciplinary framing, a biological regime shift can bear an effect on socio-cultural and –economic systems if, e.g., fishers need to adapt to losses in catches or if prices are changed with regard to the market supply (I11).

Interviewees with detailed knowledge, furthermore, considered the time span of a regime shift. On the one hand, an event “must happen pretty suddenly […] to be called a regime shift” (I15), while on the other hand a system needs to level off in the new state (I10). It is not clear which time span is defined as a norm for a regime shift. Changes can take “a long time” (I15) in, for instance, the marine realm or up to “about a million years” like the ice tides (I15). These long-term changes rather gradually take place, “without any particular difference in the dynamics” (I12) and are despite their time span still called regime shifts. Hence, understanding what a regime shift in terms of its time span actually is, is difficult to define in this context (I12).

Not only the time span for a process of a regime shift in itself varies, but regime shifts are also distinguished temporality wise into the past and future accordingly to the drivers associated with it. Regime shifts mentioned in the context of the past are in most of the cases related to anthropological drivers. The utilization pressure on the system, here the North Sea as a paradigmatic example, increased strongly since the second world war in the past 70 to 80 years (I5). In addition, the effect of climate change is conceived as becoming stronger during the past 20 years, bearing an increasing pressure on the North Sea (I9). Still, it is framed as “only ten thousand years old” (I15) having been inhabited by several species during that period. If these 10.000 years are compared to the currently 100 years of available North Sea data, “that’s very short” (I15). In terms of evolution, however, “that is a large part”, wherefore turning back to a situation “that would look like the beginning of this century” is simply not possible (I15).

In terms of the future, regime shifts are considered under the study of the development of climate change. The questions raised lie within possible usage options within the next 10 years, the spatial appearance of species, or how many of them might possibly be caught (I13). Further developments might imply that if management continues with business as usual at a MSY-level, regime shifts will appear and become more important in defining boundaries for fish stocks than management (I13). The question, however, remains, “whether we as humans will ever experience this state [former North Sea state] again” (I10)?

Regime shifts in situ – North Sea cod and neighboring examples

Interviewees used on their assessment of the regime shift concept examples from the North Sea and the Baltic Sea. As indicated in scientific literature (Beaugrand 2004; Capuzzo et al. 2018; Edwards et al. 2020), interviewees tend to refer to a North Sea regime shift in the 1980s with changes on all trophic levels as a best example (I11, I12).

In the scientific literature, the North Sea regime shift in the 1980s is negatively related to young cod survival (Beaugrand et al. 2002, 2003), and the collapse of the cod is determined as a regime shift (Sguotti et al. 2019). Related to North Sea cod, interviewees refer to the gadoid outburst in the 1960s, the strong increase of gadoid species, as a regime shift (I2, I14). The explanation lies within a temporally suddenly high abundance of cod: “the cod stock has never been as high as during the time of the gadoid outburst” (I2). In contrast to the scientific literature, interviewees do not agree in defining the subsequent decrease of North Sea cod a regime shift (I2, I12). Interviewees who frame the increase through the gadoid outburst as a regime shift, conceptualize the decrease as a decline to former levels (I2, I12). Furthermore, the shift in the North Sea in the 1980s took place on the plankton level and resulted in consequences for cod, which does not necessarily imply a regime shift on the cod level (I12). In contrast, some interviewees see the decline of the cod stock as a regime shift, but divide it into internal and external dynamics (I5, I15, I16). Internal dynamics relate to changes on population levels and are shown by one interviewee by the interplay of herring and cod stocks (I15). Since herring preys on cod eggs and larvae, the strong herring fishery after the second world war caused an increase in cod. Subsequently, fishing on the depleted herring stock was reduced, inducing an increase in herring and, consequently, a cod decrease (I15). External dynamics causing the regime shift are related to overfishing (I5, I15, I16), wherefore the cod stock “may never come back to the same extent” (I15). The appearance of the regime shift is further strengthened by highlighting the cod’s ecological importance as an indicator species for the condition of the ecosystem at large (I5). Besides the shift on population level, a climate-induced spatial shift northwards takes place by virtue of increasing water temperatures of the southern North Sea (I16). In general, climate change shifts cold water preferring species northwards and enhances the introduction of new species from the southern North Sea. This causes not only a spatial shift, but also a shift in the species composition (I2, I5, I14).

Even though interviewees expressed themselves regarding a regime shift related to North Sea cod, most interviewees only disclosed decided knowledge after they were asked by the interviewer. Examples from the neighboring Baltic Sea appeared to be more intuitive (I2, I4, I9, I13). Here, the predominant example concerns the cod-sprat relationship, where a regime shift occurred from a “cod dominated system to a sprat dominated system” (I13). As cod preys on sprat egg, a high fishing mortality on cod reduced the pressure on sprat, which in return increased (I13). Another common example for a regime shift is related to the herring stock, which experiences a prey mismatch due to increases in sea temperature and is therefore not performing well (I9).

Consequences and adaptations

Based on the examples of the regime shifts mentioned, interviewees also highlighted consequences resulting from and adaptations to shifts that have taken place. A major consequence of ecological regime shifts are changes in the social-economic system (I2, I13, I14, I16). The reduction of the high-quality food source North Sea cod stock and its spatial drift northwards, led to severe changes in the fishing fleets. From 1993 to 1996, the German fishing fleet underwent a change from several small vessels, fishing at Heligoland, to fewer large vessels, which were capable of reaching the new, northern cod fishing grounds (I16). Several fishing companies were no longer able to generate sufficient revenue due to fleet downsizing and spatial shift forcing them to go out of business (I16). Not only shifts on the population level, but also regime shifts in the North Sea species composition due to climate change appear as a short-term threat to fishing companies “because it is unclear what will happen afterwards” (I13). Besides reductions in fish stocks and changes in species composition, regime shifts implying increases in stocks can result in economic consequences. The gadoid outburst led also to a strong increase of haddock, which was therefore strongly fished by Scottish fishers. Due to contracts between fish factories and Norway, who also caught haddock, Sottish fishers could not land their fish and “discarded, an estimated 70,000 tones” (I14). Moreover, increases in species can result in changes of the target species, and therefore in the technical and economic orientation of a fleet. Irish and English fishers started fishing for edible crab in the German Bight using traps, due to a strong crab increase (I14).

Generally seen, regime shifts raise questions for management. Questions like “how should we deal with new species? How shall they be managed in the long-term?” are now and again stressed (I13). Hence, adaptation in management are needed (I4, I9, I5, I13). As a regime shift can cause irreversibility to the former state, the fisheries management system needs to adapt with new sustainable measures and fishing reference levels to the new situation which could mean less fish and lower catch levels (I9). Consequently, fishing quotas need to be adjusted to the new situation. In the case of North Sea cod, fishers need to prolong their fishing trips to reach new fishing grounds to fish their full quota and if they do not manage to do so, they lose the quota in the next year (I13) reducing their planning capabilities and therefore their livelihood security (I4).

Conceptual dimensions of tipping points

The analysis of the interviews clearly exhibits that the tipping point concept is not widely known among stakeholders. Only four interviewees (I2, I4, I10, I12) referred to the definition of the concept and applied it to examples, and criticized its application on varying levels. Interviewees (I2, I10, I12) converge in the generic definition of the concept by depicting a tipping point simply as the point where a system changes to another system state. Besides this general agreement, differences can be located in the details: two interviewees underlined that tipping points are catastrophic (I12) and determine the threshold until which a system’s resilience is still sufficient to buffer existent disturbances (I10). To discursively explore and explain these aspects, interviewees refer to examples based on environmental phenomena (I2, I10) or use data (I12) as explanatory devices. Environmentally seen, temperature can be understood as an important tipping point (I10) because a system remains in a stable state until temperature rises up to or exceeds a certain threshold. At this point in time – the so-called tipping point – “cascades are initiated which cause an abrupt change in the regime” (I10). Another tipping point concept is presented by an interviewee in the context of community shifts (I2). Here, the idea of tipping point is represented as the point at which pelagic fish species are more dominant than benthic species (I2) in the system. However, tipping points can also be related to time series data, where the tipping point determines the point in time at which two different system states a separated (I12).

Furthermore, the use of the tipping point concept is now and then critically assessed (I12) by various interviewees. Not only the concept in principle, but also underlying aspects such as its temporal reference(s), its inherent dynamics and its relevance for management are debated (I4, I10, I12). As in the case of the regime shift concept, the notion of tipping points has a high attractiveness to being used due to its conceptual and semantic imprecision. It appears to be a fancy word and “people like the sound of it” (I12) while also being used to indicate the point or threshold of an abrupt change (I2, I10, I12) in which the temporal scale is tricky to justify (I10, I12). Hence, “what does abrupt [in an ecological system] mean”? (I10). Ecological changes take place at a considerably slower temporal scale than all of a sudden (I10, I12), and rather represent gradual dynamics in reality than rapid changes as such (I12). Due to these inconsistencies, some interviewees conclude that the underlying dynamics triggering a tipping point are hardly understood (I4, I12). This can for example be seen in the fact that scientists, generally speaking, relate climate warming to tipping points, but do not clarify whether it directly or indirectly affects the system under scrutiny (I4), even if it is known that warming, as well as aspects like invasive species and predators, are involved in causing change. However, a detailed picture of the effects appears to be lacking (I4) which might have contributed to the fact that the concept of tipping points is not high on the political agenda (I4) and only plays a minor role in fisheries management.

Temporality – cause – effect - response. The concept of abrupt changes across space & time

Based on the interviews with stakeholders from different groups, one aspect can be clearly stated: abrupt changes are diverse in their *temporality*, their *causes*, their *effects*, as well as the *response* that follows them. Furthermore, this concept is considered at different levels (e.g., supranational, regional) and can be explicitly applied to different marine ecosystems (e.g., North Sea). In addition, abrupt changes are regarded in the fields of ecology, for example the abundance and distribution of fish stocks, but also of economy like fishing opportunities and social issues. The latter is here less related to fisheries, but rather expressed against the background of personal experience ("an abrupt change for all of us was of course COVID", I3).

Regarding the concepts' definition, an abrupt change is seen by interviewee as a process that does not happen in the short but in the medium to long term (I1, I5), where *temporality* can be considered on different levels, such as ecological temporality (e.g., species displacement) (I1). The speed at which an abrupt change takes place depends significantly on the strength of its *causes*, with climate change and fisheries cited as the main factors (I9). They lead to changes "that nature, and even less fisheries, can handle" (I5). This includes *impacts* on plankton in general (I11), the size of fish stocks, such as biomass (I5), and the interactions within the whole food web (I9). Considering the concept of abrupt change in general, *response*, as the end link in the chain, is related exclusively to EU fisheries policy and management pictured here as the adjusting screw of the whole (I4), with a distinction being made between short-term ("how to respond politically") and long-term measures (I4). The latter refers to a holistic approach that is intended to bring about an improvement in the management and ecosystem functioning (I4).

The four identified dimensions (*temporality*, *cause*, *effect*, *response*) are further applied to certain marine regions (regional level). The selection of which, such as the Baltic Sea, is based on the fact that there is a personal connection to it ("The Baltic Sea is close to our hearts!") (I3). However, it is not clear from this statement who is meant by "us". In deriving and describing the concept of abrupt changes with a focus on the Baltic Sea, a short-term change is described (*temporality*), without clarifying what *causes* this system change. It is only made clear that the abrupt change can be equated with drastically reduced fishing opportunities for cod and herring (*effect*) which has led to a "dilemma" in the Baltic Sea fishery (I3). However, it remains open to discussion how fisheries can or should be helped out of this dramatic situation (*response*). Another example is provided from the Northeast Atlantic, namely an abrupt change within the stock development of mackerel and herring (I9). A shift of the species as well as an expansion of their distribution is exemplified (*effect*) (I9). A temperature increase is named as the *cause*, although it is not quantified when this has occurred (*temporality*) (I9). What is clearly stated, however, is that this abrupt change has led to serious conflicts between fishing nations (I9). Similarly, in the North Sea, abrupt changes are put into the ecological context, with differentiated knowledge regarding its components (*effect*). Changes described include North Sea fish stocks, (strong collapses in the biomass and productivity) (I7, I6, I11) and plankton in general (I11) are depicted as changes, but also their interaction within the entire food web (I9). Two abrupt changes could be clearly named for the North Sea case (*temporality*): i) late 80's - early 90's (I7, I6, I11) and ii) late 90's - early 2000's (I2, I11). Contrary to the previous statement, namely that abrupt changes happen in the medium to long term, one interviewee describes this process with special regard to the decline of North Sea fish stocks as short-term ("within a short time", I7, I6). However, the *causes* "are partly understood" (I11), with overfishing ("due to overfishing the stocks have completely collapsed") being identified as one of them (I7, I6). The response of the socio-ecological system is viewed in a differentiated way by the interviewees (*response*). The abrupt changes caused, on the one hand, a surprise among the fishers, but not in an adjustment of their fishing behavior (socio-economic *response*) (I7, I6). On the other hand, a change in the entire food web (ecological *response*) was mentioned by one interviewee (I9).

Apart from a regional consideration of the abrupt change concept, the analysis also reveals a focus on the supranational level, i.e. the EU Common Fisheries Policy and associated management measures. In this regard, both the discard ban and the sharp reduction in fishing opportunities (also known as total allowable catch, TAC) for North Sea cod are understood as an abrupt change by the interviewees (I10, I4) (*effect*). An interesting aspect to note is that, in both descriptions, there is a legitimization of knowledge. Thus, either the field of work in general ("at least for the area I work in", I10) or in particular ("from a fisheries policy perspective", I4). The *temporality* of the abrupt changes in the EU administration is only determined to the "recent past" (I10), e.g. to a period of the last 10 years ("I can't say how things have gone in the last ten years", I4). Nevertheless, the *cause* of these changes is not described further and thus remains open. It is only revealed that an abrupt change in the management system was preceded by "years of arguments and discussions until changes in the regime were decided" (I1). In this context, those responsible for EU fisheries management are sharply criticized (I1), as action was only taken (abrupt changes in the EU fisheries system) when it is already almost too late (I1). The *response* is only indicated quite general ("that the measures [...] had a corresponding effect, a positive effect", I1).

Furthermore, the concept of abrupt change is considered at different levels (environmental, economic, social). Particularly when the concept is considered regionally, there is extensive knowledge about the time frame, causes, and reactions to the changes among all stakeholders. In this regard, the concept is perceived positive (e.g., introduction of the discard ban) or negative (e.g., reduction of fishing opportunities). But also, for example, the neutral consideration of an abrupt change (e.g., shift of species as in the North Sea mackerel and herring stock) is presented, whereas the *response* to this change is described as negative (e.g., conflict between fishing nations). Remarkably, abrupt changes in the context of ecology are much further in the past in terms of time, while changes in management are only related to the recent past.

4. Discussion

For the first time, we performed a socio-conceptual analysis of the concepts regime shift, tipping point and abrupt changes. Our analysis reveals that all three concepts are diversely described and framed by the groups involved, such as scientists, eNGOs and those directly involved in fisheries. Aspects like temporality, drivers and consequences determine whether a change is in fact assigned to one of these concepts or not.

The regime shift, tipping point and abrupt changes concepts were identified as black-boxed and as boundary objects at the same time. All three are used within various contexts (e.g., social, economic, management, ecology) without applying a clear explanation (black-boxed) (Jasanoff 2006; Latour 1987), and still, these concepts function as translators and bridges – i.e. boundary objects – among those involved in the framing of the concept such as different scientific disciplines and stakeholders holding various backgrounds (Kull et al. 2017; Star & Griesemer 1989). This is only possible due to the weak structure of the concepts when used commonly on the one hand, but their strong structure when used by individuals involved with boundary objects on the other hand (Star & Griesemer 1989). However, boundary objects are temporary entities and management of their content is, in terms of stable meanings, key for the development and maintenance of semantic consistency and communicative coherence across those involved in questions revolving around regime shifts, tipping points and abrupt changes (Star & Griesemer 1989). We have, moreover, shown that three dimensions of knowledge concerning the detail of the regime shift concept exist, going from non-knowledge via general knowledge to detailed knowledge (Fig. 1.4a, *knowledge*). Whereas the former implies no knowledge about the regime shift concept, the second and third include more detail by the inclusion of abrupt changes[1] and multiple system states, respectively. Similar differences in knowledges emerge for the tipping point and abrupt changes concepts, where a generic definition is agreed upon, but discrepancies in detail were revealed. Differences in these knowledges evolve from cultural beliefs, values, norms and from human experiences generated by the interaction with the environment in which our interview partners engage with them. Humans frame and perceive the environment in various ways and hence frame changes differently (Schwermer et al. 2021; Sterling et al. 2017). Consequently, the concepts used to capture them semantically vary or differ. Another commonality is the discourse around temporalities within the concepts' understanding (Fig. 1.4a, *temporality*). Temporality and temporal dimensions are defined by each person individually, and imply how time is perceived, assigned and expressed such as the past, present and future. Time itself is then practically applied to something or used for framing something (Caldas & Berterö 2012). In our analyses, we have shown that no fixed time for the processes of abrupt changes, tipping points and regime shifts exist among our interview partners. Whereas regime *shifts* are understood as processes in time, *abrupt* changes and tipping *points* rather imply particular moments in time.

[1] Here, abrupt changes are seen as being an entity included in the regime shift concept. The differentiation to the abrupt change concept itself is not made.

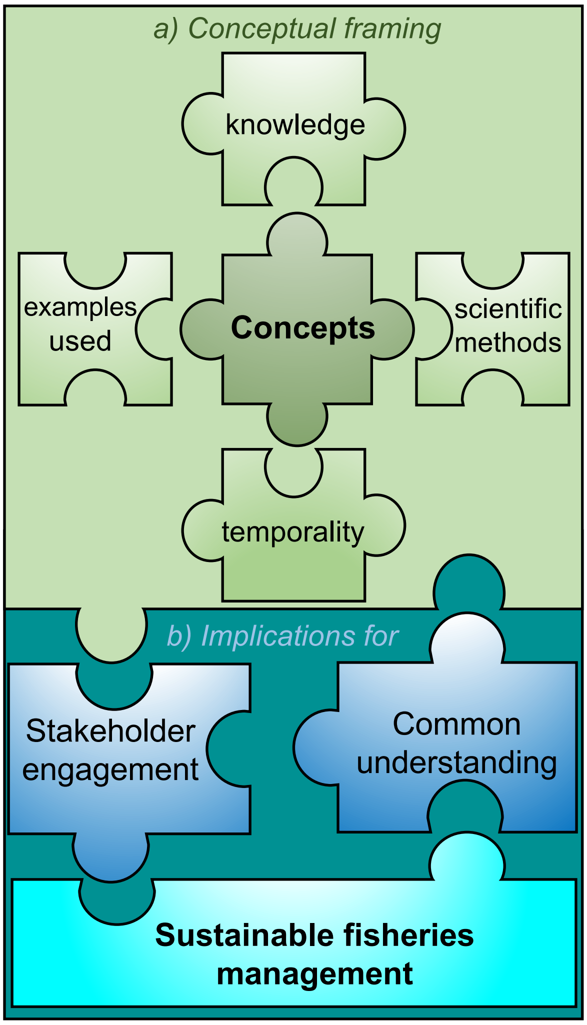

Figure 1.4. Socio-conceptual perception of the regime shift, tipping point and abrupt changes concepts. a) conceptual framing and b) the concepts' implications.

One needs to ask: what is *abrupt*? What is a tipping *point*? *Abrupt* can be defined as "sudden and unexpected" (Oxford Learner's Dictionaries 2022a) and *point* as "a particular time or stage of development" (Oxford Learner's Dictionaries 2022b). The interviews revealed that *abrupt* changes at or within certain *points* in time do not exist. Some interviewees state that, in theory, abrupt changes and tipping points shall take place rather fast and suddenly. However, they also highlight that, in reality, ecosystems underlie certain drivers and processes which can undergo short- to long-term changes. Hence, from a socio-conceptual point of view, there are no things such *abrupt* changes and tipping *points* at a particular time also revealing difficulties for the comprehension and application of the concepts.

These outcomes challenge the use of quantitative methods in science, applied to determine tipping points and regime shifts (Fig. 1.4a, *scientific methods*). Detection methods such as change point analyses, for instance, detect abrupt changes in a time series, but set the points of change to particular points in the time series (Erdman & Emerson 2007; Killick & Eckley 2014). Which of these abrupt changes detected is then indeed a tipping point or abrupt change in the regime shift context, remains with the scientists' judgement. Hence, from a quantitative method point of view, abrupt changes and tipping points align with their definitions and occur suddenly at a certain time (Erdman & Emerson 2007; Killick & Eckley 2014). The comparison of the stakeholder framing with the scientific methodological approaches shows that there is a discrepancy in the perception of abrupt changes and tipping points and the scientific possibility of detecting them. Therefore, conceptual reflection is needed to assess tipping points and abrupt changes for their temporality. The awareness that abrupt changes and tipping points are not certain points in time, but rather time spans, needs to be taken into account to enhance compliance about certain sudden events. Both, quantitative (e.g., change point analyses) and qualitative data (e.g., interviews with stakeholders) as well as their analyses, could be included if a method standardization for regime shift detection is developed. The focus is then put on how to align different framings (Star & Griesemer 1989). In this way, knowledge about the boundary object in question could become more consistent and could assist in translating and coordinating the meaning of important concepts between science, policy, administration and stakeholders (Star & Griesemer 1989). Through their involvement in scientific projects, stakeholders can for example make valid contributions to increase the relevance and robustness, as well as the understanding and acceptance of scientific results outside the academic world (Fig. 1.4b, *stakeholder engagement*) (Köpsel et al. 2021).

As we have seen, the elusiveness of the concepts makes their complexity difficult to grasp, and their application to case studies challenging. We showed that changes in the North Sea, like the decline of Atlantic cod, are considered as a regime shift in scientific literature (Sguotti et al. 2019, 2020), but not among all interviewees (Fig. 1.4a, *examples used*). These differences hold implications for fisheries management. Fisheries management needs to react to changes in the marine system to provide a sustainable governance approach to sustain the socio-ecological system (Ostrom

2009). A common understanding, if changes in the marine realm are considered as regime shifts, is crucial to adapt measures in cases of hysteresis and irreversibility (Fig. 1.4b, *common understanding*) (Scheffer et al. 2001). Decision-makers need to balance if management measures shall support a new regime, or force, if possible, the transition back to a former state. If the northward shift and the introduction of southern species in the North Sea (Baudron et al. 2020; Beare et al. 2004; Petitgas et al. 2012), for instance, are considered an irreversible regime shift, conflicts among EU fishing nations may arise and a new quota policy may be required. In addition, another challenge consists in the fact that systems constantly fluctuate and are not fully stable (Möllmann et al. 2015). Together with the inexplicit time spans defined within the three concepts, this clearly calls for a flexible management approach (Schwermer et al. 2021). Regime shift dynamics need to be incorporated into fisheries management to deal with probable changes on time and to determine if measures shall be implemented before, during or after a regime shift. Fisheries management, moreover, needs to consider the entire socio-ecological system (Ostrom 2009), like ecosystem-based fisheries management (Long et al. 2017; Westley et al. 2011), namely the sustainable exploitation of fish stocks according to sustainable reference levels and thus the preservation of the fishers' livelihoods as well as the fish markets (Fig. 1.4b, *sustainable fisheries management*).

5. Conclusion

We have explored the conceptual framing of the regime shift concept and the related concepts of tipping points and abrupt changes by highlighting that these concepts are semantically framed in various ways among stakeholders. Our analyses showed that differences in the detail of knowledge, the examples used to explain the concept and in the perception of time and temporality hold the potential to cause considerable misunderstanding for sustainable fisheries management, such as for Atlantic cod in the North Sea. But not only the increased use of the concepts in marine science (Arif et al. 2022; Möllmann et al. 2021; Sguotti et al. 2019; Stockholm Resilience Centre 2022) demands for an improved clarity to enhance a sustainable fisheries management; their strong use in media in the past decade, mainly due to the anticipated effects of climate change on the planet (van der Hel et al. 2018), promotes the use of these concepts among various user and interest groups and is a pointer to increase the urgency for a common understanding. Such an endeavor holds the potential to provide a basis for a collective ecosystem dynamics understanding and to pave the way towards acceptable management measures, which could support the sustainable use of marine resources (Schwermer et al. 2021). In contrast, the perspectives among stakeholders of having a common understanding about and similarity of the regime shift and its related concepts, whereas in reality they do not, can conceal differences in patterns and believes, as well as hide the diversity of thoughts around non-linear dynamics (Goguen 2005; Milkoreit et al. 2018). Hence, knowing that different knowledges about the details of these concepts exist is crucial for a commonly shared understanding of how and why regime shifts happen. Good and respectful communication among stakeholders can be enhanced, if the awareness of different conceptual framings – as based on varying perceptions around these concepts – is raised and if these differences are taken seriously into consideration and are discussed (Sterling et al. 2017).

The regime shift concept and its related notions of tipping points and abrupt changes remain without one clear definition but with different framings depending on the context they are used in. We have shown that these concepts are not yet well-structured and might require more time to develop into improved definitions, with consistent methods by also including knowledges from stakeholders. Hence, the heuristic “thinking” around the regime shift, tipping point and abrupt changes concepts and their application has to be unraveled into, e.g., underlying meanings, causalities, drivers and consequences to develop acceptable fisheries management measures for the sustainable use of marine resources such as fish stocks.

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Institutional Review Board Statement

All subjects gave their informed consent for inclusion before they participated in the study. This also applies for the citation of quotes from interviews which have been anonymized. The study was hence conducted in accordance with the Declaration of Helsinki.

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Supplementary Materials

Table S1.1. Interview guide. Questions asked within each interview. The interview guide consisted of six parts: i) background information interviewee, ii) Regime shifts in the North Sea, iii) Atlantic cod in more detail, iv) Cod management/policies and science, v) Future aspects, and vi) Last comments. Questions differed sometimes within the thematic blocks, depending on the stakeholder group interviewed. eNGO = environmental non-governmental organization.

Part	Main questions	Follow-up question	Stakeholder group
Background information	How did you come to the topic fisheries?	What is your scientific background? What is your experience with fisheries and fishing communities? State of the art of fisheries? Why is cod important for you? Why the specific case cod? (if applicable)	All
Regime shifts in the North Sea	Do you know about the concept „regime shift"? How would you describe the concept "regime shift"?	How would you describe "tipping points"? How relevant are these concepts? How are they applied and what use do they have for your scientific work? Since when does the concept exist in your scientific discipline?	All
	Do regime shifts matter in politics?	And tipping points? Are these related to fisheries?	Decision-maker

	How are fisheries considered on the political agenda?	Since when are fisheries considered? In which context?	Decision-maker
	What is the North Sea for you?	How would you describe the ecosystem? Which species are involved? How are they interrelated? What are possible drivers influencing the species and their ecosystem?	All
	Do you know about drastic changes in the North Sea ecosystem?	What has changed in terms of fish species? When? Where in the North Sea did they happen? Are there specific impacts causing these changes? Would you call these changes 'regime shifts'? Have these shifts affected the scientific research?	All
Atlantic cod in more detail	What do you know about cod in the North Sea?	E.g. relevance for fishing/fishers? E.g. relevance for the ecosystem? Economy of fisheries? E.g. relevance for the food web? What are relevant factors impacting the cod?	All

	Was there a regime shift/drastic change in the cod stock?	What are probable tipping points? How would you asses the current state of the art of the stock? Can the stock be recovered? (Why?/Why yes/ not?) What needs to be done for the stock to recover?	All
	What were and are consequences of the cod collapse/decline/change?	For the ecosystem? For the species composition? Who was influenced? How? Fishers? Fishery sector? How did fishers adapt to these changes? And why in this way? What adaptation measures or processes where policy induced? Do you know about social/economic/political challenges concerning the adaptive processes?	All
Cod management/ policies and science	How do you see the current cod management in the North Sea?	Do you think any changes are needed? Why? How? What will be challenges of these changes?	All

	How did the management react to the changes in the cod stocks?	E.g., licenses, quotas, restricted fishing areas? What where the consequences for the fishers given the new management strategies?	Decision-maker
	Is the current management sufficient for a sustainable fishing of the cod stock?	Do you think changes are needed? Why?/Which? Which obstacles bring these changes along?	Decision-maker
	How would you assess the role of science in the cod management?	Is it successful? Is change needed in terms of how science can be used/involved in cod management?	Science
	Do you know whether fishers are involved in the management?	If so, how? Do you know about the fishers' involvement in the management through the North Sea Advisory Council? What do you think about the fishers' contribution to management? Is this kind of involvement successful? Can stakeholder involvement be improved? How? What is the fishers' contribution to management?	eNGO Decision-maker Science

	Are you included in the fisheries management?	If so: how? Regional Advisory Council? Which contribution would you like to make? Why is your contribution meaningful? Can the contribution be enhanced? How?	Fisheries
	How is your organization related to fisheries in the North Sea?	What is your organization doing related to fishing? Is Atlantic cod in the focus of your work?	eNGO
	Does your organization cooperate with fisheries and fishers?	Why?/How? If not: Would like to involve fisheries in your work?	eNGO
	Is your organization involved in the fisheries management?	How? What is your contribution?	eNGO
Future aspects	How do you see the future related to the cod case?	Is any change in the stock expected? Are other tipping points/regime shifts expected? What is important? What needs to be taken into account? Does the occurrence of Corona (COVID-19) plays a role? Could this be seen as a “tipping point” ? (politically,	All

		socially, economically, ecologically)	
Last comments	Did we miss out something important? May I contact you again, if something important comes into my mind? Do you know someone else who would like to be asked about Atlantic cod?		All

Table S1.2. Guide of major and sub-categories.

Main category	Sub-category	Description
Regime shift	Regime Shift	*How is the concept conceptualized content wise?* All statements about regime shifts and related thoughts in all disciplines (e.g., biology, management, social, policy), as well as non-scientific understanding of the concept are included. This includes: knowledge of the concept (historical origin, relevance of the concept for the own and other stakeholders' work), definitions of regime shift (content wise and scientific-theoretical foundations), examples of regime shifts (e.g., ecological, social, economic, or political and their impacts).
	Tipping point	*How is the concept conceptualized content wise?* All statements about regime shifts and related thoughts in all disciplines (e.g., biology, management, social, policy), as well as non-scientific understanding of the concept are included. This includes: knowledge of the concept (historical origin, relevance of the concept for the own and other stakeholders' work), definitions of regime shift (content wise and scientific-theoretical foundations), examples of regime shifts (e.g., ecological, social, economic, or political and their impacts).
	Abrupt changes	*How is the concept conceptualized content wise?* All statements about regime shifts and related thoughts in all disciplines (e.g.,

		biology, management, social, policy), as well as non-scientific understanding of the concept are included. This includes: knowledge of the concept (historical origin, relevance of the concept for the own and other stakeholders' work), definitions of regime shift (content wise and scientific-theoretical foundations), examples of regime shifts (e.g., ecological, social, economic, or political and their impacts).
North Sea and related impacts	North Sea	*How is the North Sea framed?* All statements about the North Sea are highlighted here. This includes: Perception of the North Sea (aesthetics, experience, social relevance for oneself and others), ecosystem, system components (flora, fauna) and their interactions, spatial division (arguments for spatial divisions).
	North Sea – Impacts	*How are the impacts structured content wise and how do they affect the North Sea?* All statements about impacts on the North Sea system are included, e.g., abiotic and biotic, anthropogenic (e.g., fishing).
	Atlantic cod – Impacts	*How are the impacts structured content wise and how do they affect the stock?* All statements concerning impacts on the Atlantic cod are highlighted. Included are all kinds of impacts like abiotic, biotic, biologic, anthropogenic and their structure and effects within the system.
Atlantic cod	Atlantic cod	*How is the subject/the species cod developed/constructed?* All statements concerning the topic Atlantic cod are included. This means the social

		framing of Atlantic cod (relevance of cod for e.g. fisheries, tourism, ecosystem), the perception and evaluation of the stock situation (also related to stock in other regions than the North Sea).
	Atlantic cod – Development	*Which development is presented based on what evidence or assumptions?* All statements related to the Atlantic cod's development are highlighted. This category related to the process of development and includes the stock development over time, future developments (positive, negative, no change and on what basis these scenarios are developed), possible consequences due to the cod's development for the ecosystem, the fishery and the management.
	Atlantic cod – Development – Recovery	*Which potential is seen for a development and on what evidence or experience is it based?* All statements related to the Atlantic cod' recovery are included. This relates to recovery in a positive sense coming along with chances for the cod. Included are stock recoveries in the past and the future, aspects contributing to the recovery (abiotic and biotic aspects, policy, management) and their interactions, spatial and temporal recovery, comparison to cod recoveries on other regions like the Irish Sea.
Atlantic cod – Collapse and management	Atlantic cod – Collapse	*How is the concept conceptualized content wise and which examples are mentioned?* All statements concerning the collapse of the stock are included. The stock should be described as collapsed and "collapse" needs

		to be used in the citation. Included are also definitions of the concept ‘collapse’ and examples undermining the collapse.
	Atlantic cod – Management	*Which management measures are mentioned and how is their effectiveness presented?* All statements concerning the management directly related to the Atlantic cod are considered in this category. This includes the implementation of measurements (e.g., nature conservation areas, area closures), reference levels (MSC, TAC, etc.), the implementation of the scientific advice, the advice’s concept and effects.
	Atlantic cod – Brexit	*How does the Brexit affect the Atlantic cod?* All statements regarding the topic Brexit and its effects on the Atlantic cod are included.

Chapter II

Regime shift dynamics, tipping points and the success of fisheries management

Regime shift dynamics, tipping points and the success of fisheries management

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Abstract

Recovery of depleted fish stocks is an important goal for fisheries management and crucial to sustain important ecosystem functions as well as global food security. Successful recovery requires adjusting fishing mortality to stock productivity but can be prevented or inhibited by additional anthropogenic impacts such as climate change. Despite management measures to recover fish stocks being in place in legislations such as the European Union´s Common Fisheries Policy (CFP), recovery can be hindered by the occurrence of regime shift dynamics. Such non-linear discontinuous dynamics imply tipping points and bear the characteristics of abrupt change, hysteresis and non-stationary functional relationships. We here used the recent reform of the CFP as a natural experiment to investigate the existence of regime shift dynamics and its potential effects on the recovery potential of six strongly fished or even depleted commercial fish stocks in the North Sea. Using a set of statistical approaches we show that regime shift dynamics exist in all six fish stocks as a response to changes in fishing pressure and temperature. Our results furthermore demonstrate the context-dependence of such dynamics and hence the ability of management measures to rebuild depleted fish stocks, leading to either failed recovery or positive tipping.

1. Introduction

Recovery of depleted fish stocks is an important goal for fisheries management and crucial to sustain important ecosystem functions as well as global food security (EU 2013). Successful recovery requires adjusting fishing mortality to stock productivity but can be prevented or inhibited by additional anthropogenic impacts such as climate change, e.g. through temperature increase (Sguotti et al. 2019). In the European Union (EU), fisheries management targets fish stock recovery through regulations embedded in the so called common fisheries policy (CFP), first implemented in 1983, to enhance the management of fisheries and fish stocks. The CFP underwent several successive reforms (the latest in 2014) and aims for a fishery that is environmentally, economically and socially sustainable (EU 2013). One of the main features of the CFP is the introduction of the Maximum Sustainable Yield (MSY) concept, where MSY is defined as “the highest theoretical equilibrium yield that can be continuously taken from a stock under existing average environmental conditions without significantly affecting the reproduction process” (EU 2013). In EU fisheries management MSY is implemented through a target fishing mortality F_{MSY} (fishing mortality level aiming at Maximum Sustainable Yield) (ICES 2012) and MSY $B_{trigger}$, a limit reference biomass value below which F_{MSY} is adjusted (ICES 2019a). Annual stock assessments advising EU fisheries management are provided by the International Council for the Exploration of the Sea (ICES) that, among others, provides reconstructed time-series of fishing mortality (F), spawning stock biomass (SSB, the parent biomass) and recruitment of the stock (R, size at the incoming new year-class) (ICES 2012).

Within the EU, the North Sea is among the most heavily impacted areas of the world´s oceans suffering from diverse anthropogenic activities (Emeis et al. 2015). It was a hotspot of overfishing with several fish stocks suffering from unsustainable fishing pressure, with the collapse of the Atlantic cod being a prominent example (Emeis et al. 2015; Sguotti et al. 2019). Fishing pressure was reduced strongly to prevent further depletion of fish stocks, but as with cod, recovery was not successful for all species (Sguotti et al. 2019). In addition, the North Sea is currently considered a hot spot of climate change experiencing rapid warming and acidification, affecting the distribution of the North Sea fish community (Emeis et al. 2015). Cold water species experience a shift northwards, whereas subtropical species like sardine and anchovy appear more likely (Baudron et al. 2020; Beare et al. 2004; Petitgas et al. 2012). Hence, as many commercially important fish stocks in the North Sea are affected by overexploitation and climate change effects are increasing continuously, the effective implementation of the EU fisheries management to achieve sustainable reference levels is crucial for stock recovery (Sguotti et al. 2019).

Despite management measures to recover fish stocks being in place, recovery can be hindered by the occurrence of non-linear discontinuous dynamics of ecological systems (Möllmann et al. 2021; Sguotti et al. 2019, 2020). Such dynamics imply tipping points, where, e.g., a fish stock's biomass crosses a critical threshold at which two dynamic regimes can be separated, the so-called alternative states; a high biomass state above MSY and an unsustainable low biomass state. Hence, a tipping point is defined as an abrupt change in the dynamics in response to changes in internal or external pressures (Sguotti & Cormon 2018). The concept of tipping points usually implies discontinuous regime shifts of systems and includes three characteristics: 1) *abrupt change*, 2) *hysteresis*, and 3) *non-stationary functional relationships* (Beisner et al. 2003; Scheffer et al. 2001; Sguotti & Cormon 2018). *Abrupt change* is the first-order indicator of regime shifts. According to theory such rapid change or the crossing of tipping points occurs when an external pressure, e.g. fishing mortality, exceeds a threshold or through the interaction of drivers like fishing pressure and temperature, where changes in one pressure can modify the interaction between the driver and the state variable and induce the shift towards an alternative state (Beisner et al. 2003; Scheffer et al. 2001; Sguotti & Cormon 2018). If subsequently a pressure is reduced and the return path from this new alternative to the original state is different from the path that led to the new state, *hysteresis* is present. If hysteresis or even irreversibility occurs, often the two drivers interact in causing *non-stationary functional relationships* (Beisner et al. 2003; Scheffer et al. 2001; Sguotti & Cormon 2018). A non-stationary relationship implies e.g., shifts in the so-called stock-recruitment relationship (SRR). SRR is the most important relationship in fish stock dynamics and relates the SSB to R; both being essential to determine allowable catches (Yang & Yamakawa 2022). Non-stationarity in the SRR changes the relationship between SSB and R, where, in the worst case, R is no longer determined by SSB (Perälä et al. 2017). Hence, knowing the stock's SRR is crucial for a sustainable fisheries management (Yang & Yamakawa 2022).

We here used the recent reform of the CFP as a natural experiment to investigate the existence of non-linear discontinuous dynamics and its potential effects on the recovery potential of strongly fished or even depleted commercial fish stocks in the North Sea. We focused on a selection of important North Sea fish stocks since this region has experienced several regime shifts, and is a focus area of marine regime shift science (Beaugrand 2004). Therefore, we assessed the effectiveness of reducing fishing mortality to sustainable reference levels and potential recovery patterns of European plaice (*Pleuronectes platessa*), European hake (*Merluccius merluccius*), Atlantic herring (*Clupea harengus*), haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*), and Atlantic cod (*Gadus morhua*). These species are commercially relevant and cover a range of life-history strategies and taxonomic groups, i.e. pelagic and demersal as well as round and flat fishes. Here, we used fish stock (SSB, R) and fishing mortality (F) data from the International Council for the Exploration of the Sea (ICES) in the ICES Stock Assessment Database (data extracted in 2021) (ICES 2019f).

Our study revealed regime shift characteristics to exist in all six North Sea fish stocks investigated, suggesting the prevalence of discontinuous dynamics in exploited living marine resources. Our results furthermore demonstrate the context-dependence of such dynamics and hence the ability of management measures to rebuild depleted fish stocks, leading to either failed recovery or positive tipping.

2. Materials and Methods

2.1. Data

We based our analyses on stock assessment data for six North Sea fish species (plaice, hake, herring, haddock, saithe and cod) provided by the International Council for the Exploration of the Sea (ICES) in the ICES Stock Assessment Database (data extracted in 2021, see Supplementary Table S2.3) (ICES 2019f). Data for plaice comprised the years 1957-2021, for hake 1978-2021, for herring 1947-2021, for haddock 1972-2021, for saithe 1967-2021, and for cod 1963-2021. ICES stock assessment data include, among others, yearly data on spawning stock biomass (SSB), recruitment (R), and fishing mortality (F). R is represented by the population numbers at a certain age, i.e for plaice at age 1, hake at age 0, herring at age 0, haddock at age 0, saithe at age 3, and cod at age 1.

Yearly mean sea surface temperature (SST) data for the North Sea region were derived for the tGAM analysis (see below) from the National Center for Environmental Information (NCEI) (Huang et al. 2015).

2.2. Approach

We here used three characteristics (flags) of regime shift dynamics in analysing the recovery of North Sea fish species: 1) *abrupt changes*, 2) *hysteresis*, and 3) *and non-stationary functional relationships* (Beisner et al. 2003; Scheffer et al. 2001; Sguotti & Cormon 2018). We first identified abrupt changes in time-series of SSB using statistical change point analysis. Since regime shifts theoretically imply alternative stable states and these can be empirically assessed by exploring hysteretic dynamics, we assessed hysteresis in fish stocks by inspecting the temporal evolution of the relationship of F to SSB. If hysteresis exists usually important functional relationships in a system are non-stationary and multiple drivers interact. We therefore analysed the most important functional relationship in a fish stock, the so-called stock-recruitment relationship (SRR) using multiple statistical techniques.

2.3. Statistical change point analysis for detecting abrupt changes

We identified abrupt changes in time series of SSB for each fish stock using statistical change point approaches provided by the R packages *bcp* (Erdman & Emerson 2007) and *changepoint* (Killick & Eckley 2014). *bcp* calculates posterior probabilities of changes at any given point of the time series using a Bayesian approach (Erdman & Emerson 2007). We furthermore used the *BinSeg* algorithm in *changepoint*, that conducts binary segmentation based on a multiple change point search (Killick & Eckley 2014). We determined years of abrupt changes when both methods detected approximately the same change point year (± 1 year). We allowed for at least five consecutive years between change points to potentially reflect quasi-stable periods in SSB. For hake and plaice, we removed the last 8 and 10 years, respectively, of the time-series, because the strong increases at the end of the time-series masked smaller changes in previous years.

2.4. Hysteresis

We inspected hysteresis patterns in plots of F versus SSB for each North Sea stock analysed. Hysteresis is visible by a loop-like shape appearing when the recovery path of SSB in response to reduced F differs from the initial path to a more depleted SSB state. This loop-like shape indicates that for the same level of the driver alternative stable states exist in the state variable, an indication for regime shift dynamics.

2.5. Non-stationary functional relationships

We investigated non-stationarity in the so-called stock-recruitment relationship (SRR) that relates the number of new offspring in a year (i.e. the recruitment; shifted to the year of origin) to the size of the parent spawning stock biomass (SSB). For each of the six North Sea fish stocks analysed we conducted a model selection exercise comparing traditional continuous Beverton-Holt and Ricker functions to alternative breakpoint approaches as well as a linear model. Beverton-Holt and Ricker models were fitted using the R package *FSA* (Ogle et al. 2020).

The Beverton-Holt and Ricker functions are given as followed:

Beverton-Holt (Beverton & Holt 1957):

$$R = \frac{(\alpha * SSB)}{(1+\beta * SSB)} \tag{1}$$

Ricker (Ricker 1954):

$$R = SSB * e^{\alpha - \beta * SSB} \tag{2}$$

where R is the recruitment, SSB the spawning stock biomass, α and β parameters of the models (Ogle et al. 2020).

Discontinuous models incorporating breakpoints between different linear "sub-models" were fitted with algorithms provided by the R packages *segmented* (Muggeo 2008) (function ‘segmented’) and *strucchange* (Zeileis et al. 2002) (function ‘breakpoint’). In *segmented*, ‘segmented’ linear models (LM) or generalized linear models (GLMs) are fitted to portions of the data points separated by breakpoints that need to be determined a priori. New linear relationships are estimated at each break point based on breakpoint and slope parameters. If these regressions are significantly different, a break point is found (Muggeo 2008). In contrast, no a priori break points need to be determined in the *strucchange* approach. Here, deviations from linear regression models are tested for stability. Further, *m* breakpoints are assumed to exist and coefficients can shift between stable regression relationships, where *m*+1 segments have constant coefficients. Minimizing the residual sum of squares (RSS) leads to the optimal number of breakpoints (Zeileis et al. 2002). We compared the fits of a simple linear model, a linear model with logarithmic transformation of both variables (SSB and R) and a number of GLMs assuming Gaussian, Poisson, quasi-Poisson and negative binomial residual distributions. The best performing GLM was chosen based on model diagnostics and on over- or underdispersion patterns in the residuals. We here assumed only one breakpoint and used the mean of SSB as a starting value. We compared the best breakpoint models with the Beverton-Holt and Ricker as well as a simple linear model using root mean square errors (RMSE) where lowest RMSE indicates the best fitting stock-recruitment model.

2.6. Temperature influence on stock-recruitment relationships

To assess whether abrupt changes in the relationship between SSB and R are affected by changes in sea surface temperature (SST), we used the threshold generalized additive modelling (tGAM) approach provided by the R package *INDperform* (Otto et al. 2018). tGAMs are based on the following generalized additive model (gam):

$$gam\left(SSB \backsim s(R, k = 3)\right) \tag{3}$$

where k is the dimension of the basis functions for representing the smooth term defined by s().

The SST threshold is identified by fitting the GAM with the ‘thresh_gam’ function, which uses the following formula (Otto et al. 2018):

$$y \sim 1 + s\left(SSB, by = \mathrm{I}\left(1 * (R \leq threshold)\right), k = 4\right) + s\left(SSB, by = \mathrm{I}\left(1 * (R > threshold)\right), k = 4\right) \tag{4}$$

The model estimates a threshold value for temperature from the input data by minimizing generalized cross-validation (GCV) values over an interval between lower and upper quantiles of the threshold variable. The quantile values are per default 0.2 for the lower and 0.8 for the upper quantile (Otto et al. 2018). Using the 'thresh_gam' function, a sequence of evenly distributed threshold values between the defined lower and upper quantile is created. Along the sequence, a threshold GAM is implemented for every value at which a new splitting of threshold variables occurs.

For all observations where the threshold variable is below the threshold value at a certain time step (year), a smoothing function is applied. Another smoothing function is applied to the observations where the variable is higher than the threshold value. From several computed models, the tGAM with the least GCV is selected and its threshold value returned (Otto et al. 2018). The choice for or against a true temperature threshold was based on three model outputs: 1) the fitted slopes before and after the threshold had to differ, 2) at least one of the slopes needed to be significant (significance level $p < 0.05$), 3) the GCVV plot displaying GCV values of fitted tGAMs (y-axis) had to show a deep valley at the proposed threshold temperature (x-axis). To see a possible difference of the SRR before and after the threshold, the SRR was predicted using the respective tGAM, predicted data were plotted and divided into red (high temperature) and blue (low temperature) (Otto et al. 2018).

2.7. R environment and packages

All analyses were conducted within the R programming and statistical environment (R Core Team 2018). For graphics the packages 'ggplot2' (Wickham 2016) and 'patchwork' (Pedersen 2020) were used. An overview of packages and functions used in the analyses described above can be found in Table 2.1.

Table 2.1. R packages and functions used in the North Sea stocks analyses.

Analysis	Package	Function
Change/Break points	bcp (Erdman & Emerson 2007)	bcp()
	changepoint (Killick & Eckley 2014)	cpt.mean()

	segmented (Muggeo 2008)	segmented()
	strucchange (Zeileis et al. 2002, 2003)	breakpoints()
Beverton-Holt	FSA(Ogle et al. 2020)	srStarts(), srFuns()
Ricker	FSA(Ogle et al. 2020)	srStarts(), srFuns()
GLM	MASS(Venables & Ripley 2002)	glm.nb()
tGAM	INDperform(Otto et al. 2018)	thresh_gam()

3. Results

3.1. Temporal dynamics and abrupt changes

We first analysed time-series of fishing mortality (F), spawning stock biomass (SSB) and recruitment (R) to compare stock development and status among the target fish stocks of our study and to identify potential abrupt changes. For the six North Sea fish stocks, F was periodically excessively high (even > 1.0), i.e. far above the present F_{MSY} target (Fig. 2.1 – left column). This high fishing mortality lasted until the beginning of the 2000s (and partly longer) for plaice, hake, haddock and cod. During the early 2000s EU fisheries management succeeded to reduce F for all species, except for cod, to levels at or close to F_{MSY}. Plaice and hake responded immediately with strong increases to unprecedented levels in SSB, far above the limit reference level (MSY $B_{trigger}$; the threshold SSB triggering a reduction in F_{MSY} (ICES 2012)) (Fig. 2.1 – middle column). However, low responses in SSB to decreasing fishing mortalities are observed for the remaining species, in haddock only noticeable with a peak year. Importantly, cod remains exclusively below MSY $B_{trigger}$.

Statistical change point analyses (see Methods) revealed several abrupt changes, the first flag indicating regime shift dynamics in SSB (Table 2.2; Fig. 2.1 – middle column). For plaice and herring, three abrupt changes separating four semi-stable periods were found, whereas only one abrupt change was found for haddock. The identified periods for plaice and herring overlap strongly (decades: 1950s-60s, 1970s-80s, 1980s-2000s,

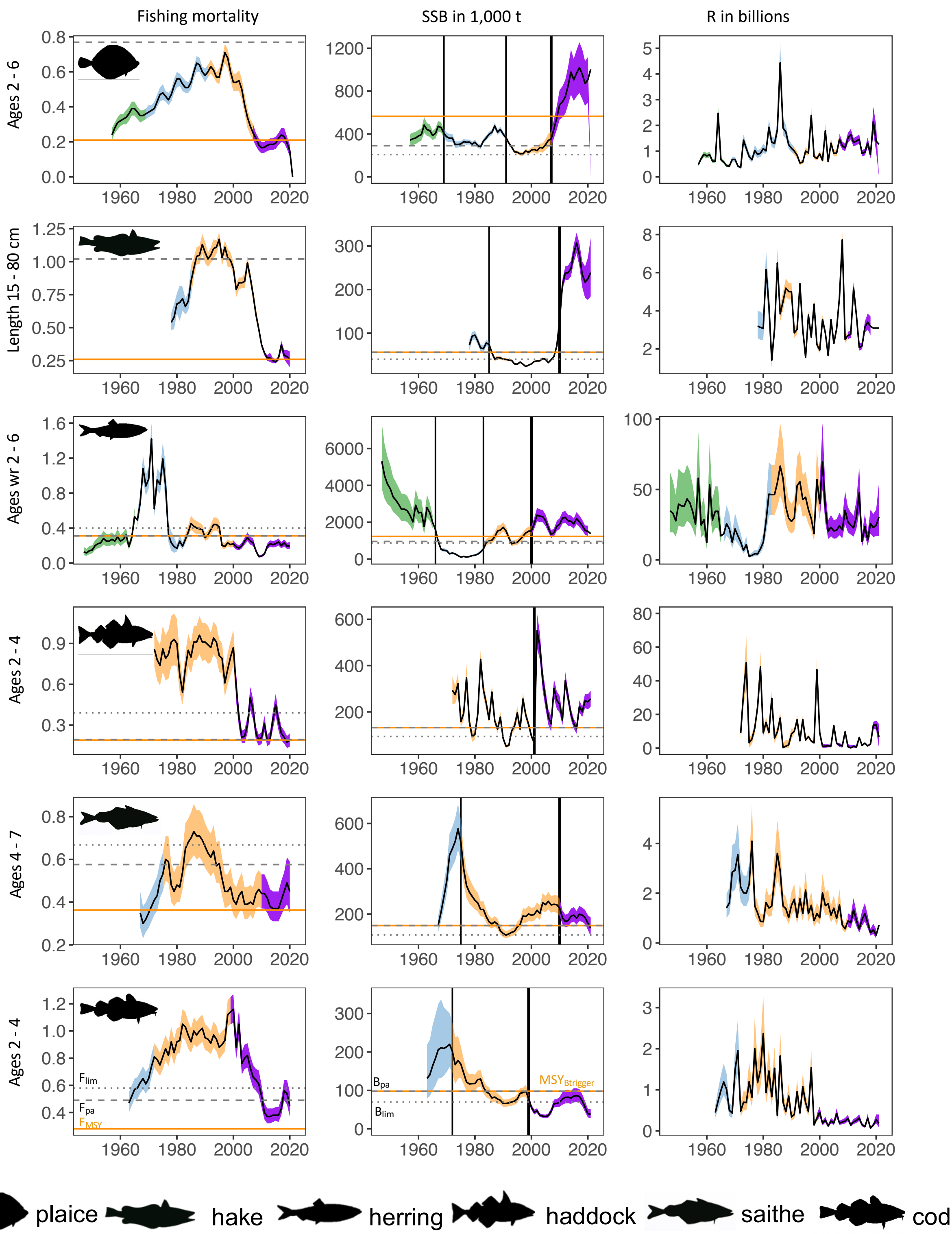

Figure 2.1. Abrupt changes in North Sea fish stocks. Time series of fishing mortality (F), spawning stock biomass (SSB) and recruitment (R). Vertical lines in SSB indicate abrupt changes detected by statistical change point analysis. Coloured ranges show identified SSB periods (see also Table 2.2); horizontal lines indicate management reference points; left column - F level aiming at Maximum Sustainable Yield (F_{MSY}), precautionary level of F (F_{pa}), limit reference point of F (F_{lim}); middle column – Level of SSB triggering specific action in management (MSY $B_{trigger}$), precautionary level of SSB (B_{pa}), limit reference point of SSB (B_{lim}) (ICES 2012).

Table 2.2. Abrupt changes in North Sea fish stocks. Periods of quasi-stability in spawning stock biomass (SSB) identified by statistical change point analyses.

Species	Period 1	Period 2	Period 3	Period 4
Plaice	1957- 1969	1970-1991	1992-2007	2008-2021
Hake	1978-1985	1986-2010	2011-2021	
Herring	1947-1966	1967-1983	1984-2000	2001-2021
Haddock	1965-2001	2002-2021		
Saithe	1967-1975	1976-2010	2011-2021	
Cod	1963-1972	1973-1999	2000-2021	

2000s-2010s) and change points only differ by eight years in maximum. Also, the periods of saithe and cod were almost in synchrony, except for the last period where the change occurred 11 years earlier for cod (decades: 1960s-70s, 1970s-2000s, 2000s-2010s). These abrupt changes preceded collapses for saithe and cod, while plaice and hake showed a positive stock development following the last abrupt change.

Apart from SSB, R is an important determinant of a population's success and a major determinant of the dynamics of commercially important fish. The number of juveniles potentially joining the parent's biomass eventually determines the size of SSB, whereas the size of SSB affects the size of recruitment (SRR) (Szuwalski et al. 2015, 2019). Whether the influence of SSB on R is greater or vice versa, depends on the stock status; depleted stocks like North Sea cod experience a higher influence of SSB on R, with R following SSB patterns (Szuwalski et al. 2015). Hence, we inspected the recruitment dynamics relating them to changes in SSB (Fig. 2.1 – right column). R was relatively stable over time in plaice and increased only slightly towards the end of the time series, which is likely a response to increased SSB. For herring, recruitment development appears to follow SSB patterns, with high R at high SSB levels and vice versa. R in hake remained largely unchanged regardless of SSB development. For the remaining stocks (saithe and cod), recruitment decreased strongly simultaneously with SSB decrease. Small occasional increases in SSB in these stocks did not lead to any improvement in R.

3.2. Hysteresis

To determine whether previously identified abrupt changes in SSB and related R patterns do reflect alternative stable states and hence true regime shifts, we studied the existence of hysteresis in the selected North Sea fish stocks, i.e. if the return path in population size (spawning stock biomass - SSB) is different after reduction of the pressure (fishing mortality - F) compared to the preceding path to depletion (the second regime-shift flag) (Beisner et al. 2003; Scheffer et al. 2001; Sguotti & Cormon 2018). Hence, by relating SSB to F we can identify hysteresis by a loop-like shape given two different paths of SSB towards and away from depletion. If the loop is fully closed, the species reached former SSB levels and fully returned to its original SSB state. In contrast, an open loop indicates recovery failure as the current state is still below former levels even though the pressure is at the same level as before. We observed hysteresis in all species, except for haddock (Fig. 2.2). We find closed hysteresis-loops for plaice, hake, herring and saithe where reduction in F to F_{MSY} has resulted in SSB levels being at least close to MSY $B_{trigger}$. Historically low F levels in plaice and hake have resulted in exceptionally high SSB states, which led to an escape from the hysteresis loop. In contrast, an open loop is observed for cod where management failed to reduce fishing pressure to F_{MSY} and hence MSY $B_{trigger}$ is not reached yet.

3.3. Non-stationary functional relationships

An important mechanistic criterium for regime shifts dynamics is non-stationarity in important functional relationships governing a dynamic system (the third regime-shift flag) (Perälä et al. 2017). SSB and R are the two most important interacting attributes of fish stocks (Yang & Yamakawa 2022). Still, the links between these two are not yet fully understood and can be disrupted by external factors, such as temperature (Perälä et al. 2017). Therefore, we here studied the stock-recruitment relationships (SRR) to determine the potential existence of non-stationarity. We compared traditional and continuous SRR models (i.e. Ricker and Beverton and Holt models) to a linear model

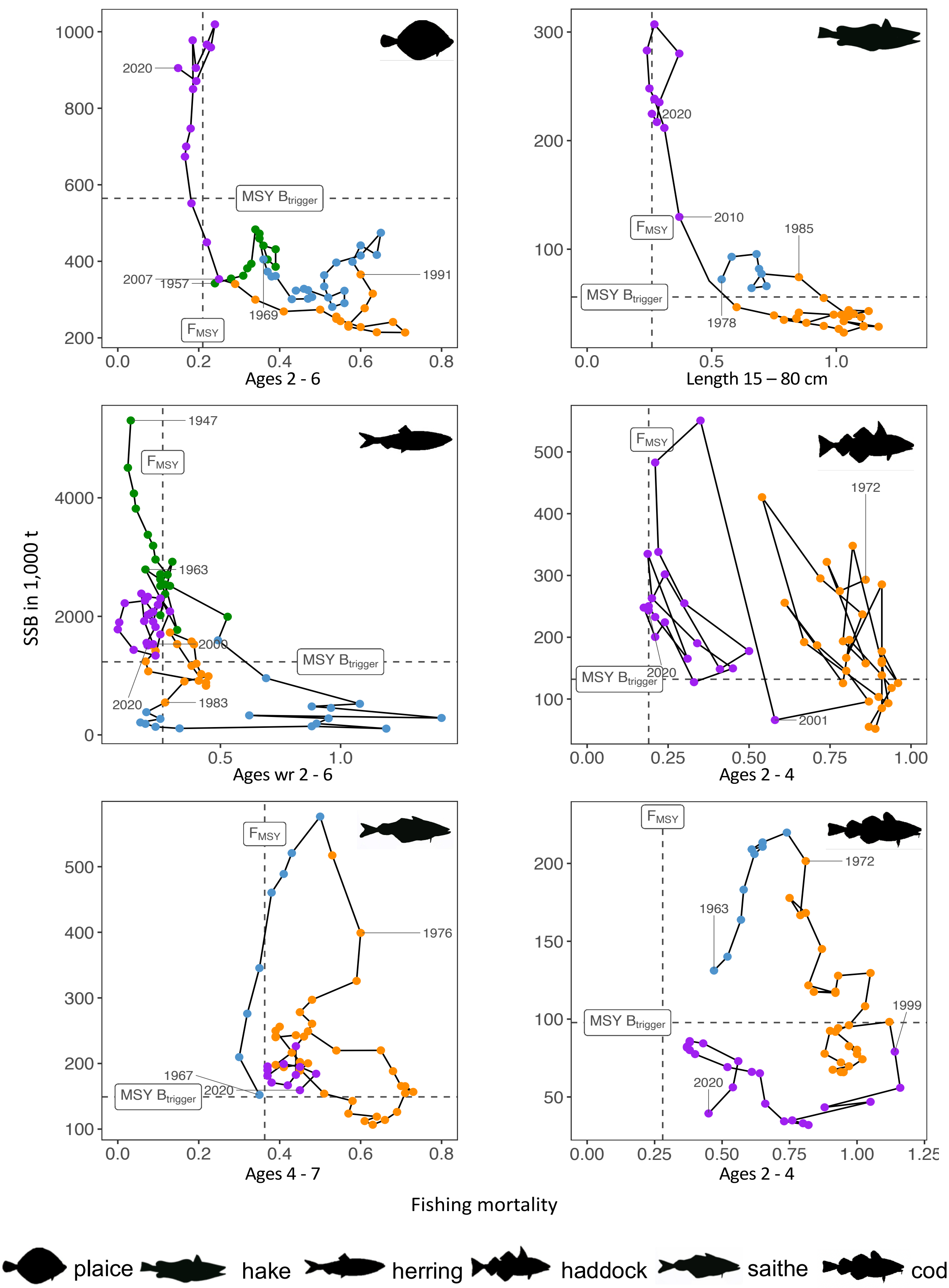

Figure 2.2. Hysteresis in North Sea fish stocks. Vertical and horizontal lines show sustainable fishing pressure (F_{MSY}) and the level of spawning stock biomass (SSB) triggering specific action in management (MSY $B_{trigger}$), respectively. Coloured points show identified SSB periods (see also Table 2.2).

and models incorporating a sudden structural change in the effect of SSB on R (see Methods). In all cases the discontinuous models provided better fits than the traditional and the linear models (comparison of models in Supplementary Table S2.1) indicating non-stationarity for all stocks.

We found for all SRRs an abrupt break point, at which the relationship between SSB and R changed (Fig. 2.3). For all stocks, except for saithe, the SRR was positive before and negative after the change point. This pattern is a sign of the typical density-dependence at which the SRR is usually dome-shaped and shows low R levels at high SSB levels as in the Beverton-Holt and Ricker curves (Szuwalski et al. 2015). For hake, e.g., the highest R occurred before density-dependence during the first (blue) and second period (orange), where SSB levels were even below the reference level MSY $B_{trigger}$. Furthermore, we only found in plaice a slight increase in R, with simultaneous high SSB levels during recent years (Fig. 2.3). Importantly, we found R in gadoid stocks, except for hake, to be very low and largely independent of the size of SSB during the recent period. Especially cod still shows very low SSB and R values in recent years and despite a slight increase in the past five years in SSB, R did not increase.

Knowing that the North Sea is a climate change hot spot with increasing water temperatures (Emeis et al. 2015), we explored whether warming has an effect on the SRR. We used Generalized Additive Models (tGAMs; see Methods) that are able to identify a threshold of a pressure like sea surface temperature (SST) at which the relationship between SSB and R is affected. A significant threshold indicates that certain levels of SST can change the SRR shown by differences in the slope (Otto et al. 2018).

We did not find any significant temperature thresholds, and therefore temperature impacts on changes in the SSR relationship, for plaice and hake (thresholds at 9.8°C); the two species with positive SSB developments (Table 2.3, Supplementary Table S2.2, Supplementary Fig. S2.1). For herring and haddock (threshold at 10.7 °C and 10.4 °C, respectively), SST has an effect on the SRR. SSB positively influences R before the threshold which is represented by a strong positive slope. At higher temperatures, crossing the threshold, the positive effect is less strong and no longer significant. For saithe and cod, SST causes a slightly different effect in the relationship before and after the threshold (10.2 °C and 10.2 °C, respectively). SSB has a strong

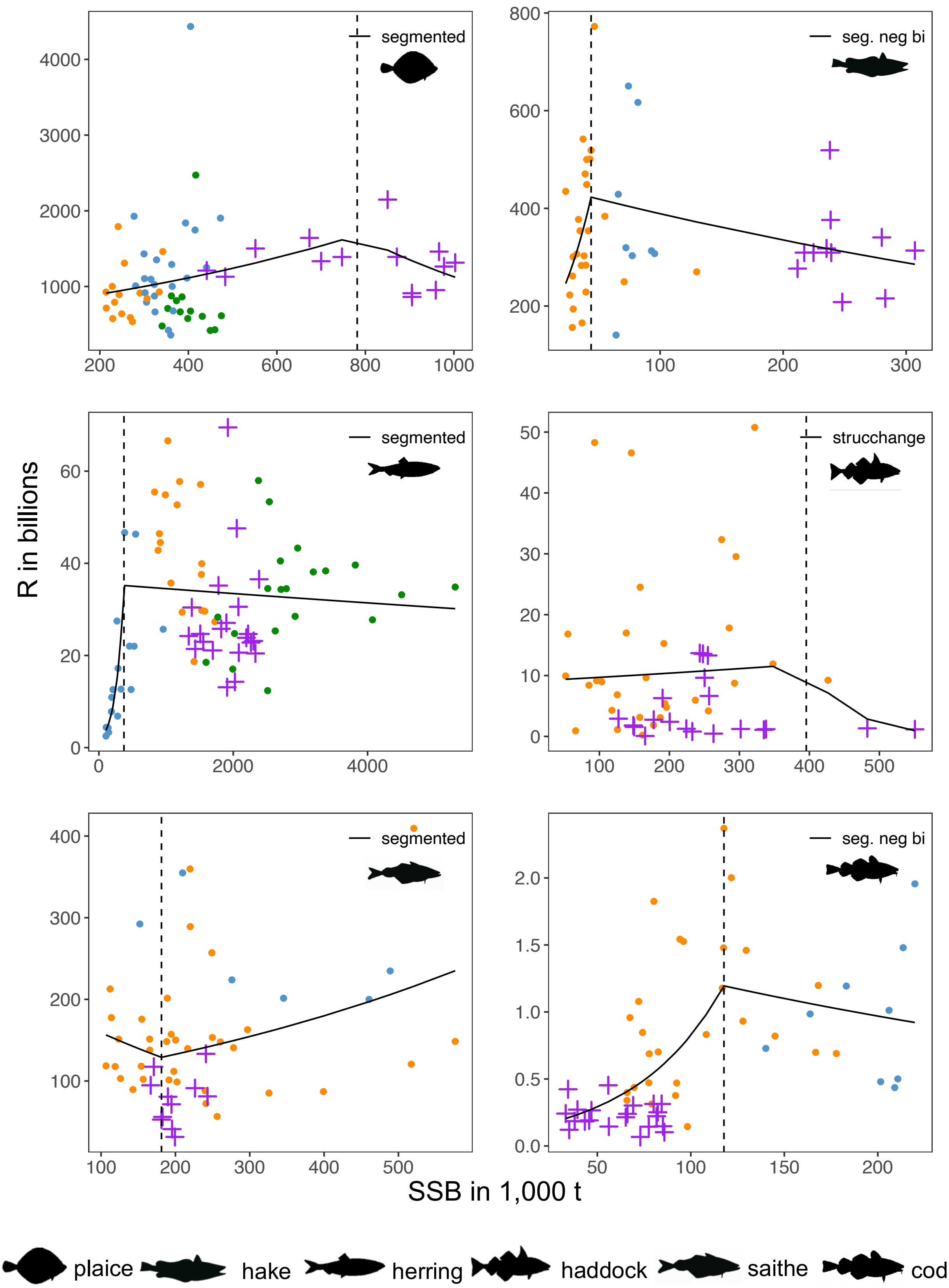

Figure 2.3. Non-stationary functional relationships in North Sea fish stocks. Break points (vertical dashed lines) in non-linear stock-recruitment relationships. Solid line represents chosen break point model, i.e. segmented negative binomial for all species. Colours represent identified spawning stock biomass (SSB) periods; crosses indicate the latest SSB period (see also Table 2.2).

Table 2.3. Non-stationarity in stock-recruitment relationships. Species-specific temperature threshold from tGAM analyses. (Detailed tGAM results in Supplementary Table S2.2).

Species	Temperature threshold	Threshold accepted
Plaice	9.8 °C	No
Hake	9.8 °C	No
Herring	10.7 °C	Yes*
Haddock	10.4 °C	Yes*
Saithe	10.2 °C	Yes
Cod	10.1 °C	Yes

* Significant relationship before the threshold only.

positive effect on R before the threshold in both stocks, which is less strong after the threshold.

4. Discussion

In our study we used the recent reform of the European Union´s Common Fisheries Policy (CFP) as a natural experiment to investigate the existence of regime shift dynamics in North Sea fish stocks, and their implications for achieving management and especially rebuilding targets. We found in all investigated fish species abrupt changes in SSB suggesting periods of quasi-stability to exist. Abrupt changes were mostly responses to changes in fishing pressure (EU 2004; ICES 2019g, 2019d, 2019e, 2019c, 2019b; Støttrup et al. 2017) interacting with environmental changes such as resulting from climate change and the positive effects of reduced eutrophication of the North Sea (A. Rijnsdorp et al. 2010; A. D. Rijnsdorp & Vingerhoed 2001; Støttrup et al. 2017). In all fish species, except haddock, we additionally identified hysteresis effects, differing in strength. With the exception of cod, all investigated North Sea fish species responded to reduced fishing mortality as a result of implementing the MSY concept in the CFP. Hence sustainable stock sizes were achieved, but the recovery occurred slower than the initial depletion. Only the cod stock failed to recover, not closing the hysteresis loop. Eventually, we also observed non-stationarity in the important stock-recruitment relationship (SRR) in all species. In total, our study delivers further support for non-linear population dynamics to prevail in commercially exploited fish species (Möllmann et al. 2021; Sguotti et al. 2019). A consequence of this results is that fisheries management cannot rely on common linear dynamic assumptions, but rather has to deal with delayed or failed recovery after implementing measures to reduced exploitation pressure as well as surprising developments such as positive tipping.

We found positive tipping dynamics in the North sea stocks of plaice and hake. These stocks recovered the fastest in response to reduced fishing mortality after the reform of the CFP and increased to record high stock sizes recently. Such dynamics can be interpreted as positive tipping, where the pressure is reduced to a point (here below F_{MSY}) that positive runaway dynamics in the population is induced. Positive tipping is in contrast to the general connotation of tipping points that are mainly seen as negative transitions in dynamic systems implying a shift from a positive to a negative state (Möllmann et al. 2021; Sguotti et al. 2019). However, it should be noted that the increases in both stocks are spatially-explicit phenomena. The increase in North Sea plaice as a whole is due to a strong increase in stock components north of Scotland as well as the offshore areas of the Netherlands, Germany and Denmark (Engelhard et al. 2011). The increase of hake in the North Sea is the result of stronger influx of individuals from the western distribution area of the northern stock component (Baudron & Fernandes 2015). Nevertheless, both stocks increased due to reduced exploitation pressure and are important examples of the effectiveness of the MSY approach of the CFP. Such unprecedented stock sizes may however induce new management challenges such as shown for hake (Baudron & Fernandes 2015).

In strong cases, regime shift dynamics with strong hysteresis and non-stationary SRR can lead to a failure to achieve management measures with cod as the best example (Möllmann et al. 2021; Sguotti et al. 2019). The North Sea cod stock appears to be locked in a low SSB state as indicated by an open hysteresis loop. Our results suggest that cod crossed a tipping point (in this case a negative one) after which recovery is difficult. Cod recovery is hindered by the detrimental effects of climate change and especially warming (Sguotti et al. 2019, 2020). Our tGAM analyses support the climate effect with a significant temperature threshold in the SRR indicating recent and further warming of the North Sea to be detrimental for cod recruitment. However, it remains clear that cod recovery in the North Sea is also limited by fishing mortalities still above the F_{MSY} target.

In addition to cod, our tGAM analyses revealed significant thermal thresholds in the SRR for herring, haddock and saithe as well. The mean SST for the North Sea over the past 20 years was at 10.8°C (Huang et al. 2015), exceeding all tGAM thresholds identified. The region records a temperature increase especially since the 1980s and mainly in the south-east (Quante & Colijn 2016). As temperature is expected to increase further due to climate change, it is assumed that effects on these vulnerable species' SRR will remain or become even more severe (IPCC 2014). No significant thermal thresholds were found for plaice and hake, indicating that these species likely can better cope with increasing temperatures as also reflected in their positive tipping dynamics.

We based our analyses on fisheries stock assessment data that have known limitations, while it is widely recognized that analysing these data provides new relevant understandings about fish stock dynamics (Möllmann et al. 2021; Sguotti et al. 2019, 2020). With this database at hand we explored recovery patterns of fish stocks in the North Sea after the recent reform of EU's CFP, implementing MSY principles (EU 2013). Our study revealed all three regime shift characteristics to exist in all six North Sea fish stocks investigated, suggesting the prevalence of discontinuous dynamics in exploited living marine resources. Our results furthermore demonstrate the dependence of such dynamics on the environmental context and hence the ability of management measures to rebuild depleted fish stocks.

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Supplementary Materials

Supplementary Table S2.1. Root Mean Square Error (RMSE) of stock-recruitment model fits. Bold highlighted RMSE values represent best fitting models with lowest RMSE.

Species	Linear	Beverton-Holt	Ricker	Segmented	Segmented logarithmic	Segmented negative binomial	Strucchange
Plaice	623348.1	635361.0	636346.8	**615952.3**	1299309.2	616685.6	*
Hake	132585.2	135802.1	138000.9	122991.0	375905.0	**122318.7**	127453.9
Herring	14647426	14057361	14148385	**12493546**	33696376	12559099	20110467
Haddock	12158017	13279671	13279671	12005541	15751640	12026556	**11659101**
Saithe	79692.51	82343.52	82853.26	**77819.88**	171123.12	77898.49	215206.41
Cod	491364.7	507607.1	507589.7	464153.8	874222.8	**451471.7**	481125.8

*no significant breakpoint model.

Supplementary Table S2.2. Results threshold generalized additive modelling. The model diagnostics include the comparison of the slopes and the p values, which each need to be different from each other to accept the threshold. *p*-values < 0.05 were considered statistically significant.

Species	n	Slopes	*p*-value	Temperature threshold (°C)	Threshold accepted
Plaice	62	1.887	0.4	9.8	No
		1.667	0.593		
Hake	42	1.667	0.000	9.8	No
		1.667	0.042		
Herring	73	3.494	0.000	10.7	Yes*
		1.667	0.014		
Haddock	48	3.372	0.034	10.4	Yes*
		1.667	0.246		
Saithe	50	3.531	0.000	10.2	Yes
		2.67	0.000		
Cod	56	2.795	0.000	10.1	Yes
		1.667	0.002		

* Significant relationship before the threshold only.

Supplementary Table S2.3. Overview of data used in analyses. Ranges of fishing mortality (F), spawning stock biomass (SSB), recruitment (R), sea surface temperature (SST).

Species	F	SSB (1,000t)	R (billions)	SST (°C)	Assessment period
Plaice	0.42-0.71 (ages 2-6)	213.890 – 1019.257	0.358303-4.434690 (age 1)	9.2-11.58	1957-2021
Hake	0.24-1.17 (length 50-80cm)	23.231-307.092	1.40670-7.72351 (age 0)	9.2-11.58	1978-2021
Herring	0.07-1.42 (ages 2-6)	105.793-5304.809	2.523740-69.493500 (age 0)	9.2-11.58	1947-2021
Haddock	0.18-0.96 (ages 2-4)	51.828-550.753	0.065563-50.765467 (age 0)	9.2-11.58	1972-2021
Saithe	0.3-0.73 (ages 4-7)	106.632-576.387	0.041095-4.09407 (age 3)	9.2-11.85	1967-2021
Cod	0.37-1.16 (ages 2-6)	31.978-219.8379	0.067402-2.370072 (age 1)	9.2-11.85	1963-2021

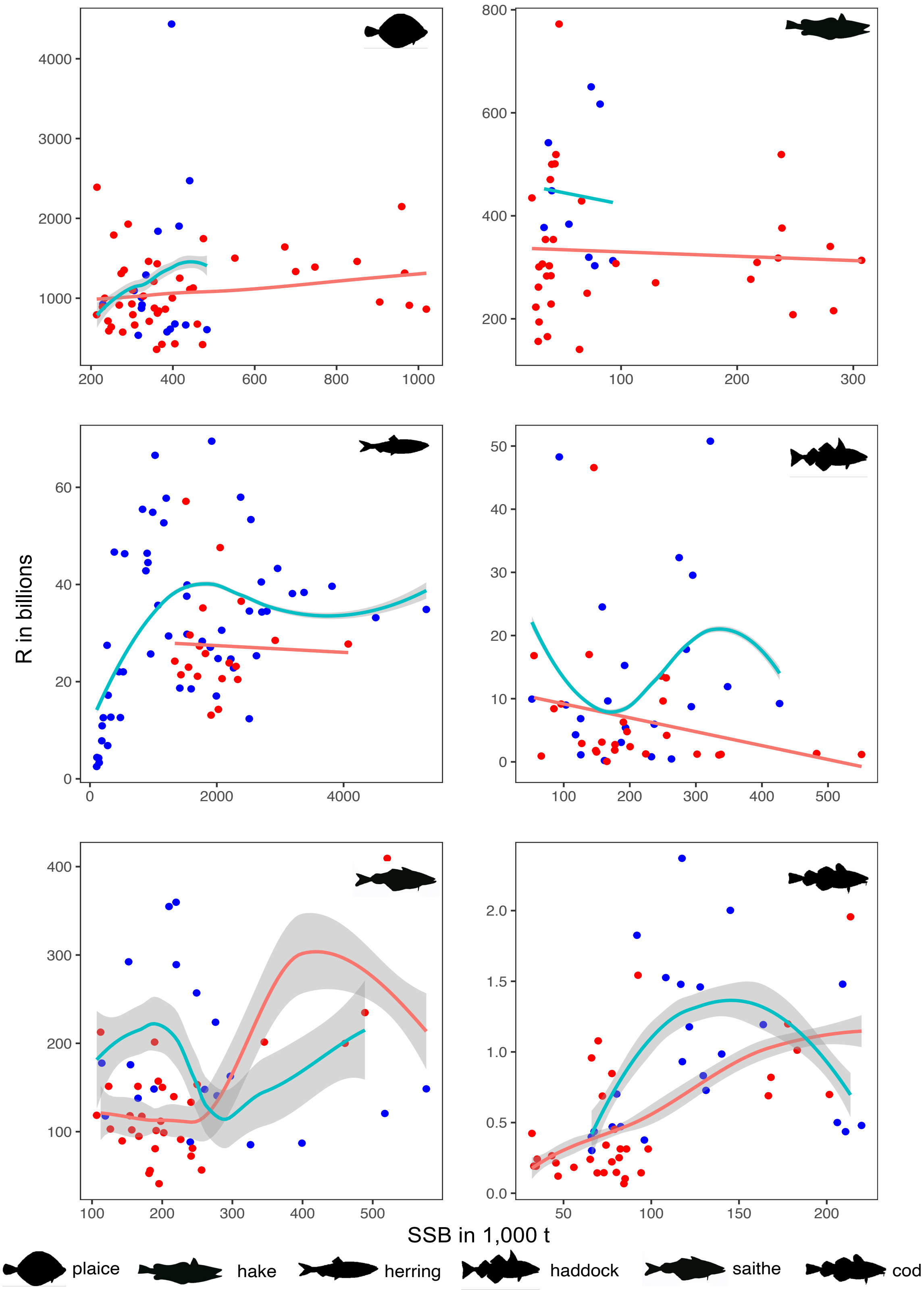

Figure S2.1. Threshold GAM models. Model outcomes showing stock-recruitment relationship values before (blue) and after (red) the threshold. Solid line represents predicted model data using a LOESS-smoother for trend visualization. In grey the confidence interval of the line is shown. Points show original data. Spawning stock biomass (SSB), recruitment (R).

Chapter III

Discontinuous dynamics in North Sea cod (*Gadus morhua*) by ecosystem change

Discontinuous dynamics in North Sea cod (*Gadus morhua*) caused by ecosystem change

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Abstract

Marine ecosystems worldwide experience abrupt changes and regime shifts in structure and functioning due to interacting effects of multiple stressors. North Sea cod (*Gadus morhua*) is a key example of being strongly overexploited for decades, causing an abrupt stock decrease below scientifically advised sustainable levels. Despite reductions in fishing pressure in recent years, North Sea cod has not recovered yet. Why recovery is hindered and especially how ecosystem dynamics interacted with fishing to create a stable low cod stock is an open question. Here we sequentially apply change point and principle component analysis as well as stochastic cusp modeling to show that North Sea cod recovery is limited due to an interaction of fishing pressure, internal stock dynamics and external environmental changes. We found that cod biomass experienced nonlinear discontinuous dynamics given the interaction of fishing pressure and climate change induced increases in temperatures, wind and the NAO. Our results further demonstrate discontinuity in the biomass due to low recruitment caused by a discontinuous relationships between stock biomass and environmental changes characterized by climatic and zooplankton variables. Our study indicates that increasing climate-induced changes in the environment will trap North Sea cod in a depleted state, limiting its chance to regain its role as a main target species for fisheries. Hence, we highlight the importance to incorporate discontinuous dynamics in fisheries management approaches to achieve sustainable exploitation levels and to promote recovery of depleted fish stocks.

Keywords: recovery, collapse, regime shift, stochastic cusp model

1. Introduction

People and communities worldwide depend strongly on the services oceans provide and livelihoods are built upon the provision of food, the cultural beauty, and the trade of marine commodities. The awareness that these goods are under enormous anthropogenic pressures is increasing and efforts to recover those losses are enforced (Ingeman et al. 2019; Palmer et al. 2004). Recovery of deteriorated marine ecosystems is differently defined depending on who is involved, what is assessed and which goals are formulated (Lotze et al. 2011). Definitions of recovery comprise the restoration of underlying ecosystem functions and processes, recovery goals like system stability (Ingeman et al. 2019), or the recuperation of marine populations and their habitats (Duarte et al. 2020). In fisheries management, recovery is achieved if biomass levels reach a level according to the maximum sustainable yield concept (B_{MSY}), which enables sustainable fishing (Duarte et al. 2020). The European Union (EU) in more detail applies the maximum sustainable yield (MSY) approach through the common fisheries policy (CFP). Achieving the MSY is considered as recovery, where the management follows the implementation of reference levels with respect to fishing mortality and biomass, i.e. F_{MSY} and MSY $B_{trigger}$ (ICES 2012a).

Ecosystems can also recover from different levels of disturbance, where i) at a complete recovery the system regains its initial state, ii) at a partial recovery it arrives at an alternative or diminished state, and lastly iii) the system may remain harmed in the long-term or its state may even become irreversible (Duarte et al. 2020; Lotze et al. 2011). Limited recovery is theoretically enforced if drivers are not reversed and by the appearance of abrupt shifts in system dynamics, so-called “regime shifts”. Regime shifts occur if resilience of a system (or population) is low and its structure and functioning is being altered (Beisner et al. 2003; Conversi et al. 2015). The underlying theory implies the characteristics ‘abrupt changes’, ‘alternate stable states’, and ‘hysteresis’ (Beisner et al. 2003; Scheffer et al. 2001). Depending on the relationship between a pressure and the response variable, a shift can occur logistically or discontinuously. Discontinuity implies the occurrence of hysteresis, where the path of reaching a new alternative stable state differs from the path of returning to the original state (Conversi et al. 2015; Scheffer et al. 2001; Sguotti et al. 2019).

Regime shifts are a well-documented phenomenon in the marine realm especially in the North Sea ecosystem, observed over several trophic levels (Weijerman et al., 2005; Kenny et al., 2009). Regime changes were especially reported for phyto- and zooplankton and related hydroclimatic changes such as the indices of the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO) (Edwards et al. 2013; Fromentin & Planque 1996; Reid & Edwards 2001), as well as local temperature (Capuzzo et al. 2018; Edwards et al. 2020; Nohe et al. 2020). A major regime shift was detected during the 1980s, including pronounced changes in the phytoplankton due to increasing temperature (Beaugrand 2004; Beaugrand & Reid 2003; Lynam et al. 2017). Generally, phytoplankton biomass increased steadily in recent decades (McQuatters-Gollop et al. 2011), and characteristically a change in the ratio between diatoms and dinoflagellates has been observed (Hinder et al. 2012). Recently, further warming combined with a decrease of eutrophication since the 1990s caused a change in bloom patterns and an increase in diatom and dinoflagellate biomass (Nohe et al. 2020). Changes in primary production have been further related to shifts in zooplankton community affecting the productivity of fish populations (Kenny et al., 2009; Lynam et al., 2017), especially where a changing secondary production may increase stress on already depleted fish stocks (Edwards et al. 2020).

An instructive case for studying recovery as well as regime shift dynamics is Atlantic cod (*Gadus morhua*). Atlantic cod populations are key examples of overfishing and many collapsed cod stocks did not recover even though fishing pressure has often been reduced strongly (Rose 2019; Sguotti et al. 2019). In the North Sea, cod historically experienced a strong increase during the so called ‘Gadoid Outburst’, characterized by favorable feeding conditions for gadoid species in the North Atlantic during the 1960s (Cushing 1980). Subsequently, fishing pressure has been increased to very high levels causing the stock to decline strongly (Cook et al. 1997). In combination with a diminished young cod production and a decrease of optimal thermal habitat due to increased warming of the North Sea (Blanchard et al. 2005; O’Brien et al. 2000; Rindorf & Andersen 2008), the stock collapsed eventually and fell below all scientifically advised safety levels since the late 1980s (ICES 2020). Furthermore, the decrease of thermal range combined with fishing pressure led to a northward shift of the cod stock (Engelhard et al. 2014). Since the North Sea stock consists of three distinct populations centered around the Viking bank, the Dogger bank (the South proper) and the north-west (Romagnoni et al. 2020), it can be assumed that the southern population is affected most by these stressors. A recovery plan was established in the 1990s to stop cod from declining and to enhance recovery (ICES 2012b). Still, North Sea cod stock did not recover and especially recruitment still remains at historically low levels since 1998 (ICES 2020). This failed recovery despite a strong reduction in fishing pressure is typically pointing towards hysteresis in cod dynamics, a typical sign of a regime shift in the fish stock or its supporting ecosystem (Sguotti et al. 2019).

We here studied whether regime changes in the North Sea ecosystem can be linked to the failed cod recovery. We explored cod-ecosystem links using stochastic cusp modelling (Grasman et al. 2009); a modelling approach based on catastrophe theory. Catastrophe theory became popular in the 1970s (Zeeman 1979), but has been largely ignored afterwards (Sguotti et al. 2019). Recently, stochastic cusp modelling is increasingly applied in diverse scientific fields such as economics (Diks & Wang 2016), sociology and psychology (Guastello et al. 2012; Sideridis et al. 2016), and also in fisheries (Möllmann et al. 2021; Sguotti et al. 2019, 2020). The theory’s scope comprises investigating sudden changes in dynamic systems in response to multiple interaction of external drivers (Grasman et al. 2009; Poston & Stewart 1978; Sguotti et al. 2019). Importantly, the stochastic cusp modelling approach allows for i) evaluating discontinuity in system dynamics implying hysteresis in response to external drivers, and ii) testing for stability of system states at any point in time (Grasman et al. 2009; Zeeman 1979). Even though regime shifts in North Sea cod stocks are intensively studied, the drivers of these shifts are not fully understood (Sguotti et al., 2019). Our study provides evidence for non-linear discontinuous population dynamics in North Sea cod implying hysteresis in the recovery of the fish stock to reduced fishing mortality. We relate the failed cod recovery to low recruitment in response to lower trophic North Sea ecosystem changes, i.e. changes in phyto- and zooplankton productivity as a result of climate-induced temperature rise. Our study hence demonstrates how climate-induced ecosystem dynamics can limit the recovery of a depleted fish stock, being important information for ecosystem-based fisheries management.

2. Materials and Methods

2.1. Data

The main goal of our study was to study the potential existence of discontinuous dynamics in North Sea cod, and to understand the underlying mechanisms limiting cod stock recovery. Therefore we gathered a wide range of biotic and abiotic data to obtain a holistic picture of ecosystem dynamics and to identify potential external pressures on the stock.

For analyzing stock dynamics we retrieved data on North Sea cod spawning stock biomass (SSB), recruitment (R), and fishing mortality (F) from the International Council for the Exploration of the Sea (ICES) Stock Assessment Database (ICES 2019). We investigated climate effects on cod using indices of the North Atlantic Oscillation (NAO) (Climate Prediction Center 2020) and the Atlantic Multidecadal Oscillation (AMO) (Enfield et al. 2001), provided in monthly values from the Climate Prediction Center of National Oceanic and Atmospheric Administration (NOAA). Both, the NAO and AMO, are hydro-climatic indices known to affect oceanographic changes in the North Sea (Drinkwater et al. 2003; Knight et al. 2006). Whereas the NAO index is based on atmospheric pressure differences at sea level between the Azores High and the Icelandic Low (Drinkwater et al. 2003), the AMO index builds upon Atlantic sea surface temperature (SST) variations in the Northern Hemisphere (Knight et al. 2005). We used the NAO winter index, which is computed based on the mean pressure difference from December to March between Iceland and Lisbon, Portugal. The NAO effect is considered to have its greatest effect on the boreal environment during these months, where a positive NAO reflects high westerly winds (Drinkwater et al. 2003; Hurrell 1995). The AMO has been identified as a coherent mode of natural variability occurring in the North Atlantic Ocean with an estimated period of 60-80 years, and based upon the average anomalies of sea surface temperatures (SST) in the North Atlantic basin, typically over 0-80N. In general the AMO has great effects on the northern hemisphere's climate, and influences rainfall and sea surface temperature in North Western Europe (Alheit et al. 2014; Edwards et al. 2013; Knight et al. 2006). We here calculated the yearly mean of the AMO.

Since local temperature greatly affects the ecosystem, we also gathered annual sea surface temperature (SST, °C) and sea bottom temperature (SBT, °C) data (Nunez-

Riboni et al., 2015). We further explored the effect of the North Sea Inflow (in Sverdrup) on cod dynamics. The inflow of zooplankton rich water and simultaneous changes in temperatures of deep waters are expected to affect North Sea cod recruitment (Akimova et al. 2016). Monthly inflow data were derived from simulations with the NORWECOM model (Hjøllo et al. 2009). These inflow data cover the Orkney-Utsir transect along the longitude 59.17N over the entire water column (Hjøllo et al. 2009). As NAO and AMO are also related to local changes in winds and currents, we additionally retrieved respective data from NOAA and the Integrated Climate Data Center University of Hamburg. We calculated annual mean wind data from daily u-wind and v-wind data at a level of 10m (Kalnay et al. 1996), and yearly mean current data from daily u- and v-current data (Balmaseda et al. 2013; Mogensen et al. 2012), aggregated across the whole North Sea, using the following Pythagorean equation:

$$\text{magnitude} = \sqrt{u^2 + v^2}, \tag{1}$$

where magnitude (m s^{-1}) = wind/current speed, u = u-wind/-current (towards east), v = v-wind/-current (towards north).

We furthermore used phyto- and zooplankton abundance indicators derived from the Continuous Plankton Recorder (CPR) survey (Johns 2019) to characterize North Sea ecosystem changes, specifically the phytoplankton color index, the abundance of diatoms and dinoflagellates, and the abundance of small and large copepods (Bedford et al. 2020; Capuzzo et al. 2018). We used annual means for the complete North Sea from spatially resolved monthly data across the entire North Sea for each of the biotic variables.

All data were combined to a data matrix with annual values covering the entire North Sea for the period 1963 until 2018, i.e. the period covered by the cod stock assessment data we used.

2.2. Statistical analyses

We applied a combination of statistical modelling approaches to analyze the potential effects of biotic and abiotic variables on the recovery of the North Sea cod stock. We first applied statistical change point analyses to SSB time series to identify abrupt changes indicating regime shifts in the cod stock. To further understand common trends in abiotic, biotic and cod stock dynamics, we conducted a Principal Component Analysis (PCA) (Kassambra 2017) and Constrained Clustering (Diekmann et al. 2012; Juggins 2020). Eventually, we used the stochastic cusp modelling approach (Grasman et al. 2009) to identify the interactions between abiotic and biotic variables potentially causing discontinuous dynamics in cod SSB and R.

2.2.1. Change point analyses

We identified abrupt changes in North Sea cod stock dynamics using statistical change point analyses on time series of spawning stock biomass (SSB). Different change point approaches exist that encompass distinct statistical concepts and hence often the change points identified in a time series slightly vary. Hence, we applied four common methods and only accepted change points if at least two of the methods detected a change point at approximately the same location (± 1 year). The Bayesian change point analysis (Erdman & Emerson 2007) uses a Bayesian approach to estimate the probability of change in a specific year of a time series. The ‘bcp’ function (in the bcp R package (Erdman & Emerson 2007)) makes use of an estimate of a posterior mean as the primary result. Hereby, a Markov chain Monte Carlo analysis is ran to calculate the posterior probability that the change of the mean between two points is significant (Erdman & Emerson 2007). As commonly applied, we here assumed years with a posterior probability > 0.7 to be a significant change point. Secondly, we used the ‘cpt.mean’ function from the R package ‘changepoint’ (Killick & Eckley 2014) using the ‘BinSeg’ function (Scott & Knott 1974). ‘BinSeg’ searches for a maximum number of change points using a multiple change point search. A statistical single change point test is performed for the entire data series. The method encompasses splitting the time series into two at the detected change point. The procedure is repeated until no further change points are found in the time series (Killick & Eckley 2014). Moreover, we applied the segmented analysis from the ‘segmented’ R package (Muggeo 2008), which uses the fit of regression models as a basis for the change point analyses; here called break points. After setting the number of change points to be found beforehand, the method estimates new linear relationships at each break point based on break point and slope parameters. A break point is found if the regressions are significantly different (Muggeo 2008). Eventually we used the breakpoint analysis from the 'strucchange' R package (Zeileis et al. 2002, 2003). In contrast to the segmented method, change points do not need to be determined a priori using the strucchange approach. The method tests for the stability of deviations from linear regression models. It implies that coefficients can shift between stable regression relationships assuming the existence of *m* breakpoints. Hence, *m*+1 segments have constant coefficients. The ultimate number of breakpoints is found by minimizing the residual sum of squares (RSS) (Zeileis et al. 2003).

2.2.2. Principal component analysis and constrained clustering

In order to understand how the biotic community and abiotic variables changed over time, which variables drive these changes the most and to use the main mode of variability of these changes we performed a principal component analysis (PCA). A PCA extracts the main modes of variability from a multivariate data set by creating new variables, the so-called principal components, which represent a linear combination of the original variables (Kassambra 2017). Here, we applied the PCA on three data matrices: 1) all abiotic and biotic variables combined, and 2) for abiotic and 3) biotic variables, separately. Cod SSB and R were treated as supplementary quantitative variables in the analyses, meaning they were not included in the PCA calculations but are still shown in the results. We extracted for each case the principal components 1 (PC1) and PC2 from the PCA outcome as representatives of general abiotic and biotic trends over time. To determine clusters in years with common trends in abiotic and biotic variables, we applied the Constrained Hierarchical Clustering (Diekmann et al. 2012; Juggins 2020) method on the data, using the Euclidean distance. Clusters were distinguished using graphical interpretation of CONISS broken stick and CONISS cluster plots.

2.2.3. Stochastic cusp modelling

As a focus of our analysis we used the stochastic cusp model to test for discontinuous dynamics in North Sea cod. The model is based on catastrophe theory implying a canonical cusp form and describes abrupt changes between equilibria of a state variable (z_t) due to changes in two control parameters (α,β). Parameter α is the so-called asymmetry parameter and affects the dimension of the state variable directly and can be managed policy wise (Grasman et al. 2009; Sguotti et al. 2019). The control parameter β, the so-called bifurcation variable or splitting factor, determines the path of the relationship between the state variable and the asymmetry parameter, which can change from linear to non-linear continuous (logistic) to discontinuous (Grasman et al. 2009; Sguotti et al. 2019). Hence, using the stochastic cusp model the interactive effect of two simultaneous or cumulative drivers on the state variable can be determined (Diks & Wang 2016; Sguotti et al. 2019).

The rate of change of this relationship is represented by the following cubic equation:

$$V(z_t;\alpha,\beta) = \frac{1}{4}z_t^4 - \frac{1}{2}\beta z_t^2 - \alpha z_t, \qquad (2)$$

Where $V(z_t;\alpha,\beta)$ is a potential function of the rate of change of the system (z_t), which is represented by the slope depending on the two control parameters (α, β) (Grasman et al. 2009; Sguotti et al. 2019).

A white noise, the Wiener process, is added to transform Equation (2) into a stochastic differential equation. One assumes that the function of Equation (2) governs the state variable (z_t), and that the driving noise includes the variance σ_z^2:

$$-\frac{\delta V(z,\alpha,\beta)}{\delta z} = \left(-z_t^3 + \beta z_t + \alpha\right)dt + \sigma_z dW_t = 0. \qquad (3)$$

The left hand side represents the drift term, σ_z the diffusion parameter, and W_t the Wiener process (Diks & Wang 2016; Grasman et al. 2009; Sguotti et al. 2019).

Here, we applied the model twice using SSB and R as the state variable, respectively. The manageable asymmetry parameter was related to fishing pressure for SSB, and to SSB for R. The splitting factor β was represented by the abiotic and biotic parameters, as well as trends of the full community given by PC1s and PC2s. In addition, the splitting factor was predicted by a combination of abiotic and biotic PCs to investigate effects of combined abiotic and biotic changes on the relationship between the state variable and the asymmetry parameter.

The canonical state variable (z_t) is estimated with a linear function with one or more observable state variables (Equation 4a). The parameters, α and β, are estimated using linear functions of independent variables (Equations 4b and 4c) (Diks & Wang 2016; Grasman et al. 2009):

$$z_t = w_0 + w_1 \text{SSB}, \tag{4a}$$

$$\alpha = \alpha_0 + \alpha_1 \text{Fishing pressure}, \tag{4b}$$

$$\beta = \beta_0 + \beta_1 \text{Abiotic and/or Biotic Driver}, \tag{4c}$$

where w_0, α_0, and β_0 are the intercepts and w_1, α_1, and $\beta_1$are the slopes of the models

These estimated parameters were fit into Equation 3. The canonical form of the cusp function contains equilibrium points, which are defined by a function of the control parameters (Grasman et al. 2009; Sguotti et al. 2019):

$$-\frac{\delta V(z, \alpha, \beta)}{\delta z} = -z_t^3 + \beta z_t + \alpha = 0. \tag{5}$$

Given Equation 5, a Cardan discriminant was derived to distinguish the different possible solutions of the number of equilibria: there is one equilibrium if δ > 0, and three if δ < 0 (Diks & Wang 2016; Grasman et al. 2009; Sguotti et al. 2019):

$$\delta = 27\alpha^2 - 4\beta^4 \tag{6}$$

The cusp model R package produces a 3D surface as an outcome, which shows linear, logistic and discontinuous relationships between the state variable and the control parameters. These three relationships are tested statistically against each other. The discontinuous path includes in addition a folded area, the so called bifurcation set

(Grasman et al. 2009; Sguotti et al. 2019). The 3D surface can be visualized in 2D where the bifurcation set (area of instability) is highlighted in blue, and the α and β parameters are on the x- and y-axis, respectively. Points within the bifurcation area represent the unstable state of the system ($\delta > 0$). At the boundary of the bifurcation set, the Cardan's discriminant δ equals zero. Points outside of the bifurcation area indicate the stable alternate states and high resilience to pressures. If the relationship is indeed discontinuous, the path runs through the bifurcation area and might indicate the presence of hysteresis (Diks & Wang 2016; Petraitis & Dudgeon 2016).

Given the high number of covariates and their combinations representing β, we performed a model selection procedure using a combination of an information-theoretic approach (Burnham & Anderson 2002) and the classical stepwise model selection. Five models each were specified a priori for SSB and R, and then modified using back- and forward selection. A total of 14 and 13 models for SSB and R were tested, respectively (See online supplementary materials Table SM1 for all model outcomes).

We validated the cusp model outcomes according to criteria recommended by Grasman *et al.*, (2009), and developed by Cobb (1998). First, we assessed whether the cusp fit is superior to a linear or a logistic regression based on the goodness of fit, using Cobb's pseudo-R^2 and the Akaike's information criterion (AIC). Secondly, we determined the significance of the state variable slope coefficient, which should be significantly different from zero. Thirdly, the percentage of observations (α and β pairs) within the bifurcation area should at least be 10% (Cobb 1998; Grasman et al. 2009). Eventually, we chose the best fitting cusp models based on the highest R^2 value, and based on our focus on discontinuity and hysteresis presence in the state variables SSB and R to detect the occurrence of true regime shifts.

We performed all analyses within the statistical and programming environment of R (R Core Team 2018). The change point analyses were performed with the packages bcp (Erdman & Emerson 2007), changepoint (Killick & Eckley 2014), segmented (Muggeo 2008) and strucchange (Zeileis et al. 2002, 2003). The PCA was conducted using the packages stats (R Core Team 2018) and factoextra (Kassambra & Mundt 2019), the constrained clustering method was supported by the packages vegan (Oksanen et al. 2020) and rioja (Juggins 2020), and the stochastic cusp modelling was implemented with the package cusp (Grasman et al. 2009).

3. Results

3.1. North Sea cod stock dynamics

The North Sea cod stock experienced a strong decline in SSB and R since the early 1970s (Fig. 3.1). We determined major abrupt changes in SSB in 1975 and 2006 using statistical change point analysis, indicating three regime periods (Fig. 3.1a). The first regime was characterized by a steep increase in SSB followed by a decline. The initial regime is the only period within the study period where the SSB was above all biomass management reference points indicating a sustainable stock size. Within the second regime SSB declined continuously until 2005 crossing all reference points. After 2006, SSB of North Sea cod increased slightly, but did not recover above MSY $B_{trigger}$. R showed a similar development as SSB until the end of the second regime, but remained low during the third regime (Fig. 3.1b). Fishing mortality of North Sea cod was above the reference point F_{MSY} during the whole assessment period indicating unsustainable fishing pressures (Fig. 3.1c). Fishing pressure constantly increased until the late 1990s, subsequently declined in the early 2000s, but never reached the present management target of F_{MSY}. In recent years fishing mortality is observed to increase again.

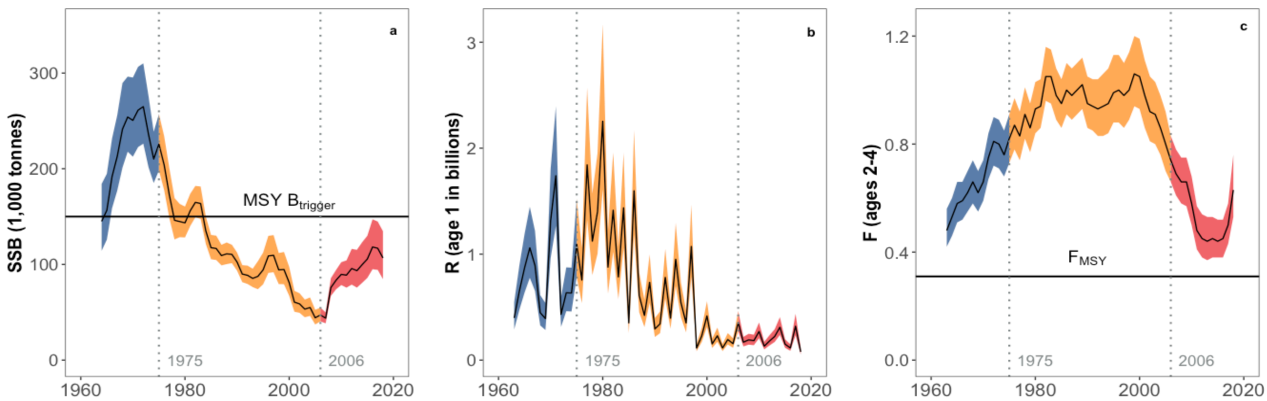

Figure 3.1. North Sea cod stock dynamics. a – spawning stock biomass (SSB), b – recruitment (R), and c – fishing mortality (F). Vertical lines in a – c indicate abrupt changes in SSB identified by statistical change point analyses; colors distinguish the three regimes identified; horizontal lines in a and c indicate management reference points (Level of SSB triggering specific action in management (MSY $B_{trigger}$), F level aiming at Maximum Sustainable Yield (F_{MSY})) (ICES 2012a).

3.2. North Sea ecosystem changes

A major question of our study was how cod stock dynamics are embedded in overall ecosystem developments in the North Sea. We divided the ecosystem into biotic (Fig. 3.2) and abiotic (Fig. 3.3) dynamics. Major changes in the large and small copepods took place around the 1980s, implying a strong decrease in abundances (Fig. 3.2a,c). A strong increase in phytoplankton (Fig. 3.2b) in the late 1980s came along with a strong decline and increase of dinoflagellates (Fig. 3.2d) and diatoms (Fig. 3.2e) , respectively, from the 2000s onwards.

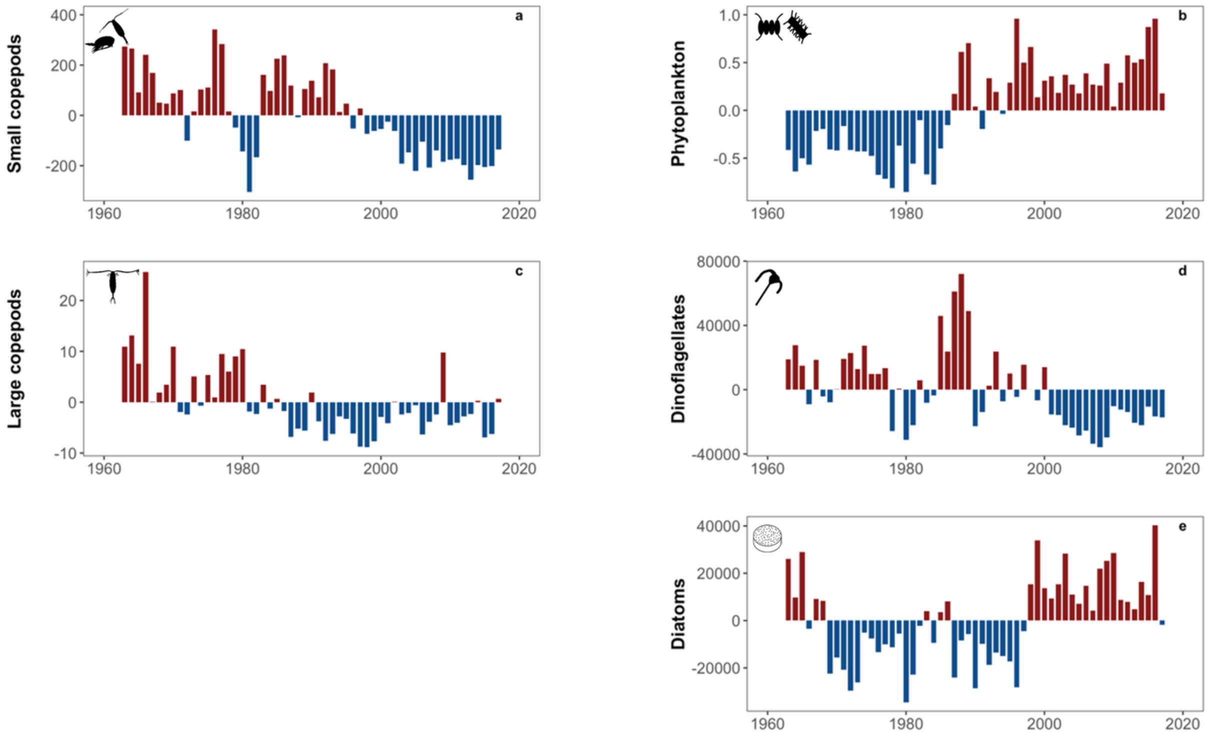

Figure 3.2. Biotic North Sea ecosystem changes. Anomalies of the biotic community in the North Sea; small copepods (count), Phytoplankton (Phytoplankton Plankton Color Index), large copepods (count), dinoflagellates (count), diatoms (count).

Similar developments with major changes in the 1980s and 2000s took place in the abiotic environment (Fig. 3.3). The NAO, inflow, wind, and current indicators increased steadily from 1980 onwards, shown by a switch from a negative to a positive anomaly (Fig. 3.3a,c,e,g). The AMO, SBT, and SST (Fig. 3.3b,d,f) show increases later in time, around 2000.

For an overall understanding of the ecosystem developments we conducted a comprehensive assessment of North Sea ecosystem changes using principal component analyses (PCA) based on these biotic and climatic variables (Fig. 3.4).

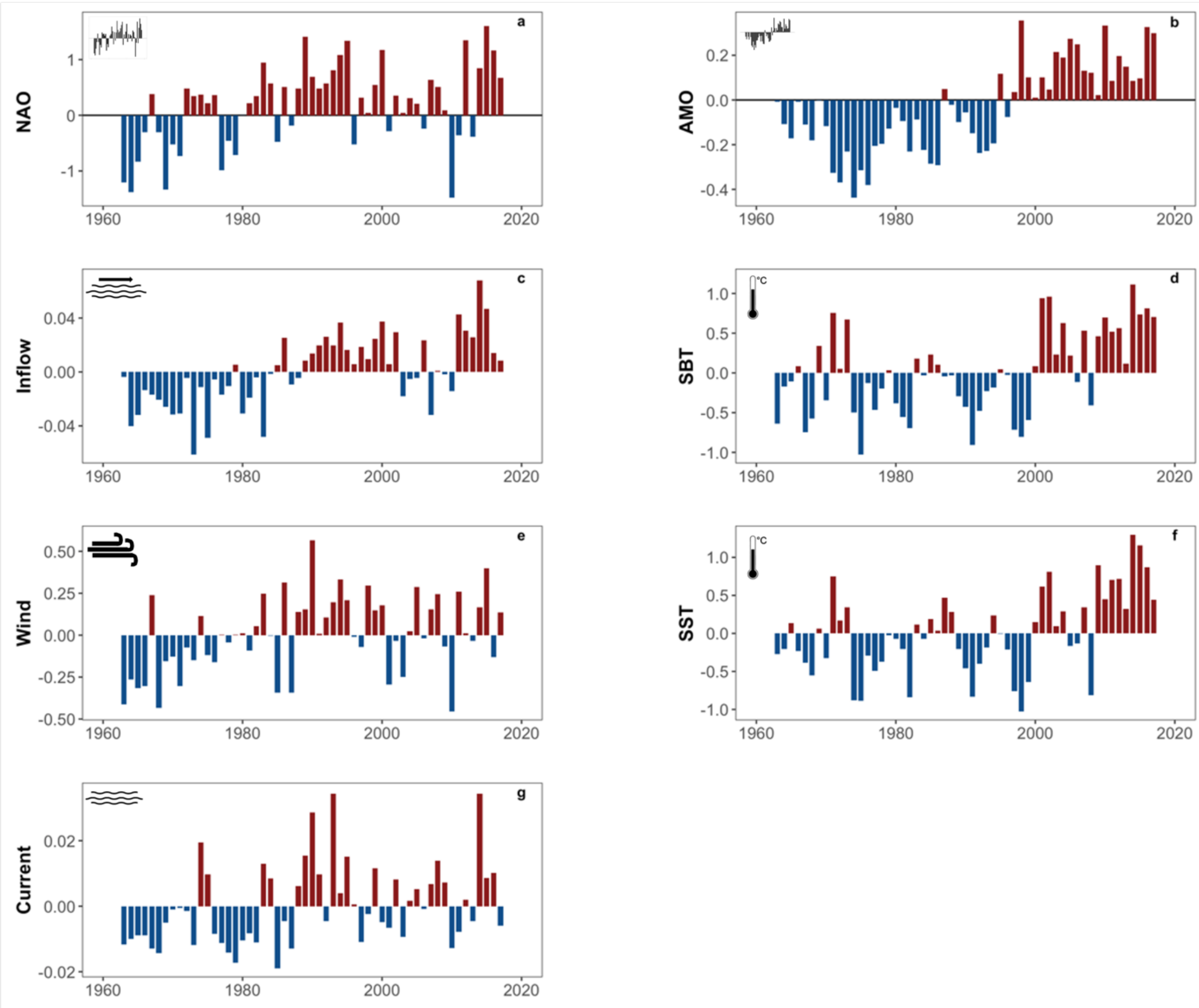

Figure 3.3. Abiotic North Sea ecosystem changes. Anomalies of the abiotic variables; North Atlantic oscillation (NAO), Atlantic multidecadal oscillation (AMO), inflow (Sverdrup), sea bottom temperature (°C, SBT), wind (m s^{-1}), sea surface temperature (°C, SST), current (m s^{-1}).

The analysis, including all relevant biotic and abiotic variables (Fig. 3.2,3.3), revealed a main ecosystem component (PC1) that increased continuously over the entire study period (Fig. 3.4a, see online supplementary materials Fig. SM3.1,3.2 for distinct biotic and abiotic PCA). The main variables contributing to PC1 are phytoplankton (represented by the phytoplankton color index), the North Sea inflow and the NAO. Phytoplankton and the inflow increased with PC1, with an abrupt change of the former already in the early 1980s and for the latter later in the 1990s. PC2 experienced a continuous decline until the late 1990s and an abrupt change to a higher level subsequently (Fig. 3.4b). Variables mainly associated to PC2 are climatic like SBT, wind and SST. Especially temperature variables display a positive relationship with PC2.

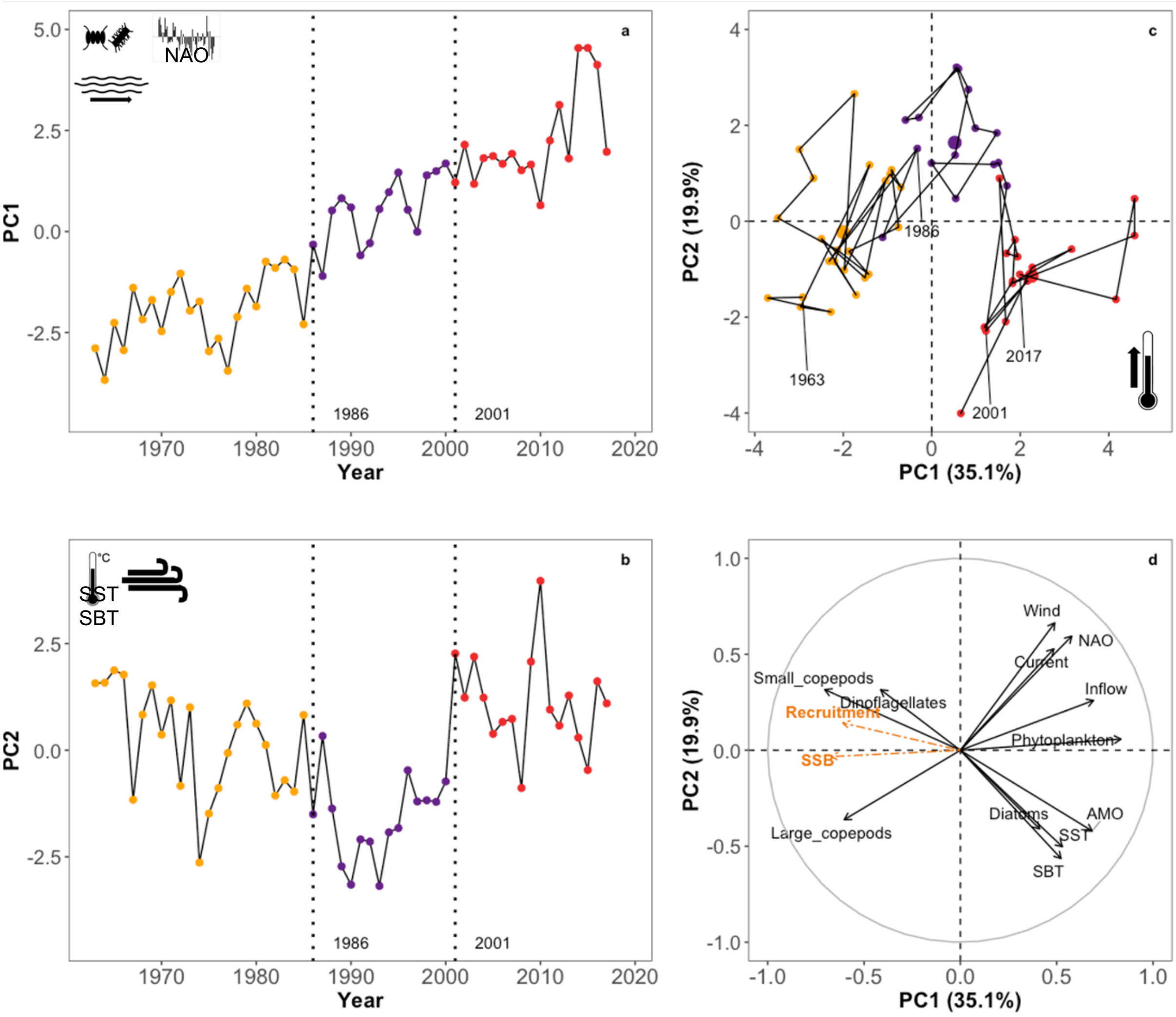

Figure 3.4. Major trends in North Sea ecosystem dynamics. Results of Principal Component Analysis a.– PC1 trajectory over time, b – PC2 trajectory over time, c – PCA individuals, e – PCA variables (spawning stock biomass (SSB), sea bottom temperature (SBT), sea surface temperature (SST), Atlantic Multidecadal Oscillation (AMO), North Atlantic Oscillation (NAO), Phytoplankton (Phytoplankton Color Index)). SSB and recruitment are supplementary quantitative variables (orange); vertical lines in a and b indicate transitions between clusters identified by constrained clustering analyses in c; cluster 1 in yellow (1963-1985), cluster 2 in purple (1986-2000), cluster 3 in red (2001-2017); icons represent main variables contributing to PC.

We separated three main periods in the North Sea ecosystem using constrained clustering on these PCA results (Fig. 3.4c,d). The periods revealed coincided with the major changes in the abiotic and biotic variables. A first (1963-1985) and a third cluster (2001-2017) demonstrate opposite configurations in the ecosystem. A large and productive cod stock (high SSB and strong R) and high abundances of copepods are characteristic for the first period, but all variables show low values recently. In contrast, the recent period is characterized by increased physical variables that provide evidence for the recent warming of the North Sea, while the initial period can be described as a cold regime. The second cluster (1986-2000) represents the transition between the two more extreme periods.

3.3. Discontinuous cod stock dynamics

The main aim of our study was to understand North Sea cod SSB and R dynamics and detect potential regime shift dynamics. We modelled the interactive effects of biotic and abiotic changes with (i) fishing mortality (F) on SSB, and with (ii) SSB on R. We used the stochastic cusp model approach to investigate the effect of the interactions between these drivers on SSB and R, and also to additionally test for regime stability and potential irreversibility or hysteresis of the system. Our model selection procedure revealed for SSB six, and for R two relevant cusp models implying discontinuous dynamics (Table 3.1). The discontinuous dynamics in the models with SSB as the state variable are strong since the R^2 of the cusp models are far better than the logistic ones. Instead, the cusp models with R are only slightly better than the logistic models (Table 3.1, Cobb's pseudo-R^2).

First, we analyzed the dynamics of SSB as a function of the interaction between R and fishing mortality (F) (Fig. 3.5a). At the beginning of the time series, R was high, F low and SSB high and within the unstable area (Fig. 3.5a - blue points).

Afterwards, SSB increased to a high biomass and reached stability, outside the bifurcation area going hand in hand with a high R but also high F (Fig. 3.5a - orange points). Around 2000 SSB collapsed and R decreased rapidly; subsequently F was reduced. But despite the decline of F, SSB remained low and reached in the last period the unstable bifurcation area where 3 equilibria are possible (Fig. 3.5a - red points). These results indicate that SSB went through a regime shift due to the interactive effect of F and R highlighting the presence of hysteresis. Indeed, the decrease in F did not facilitate an increase of SSB towards previous levels, due to the decline in R.

Table 3.1. Stochastic cusp model outcomes. Statistical results of selected cusp analyses; z_t - state variable, α - asymmetry parameter, β - bifurcation parameter, AIC – Akaike information criterion, SSB - spawning stock biomass, R -recruitment, F - fishing mortality.

z_t	α	β	Model	AIC	Cobb's pseudo-R^2	% within bifurcation area
SSB	F	Recruitment	Linear Logist Cusp	1350.29 1346.54 121.54	0.36 0.43 0.50	36.36
SSB	F	PC2 biotic and abiotic	Linear Logist Cusp	1371.17 1366.35 143.03	0.06 0.17 0.54	50.91
SSB	F	NAO	Linear Logist Cusp	1367.10 1365.46 144.76	0.13 0.19 0.56	45.45
SSB	F	SST	Linear Logist Cusp	1365.23 1364.09 142.67	0.16 0.21 0.46	40.00
SSB	F	SBT	Linear Logist Cusp	1364.50 1365.67 138.46	0.17 0.18 0.35	36.36
SSB*	F	Large copepods	Linear Logist Cusp	1359.96 1361.59 132.90	0.24 0.29 0.40	52.72
R*	SSB	PC1 + PC2 biotic and abiotic	Linear Logist Cusp	1552.08 1547.09 98.47	0.43 0.50 0.58	83.33
R	SSB	Small copepods	Linear Logist Cusp	1560.96 1550.31 166.80	0.31 0.45 0.49	50.00

*The bimodality of the residuals of these models is not strong.

In a next set of stochastic cusp models we used indicators of abiotic and biotic variables as splitting factors to test how these indirectly interact with F to steer SSB dynamics (Fig. 3.5b-f). In a first model we tested the effect of the interaction between PC2, hence wind and SST and SBT, and F on the SSB. First, PC2 was at an intermediate state and fishing was low, and SSB was high in the unstable area (Fig.

3.5b – blue points). After 1976, F increased to high levels, PC2 decreased, indicating lower wind magnitudes and surface and bottom temperatures, and SSB entered the stable area (Fig. 3.5b – orange points). In the 2000s, PC2 increased and F decreased strongly, while SSB reached low levels within the cusp area (i.e. unstable state) (Fig. 3.5b – red points).

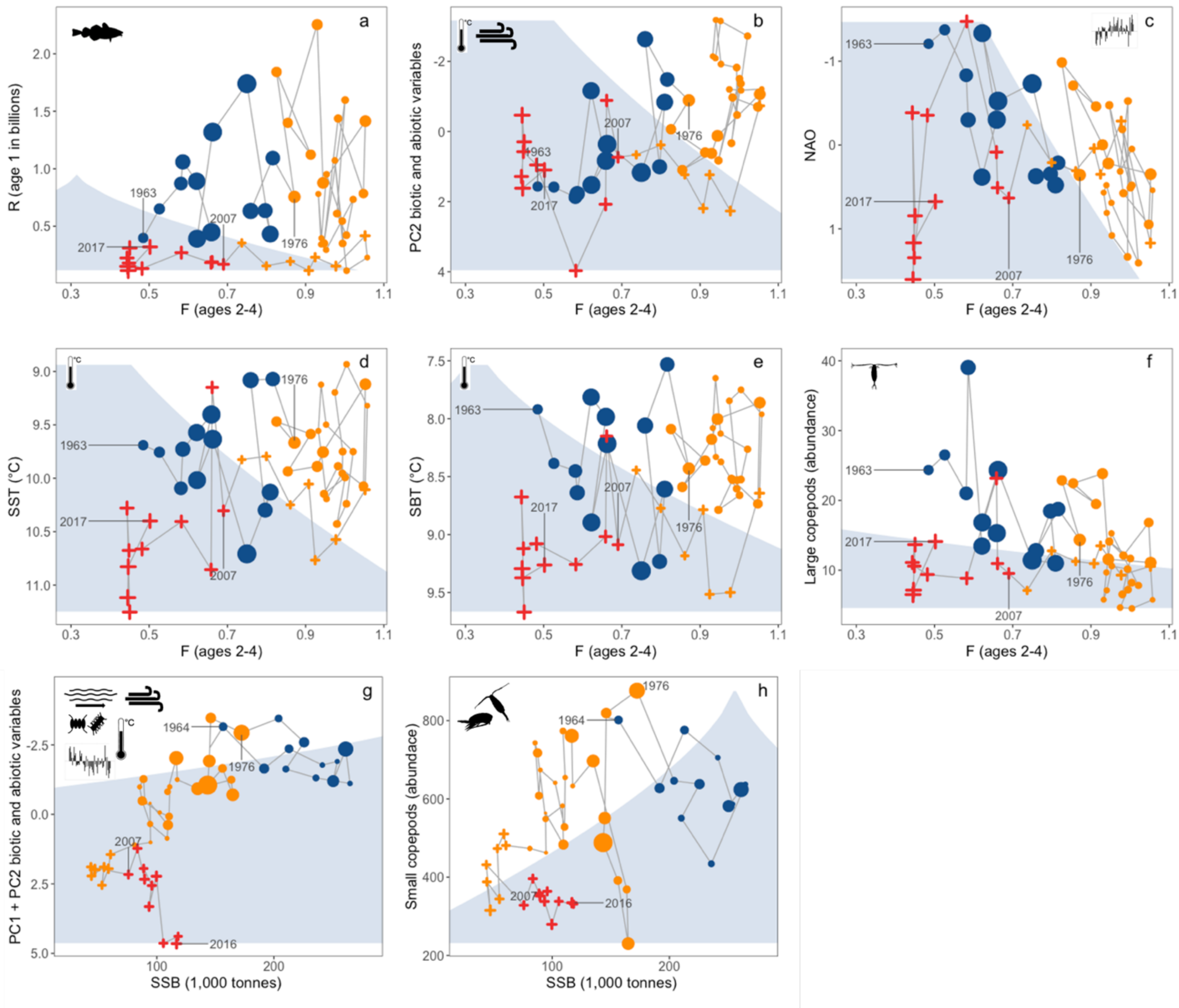

Figure 3.5. Abrupt changes in Atlantic cod stock dynamics. Results of stochastic cusp modeling with spawning stock biomass (SSB, a-f) and recruitment (R, g-h) as the state variables. a – cusp model with fishing mortality (F) and recruitment (R), b – cusp model with F and overall PC2, c – cusp model with F and NAO, d – cusp model with F and sea surface temperature (SST), e – cusp model with F and sea bottom temperature (SBT), f – cusp model with F and large copepods, g – cusp model with SSB and PC1 plus PC2 abiotic variables, h – cusp model with SSB and small copepods; size of points represents size of SSB (a-f) and recruitment (g-h), light blue area indicates the bifurcation area; colors show regimes identified in SSB by statistical change points analyses (Fig. 3.1); crosses highlight last 16 years of time period.

The previous model showed the importance of climatic influences (temperatures and wind), which are strongly related to the changes in the NAO. Hence, we tested how the interaction between the NAO and F affects SSB (Fig. 3.5c). Initially, the model shows a low NAO and low fishing, but a high SSB within the unstable area (Fig. 3.5c – blue points). After 1976, the NAO fluctuated strongly between positive and negative values, F increased strongly, and SSB decreased and entered and remained in the stable area (Fig. 3.5c – orange points). After 2005, the NAO increased further and F decreased strongly, wherefore SSB reached the unstable area and remained at low values (Fig. 3.5c – red points).

In subsequent models, we tested the climatic conditions SST and SBT, which are closely related to the NAO, separately, as they are main drivers inducing changes in the North Sea ecosystem and consequently in population processes of cod. Thus, we modelled SSB based on the interaction of F and SST as well as F and SBT (Fig. 3.5d,e) and obtained similar outcomes for both models. At the beginning of the study period, SSB was high within the cusp area, F started to increase and SST/SBT was intermediate and fluctuating (Fig. 3.5d,e – blue points). Afterwards, F reached high levels and SST/SBT increased slowly, whereas SSB decreased and entered the stable area (Fig. 3.5d,e – orange points). From 2000 onwards, the temperatures increased steadily resulting in a depleted and unstable SSB despite the decline in F (Fig. 3.5d,e – red points). This outcome confirms the previous models and shows that climatic variables have a great impact on the dynamics of SSB of Atlantic cod.

The next model incorporated the interaction of large copepods and F and their effect on SSB (Fig. 3.5f). At the beginning of the time series, F was intermediate and large copepods were highly abundant, and SSB was at high levels and outside the unstable cusp area (Fig. 3.5f – blue points). After 1976, F was reduced and the abundance of large copepods decreased strongly. At that time, SSB entered the bifurcation area (Fig. 3.5f – orange points). During the last period, F was further reduced and the abundance of large copepods remained low, keeping SSB in a low state within the unstable area (Fig. 3.5f – red points). The results of these cusp models are all similar and indicate that SSB underwent true regime shifts due the interaction between F and changes in climate and the biotic ecosystem variables influencing R. Moreover, all these models show that SSB is presently in a low state and trapped in the unstable area, highlighting the presence of hysteresis.

Our first four models indicated that environmental drivers are important for the dynamics of North Sea cod and that low recruitment levels hinder the recovery of SSB. Thus, in a second set of models we studied how environmental drivers affect R to determine underlying causes keeping R low. First, we investigated the additional effect of PC1 (phytoplankton, inflow, NAO, large copepods) and PC2 (SBT, wind, SST) resulting from the common PCA of biotic and abiotic variables and SSB on R (Fig. 3.5g). The model shows initially a high SSB and a low PC1+PC2, and a high R (Fig. 3.5g – blue points). In 1976, SSB reached intermediate levels and PC1+PC2 did not change, wherefore R entered the stable area with high values (Fig. 3.5g – orange points). In the 1980s, SSB declined and PC1+PC2 increased, while R entered the cusp area. At present, SSB is in a very low state and PC1+PC2 increased strongly, pushing R progressively into the unstable area (Fig. 3.5g – red points).

The previous model highlighted that the interaction of abiotic and biotic variables caused changes in R dynamics. Subsequently, we studied the effect of changes in small copepods as possible effects on cod recruitment since they are important prey items (Fig. 3.5h). At the beginning of the time series, small copepods were highly abundant, SSB was high, and R was in the unstable area being high as well (Fig. 3.5h – blue points). After 1976, SSB started to decline and small copepods declined slightly, whereas R decreased in the stable area (Fig. 3.5h – orange points). In the last period, the combination of low SSB (even if slightly increasing) and low abundances of small copepods trapped R into the unstable area in a very low state (Fig. 3.5h – red points). This confirms the results of the previous model and highlights that biotic and abiotic variables are relevant to model recruitment. Moreover, the models highlight that R underwent true regime shifts and is at present in a very low state and inside the instability area.

4. Discussion

In our study we demonstrated that North Sea cod experienced regime shifts in SSB and R, including hysteresis, despite reduced fishing mortality. Low cod recruitment together with unsustainable fishing pressure caused a failed cod recovery. Low recruitment was as a result of North Sea ecosystem changes at lower trophic levels, e.g. in phyto- and zooplankton productivity, due to climate-induced temperature rise and global changes. We demonstrate how changes in the ecosystem context can limit the recovery of an already depleted fish stock, impeding management measures, which is important information for ecosystem-based fisheries management.

Our analyses on the ecosystem components (environment and lower trophic levels, i.e., phyto- and zooplankton) confirmed the major regime shift identified in the North Sea during the 1980s (Alheit et al. 2005; Edwards et al. 2013; Fromentin & Planque 1996; Reid et al. 2016; Reid & Edwards 2001). The regime shift was caused by an increase in water temperature due to positive changes in the global climate indices NAO and AMO (Beaugrand et al. 2002). These changes affected and increased wind direction and strength and the North-Atlantic inflow, which are characteristically influencing the lower trophic levels like phyto- and zooplankton in the North Sea (Fromentin & Planque 1996; Reid et al. 2001, 2003). The phytoplankton increased strongly and changed from a diatom dominated to a dinoflagellate dominated assemblage (Alheit et al. 2005; Beaugrand 2004; Beaugrand & Reid 2003; Reid et al. 2016). Shifts in phytoplankton combined with the increase in water temperature induced changes in the higher trophic level of zooplankton. A temperature induced increase of warm and a decrease of cold water related species took place, and the phytoplankton increase induced a reduction of *Calanus finmarchicus* and an increase of *Calanus helgolandicus* abundance. The former was a major prey species for young cod, wherefore the regime shift in the 1980s was the first to be recognized as being related to Atlantic cod survival in the North Sea (Beaugrand et al. 2002, 2003).

Our results add upon earlier studies where the stochastic cusp model has revealed regime shifts and hysteresis in North Atlantic cod stocks related to the interaction of fishing pressure and temperature changes (Möllmann et al. 2021; Sguotti et al. 2019, 2020). In addition to temperature as a proxy for climatic changes, we used distinct environmental and biological drivers in the models to understand why the North Sea cod is maintained at a low state. We found that SSB recovery is limited by the interaction of fishing mortality and external abiotic and biotic dynamics like increasing temperature and decreasing abundance of large copepods. The SSB is currently trapped in a low state and given expected further increases in external drivers like climate change induced water temperatures (IPCC 2022), the recovery potential of SSB is low.

We have also shown that cod SSB recovery depends strongly on recruitment. R is unstable since 20 years due to interactions between low SSB and increasing climate change effects. We found that not only ecosystem changes like NAO induced increases in wind (Stige et al. 2006) and sea temperature (Planque & Frédou 1999; Rindorf et al. 2020) related to the regime shift in the 1980s maintain R in the low state, but that also an ecosystem shift in the 2000s hinders R recovery. The shift occurred due to a high AMO causing warming of the sea temperature and eventually turning a dinoflagellate dominated into a diatom dominated phytoplankton community. In contrast to Lynam et al. (2017) reporting a decrease in diatoms given increased phytoplankton and decreased large copepods, we saw that an increase in diatoms goes hand in hand with increasing positive temperature (AMO) and decreasing abundances of small copepods. The decrease is further caused by the reduction in dinoflagellates, which are an important food source for small copepods (Alvarez-Fernandez et al. 2012). Hence, under potentially good environmental conditions, implying lower temperatures for example, these cascading effects could reverse and recruitment could increase to favour a recovery through a good year class. Also, the chance for recovery can be enhanced by further decreases in fishing mortality. Environmental stressors have a strong impact in especially open ecosystems (Conversi et al. 2015), and despite their bottom-up effects, the top-down impact of fisheries is stronger in benthic systems as for cod (Kenny et al. 2009). Hence, further reductions in fishing may push SSB into a stable area to support recruitment recovery.

We here demonstrated the potential of the stochastic cusp model approach to consider interactions between abiotic and biotic drivers and hence broaden the understanding of underlying reasons causing limited recovery of North Sea cod. Our study has limitations given known uncertainties within the stock assessment data we used (Sguotti et al. 2019). The stochastic cusp model approach is increasingly applied in various scientific disciplines (Diks & Wang 2016; Grasman et al. 2009). Still, it is only recently used in ecology and especially only applied little in fisheries science (Möllmann et al. 2021; Sguotti et al. 2019, 2020). The approach requires improvement to account for autocorrelation in time series data, and to enhance model comparison given uncertainties using the Akaike information criterion (AIC) and the Cobb's pseudo-R^2 (Sguotti et al. 2019).

Here, we studied Atlantic cod in the North Sea as one stock and did not distinguish between the three sub-populations (Romagnoli et al. 2020). Still, North Sea cod is affected differently in the different areas, with especially the cod population in the southern North Sea being negatively affected. The increases in temperature cause the cod to experience a northward shift of its most southern boundary and hence decreasing its distribution area (Baudron et al. 2020). The study of discontinuous dynamics in the spatial sphere of cod is an undiscovered field and hence a useful approach to complete the understanding of North Sea cod dynamics.

Eventually our study indicates that North Sea cod experienced non-linear discontinuous population dynamics. Despite decreased fishing pressure, climate change induced long-term impacts enhance effects of abiotic and biotic drivers on the stock and increase the likelihood that the stock will not recover and will rather be trapped in a SSB and R and in a low resilience (Lotze et al. 2011). The definition of recovery of the cod population is mainly set within the management context (MSY level) and entails an ‘increase towards a specific target’ (Lotze et al. 2011). To reach the MSY, a management on EU level which incorporates sustainable fishing at ICES reference levels is acquired (ICES 2012b). Additionally, it is fundamental to understand discontinuous dynamics in fisheries management to prevent abrupt failures given linear management approaches. Hence, management is required to consider abrupt changes related to climate change, especially given the steady increase in ocean warming in the North Sea (IPCC 2022). Even though F was reduced strongly, cod did not recover due to profound and abrupt ecosystem changes and probably changes in species composition.

Management goals to ‘increase towards a specified target’, like biomass towards MSY-level, and to account for shifts of social, demographic and functional components on population and ecosystem level, should be implemented to enhance the restoration of a system to more natural robust or a pristine structure (Lotze et al. 2011). Further North Sea species might experience similar abrupt discontinuous dynamics like cod due to overfishing and climate change. Hence, we highlight the importance to incorporate discontinuous dynamics in fisheries management approaches to achieve sustainable exploitation levels and to promote recovery of depleted fish stocks.

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Supplementary Materials

Table S3.1. All stochastic cusp model outcomes. Statistical results of all cusp analyses; z_t - state variable, α - asymmetry parameter, β - bifurcation parameter, AIC – Akaike information criterion, SSB - spawning stock biomass, R -recruitment, F - fishing mortality. % within bifurcation area is only shown for cusp models, dark panels show models selected.

z_t	α	β	Model	AIC	Cobb's pseudo-R^2	% within bifurcation area
SSB	F	Recruitment	Linear Logist Cusp	1350.29 1346.54 121.54	0.36 0.43 0.50	36.36
SSB	F	PC2 biotic and abiotic	Linear Logist Cusp	1371.17 1366.35 143.03	0.06 0.17 0.54	50.91
SSB	F	NAO	Linear Logist Cusp	1367.10 1365.46 144.76	0.13 0.19 0.56	45.45
SSB	F	SST	Linear Logist Cusp	1365.23 1364.09 142.67	0.16 0.21 0.46	40.00
SSB	F	SBT	Linear Logist Cusp	1364.50 1365.67 138.46	0.17 0.18 0.35	36.36
SSB	F	Large copepods	Linear Logist Cusp	1359.96 1361.59 132.90	0.24 0.29 0.40	52.72
SSB	F	Diatoms	Linear Logist Cusp	1355.03 1349.46 137.19	0.30 0.39 0.33	/
SSB	F	Dinoflagellates	Linear Logist Cusp	1363.21 1347.11 136.258	0.19 0.42 0.41	/
SSB	F	Small copepods	Linear Logist Cusp	1359.98 1339.76 136.10	0.23 0.49 0.23	/
SSB	F	Phytoplankton	Linear Logist	1344.62 1319.37	0.42 0.65	/

			Cusp	124.28	0.39	
SSB	F	Inflow	Linear Logist Cusp	1347.25 13344.65 133.94	0.39 0.44 0.39	/
SSB	F	AMO	Linear Logist Cusp	1333.36 1329.38 115.48	0.52 0.58 0.54	/
SSB	F	PC1 biotic and abiotic	Linear Logist Cusp	1328.14 1310.78 110.21	0.57 0.70 0.55	/
SSB	F	PC1+PC2 biotic and abiotic	Linear Logist Cusp	1325.82 1312.28 108.53	0.60 0.70 0.58	/
R	SSB	PC1 + PC2 biotic and abiotic	Linear Logist Cusp	1552.08 1547.09 98.47	0.43 0.50 0.58	83.33
R	SSB	Small copepods	Linear Logist Cusp	1560.96 1550.31 166.80	0.31 0.45 0.49	50.00
R	SSB	SST	Linear Logist Cusp	1563.45 1549.88 121.93	0.27 0.45 0.22	/
R	SSB	SBT	Linear Logist Cusp	1561.32 1549.556 119.334	0.30 0.46 0.26	/
R	SSB	Diatoms	Linear Logist Cusp	1561.90 1549.33 119.35	0.29 0.48 0.24	/
R	SSB	Dinoflagellates	Linear Logist Cusp	1565.29 1547.89 123.78	0.25 0.47 0.25	/
R	SSB	Large copepods	Linear Logist Cusp	1560.24 1547.14 120.95	0.31 0.48 0.25	/
R	SSB	Phytoplankton	Linear Logist Cusp	1550.94 1537.39 108.64	0.42 0.57 0.41	/

R	SSB	Inflow	Linear Logist Cusp	1565.13 1551.58 126.17	0.25 0.44 0.19	/
R	SSB	AMO	Linear Logist Cusp	1557.30 1546.90 103.95	0.35 0.48 0.47	/
R	SSB	NAO	Linear Logist Cusp	1565.25 1549.45 128.01	0.25 0.46 0.16	/
R	SSB	PC1 biotic and abiotic	Linear Logist Cusp	1550.27 1545.92 99.68	0.42 0.48 0.47	/
R	SSB	PC2 biotic and abiotic	Linear Logist Cusp	1565.51 1545.74 125.35	0.24 0.48 0.26	/

To gain a deeper understanding into the different effects of biotic and abiotic variables, we performed distinct PCAs (Fig. S3.1,2). Both PCAs show a strong and steady increase in the main principle component (PC1) (Fig. S3.1a,2a) and a continuous decline in PC2 until the 1990s, being stronger for the biotic system. An abrupt increase in PC2 took place in 1997 and 2001 for the biotic and abiotic variables, respectively (Fig. S3.1b,2b). The main biotic variables contributing to PC1 are small copepods and phytoplankton, while PC2 is strongly determined by dinoflagellates and large copepods. As for the overall PCA analyses, three periods could be identified for the biotic variables as well (Fig. S3.1c,d). The first cluster (1963-1985) determines a high SSB and recruitment, and strong appearances of dinoflagellates and large and small copepods. In contrast, the third cluster (1998-2017) demonstrates a low SSB and recruitment, and high abundances of diatoms and phytoplankton, being the biotic opponents to PC1.

We found a similar strong distinction within abiotic variables (Fig. S3.2). PC1 represents climatic variables with strong contributions by the NAO, inflow, current and wind. The warming variables SBT and SST contrarily strongly contribute to PC2. Here, we also identified three clusters using constrained clustering (Fig. S3.2c). The low reproductive stock (SSB and recruitment) characterizes the first cluster (1963-1987) solely (Fig. S3.2c,d). The second (1988-2000) and third clusters (1989-2017) highlight the distinction between variables characterizing atmospheric dynamics and thermal conditions, as well as the upcoming relevance of abiotic variables for the cod stock. The second period experienced a high NAO, strong winds, currents and North Sea inflow, whereas the recent period demonstrates increased warming.

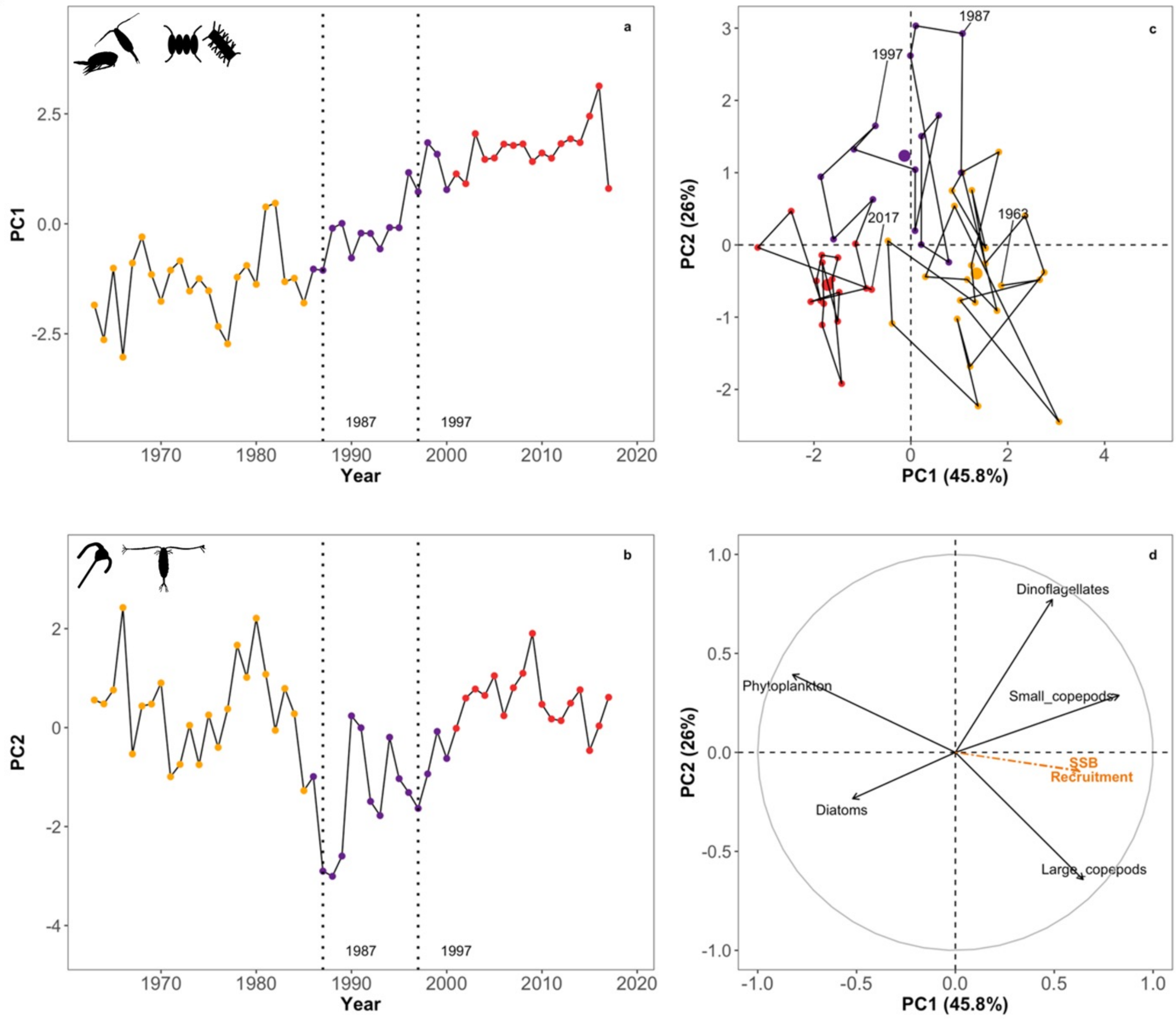

Figure S3.1. Biotic North Sea ecosystem dynamics. Results of Principal Component Analysis a.– PC1 trajectory over time, b – PC2 trajectory over time, c – PCA individuals, d – PCA variables (spawning stock biomass (SSB), Phytoplankton (Phytoplankton Color Index). SSB and recruitment are supplementary quantitative variables (orange); vertical lines in a and b indicate transitions between clusters identified by constrained clustering analyses in c; cluster 1 in yellow (1963-1986), cluster 2 in purple (1987-1996), cluster 3 in red (1997-2017); icons represent main variables contributing to PC.

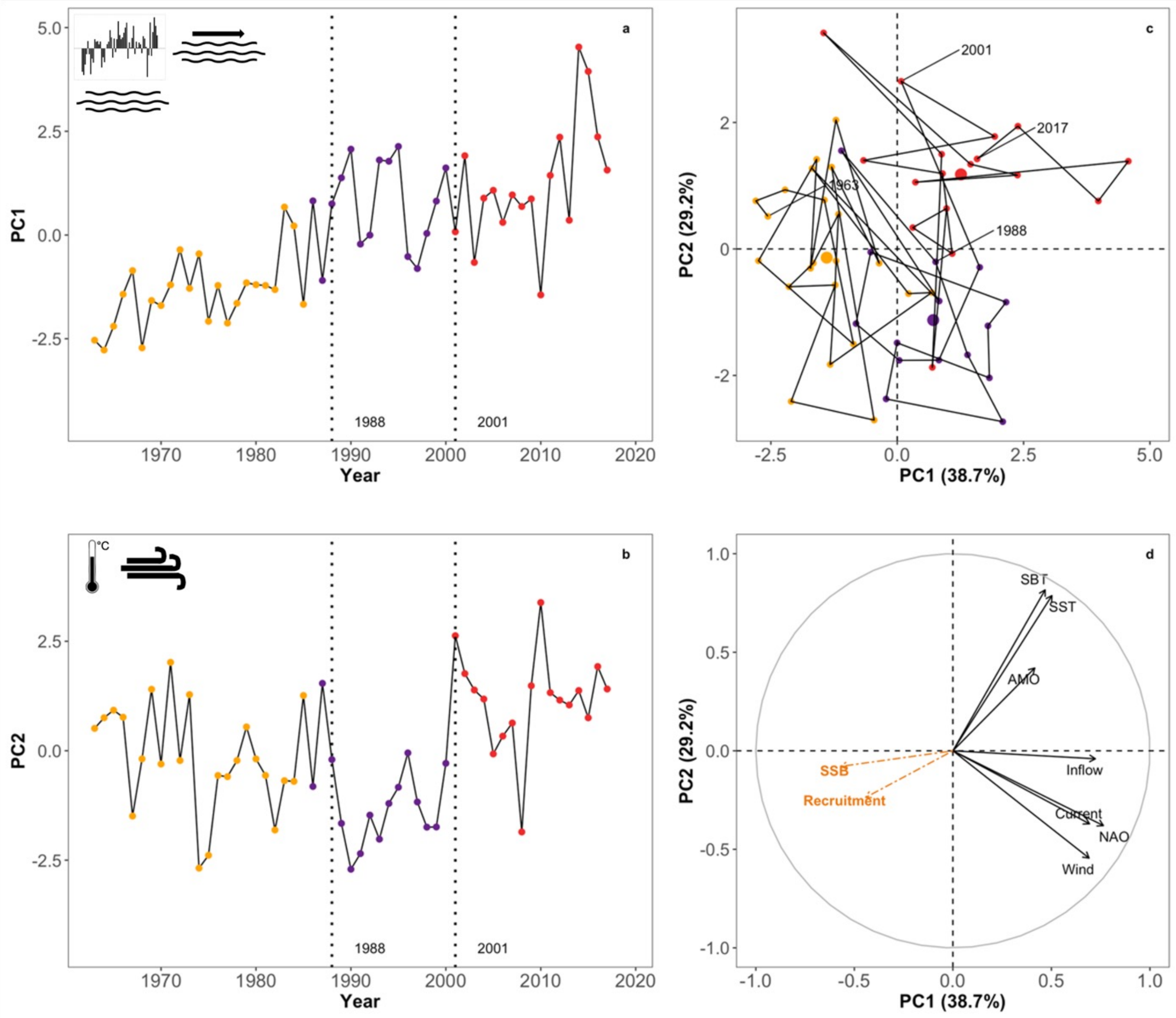

Figure S3.2. Abiotic North Sea ecosystem dynamics. Results of Principal Component Analysis a.– PC1 trajectory over time, b – PC2 trajectory over time, c – PCA individuals, f – PCA variables(spawning stock biomass (SSB), sea bottom temperature (SBT), sea surface temperature (SST), Atlantic multidecadal oscillation (AMO), North Atlantic oscillation (NAO), Phytoplankton (Phytoplankton Color Index)). SSB and recruitment are supplementary quantitative variables (orange); vertical lines in a and b indicate transitions between clusters identified by constrained clustering analyses in c; cluster 1 in yellow (1963-1987), cluster 2 in purple (1988-2000), cluster 3 in red (2001-2017)); icons represent main variables contributing to PC.

Chapter IV

Irreversibility of regime shifts in marine ecosystems

Irreversibility of regime shifts in marine ecosystems

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Abstract

Human impacts can induce ecosystems to cross tipping points and hence unexpected and sudden changes in ecosystem services that are difficult or impossible to reverse. The world´s oceans suffer from cumulative anthropogenic pressures like overexploitation and climate change and are especially vulnerable to such regime shifts. Yet an outstanding question is whether regime changes in marine ecosystems are irreversible. Here we first review the evidence for regime shifts in the North Sea ecosystem, one of the heaviest impacted and best studied marine ecosystems in the world. We then used catastrophe theory to show that fishing and warming have caused a previously undetected and potentially irreversible regime shift. Our study emphasizes the powerful combined effects of local and global human impacts in driving significant ecosystem shifts and suggests that adaptation is likely the central avenue forward for maintaining services in the face of global climate change.

Keywords: Regime shifts, Irreversibility, Hysteresis, Ecosystem resilience, Stochastic cusp modelling, Marine ecosystems

1. Introduction

In the face of global change, ecosystem resilience is necessary to maintain the critical services ocean ecosystems provide, yet we still know relatively little about how many human impacts an ecosystem can take before it is irrevocably changed. In some circumstances, the accumulation of human impacts has induced ecosystem reorganizations called "regime shifts", defined as abrupt changes in the structure and function of ecosystems (Beisner et al. 2003; Scheffer et al. 2001; Scheffer & Carpenter 2003). When regime shifts occur, previously abundant commercially-harvested species can be replaced by more tolerant species that are able to thrive under the new more heavily impacted conditions (Beaugrand 2004; Vasilakopoulos et al. 2017). These changes can be socially and economically costly when they require adaptation by ocean users, including significant modifications to harvest methods, supply chains, and infrastructure (Carpenter 2001; Levin & Möllmann 2015; Scheffer et al. 2001). As a result, avoiding regime shifts, or reversing them, is often preferred. However, reversals can be slow and are not always possible, because of hysteresis – the delayed return to previous conditions following a regime. Therefore, there is continued interest and value in understanding what drives regime shifts, and there is significant uncertainty whether regime shifts can be reversed, and what management solutions exist in case of irreversibility (Levin & Möllmann 2015; Selkoe et al. 2015).

While it is evident that avoiding irreversible regime shifts in a social-ecological system is fundamental in order to maintain services, the management application is not straightforward. The consideration of abrupt non-linear change in management is often undermined by the lack of consensus on the definition of the word "regime shift" and by methodological limitations. The former derives from the use of the same word "regime shift" in completely opposite contexts. Indeed, regime shift is used sometimes to describe a simple "phase shift" not characterized by hysteresis and sometimes to describe alternative stable states characterized by hysteresis (Scheffer et al. 2001; Selkoe et al. 2015). This lack of an agreed definition creates confusion in the scientific community around the concept and a certain level of disbelief in its importance. The presence of multiple definitions with opposite dynamics (with or without hysteresis) have repercussion also on their detection. Simple statistical change point analyses can be useful to identify phase shifts without hysteresis, but are not enough to detect the presence of irreversible regime shifts (Andersen et al. 2009). However, the majority of the paper studying regime shifts employ these types of methods and do not quantify or detect hysteresis. Moreover, often the drivers of regime shifts are not statistically tested.

Identifying the drivers of regime shifts can be relatively straightforward using empirical data. In general, human impacts such as fishing pressure and environmental drivers like temperature can be regressed against different types of ecosystem metrics to determine which combination of drivers caused observed shifts (Andersen et al. 2009; Beaugrand 2004). Understanding whether a regime shift is reversible or irreversible, thus quantifying hysteresis, is however far more challenging and has rarely been done using empirical data (Schmitt et al. 2019; Sguotti & Cormon 2018; Vasilakopoulos et al. 2017). Hysteresis and irreversibility are due to powerful feedbacks loops (Beisner et al. 2003). These feedbacks stabilize the new regime through the creation of new interactions among species, new energy pathways and new system structures making it difficult or impossible to transit back to the previous system state even if the original driver of the regime shift is removed or alleviated. Thus, to determine whether a regime shift is reversible or not we need to answer two main questions. 1) How strong is the hysteresis? In other words, how much do we need to alter the drivers in order to disrupt the feedback loops formed in the new system? 2) Is management able to revert the drivers? Some drivers such as fishing or pollution can be reduced, while other pressure such as global climate change are likely more difficult to reverse (Hoegh-Guldberg & Bruno 2010).

Here, we study regime shifts in the North Sea large marine ecosystem which is experiencing rapid warming and also intensive fishing pressure and is one of the most heavily human impacted areas in the world (Emeis et al. 2015). Firstly, we conducted a literature review to check what regime shifts have been documented and which methods were used to detect them. Previous analyses have documented regime shifts in the North Sea in subsets of the ecosystem such as plankton or fishes in the 1980s and 1990s (Beaugrand 2004; deYoung et al. 2008; Wouters et al. 2015), however using models not able to quantify hysteresis. Our study seeks to document a new regime shift in the most recent warming period, and moves beyond regime shift detection, to understand whether cumulative impacts on the North Sea are irreversible. To conduct a comprehensive analysis of regime shifts in the North Sea, using all trophic levels of the ecosystem, we use stochastic cusp modelling, an approach derived from catastrophe theory. We show the interactive effects of global warming and changes in fishing pressure in driving the most recent regime shift in the system and document the existence of hysteresis. If reduced, fishing pressure could help to increase the yield of the currently exploited species; however, simply removing fishing pressure is unlikely to reverse the regime shift, which is maintained by other feedbacks. Moreover, since climate change is not currently reversible and can only be mitigated, we suggest that the new regime in which the North Sea resides now is irreversible and thus major adaptations need to be undertaken in order to maximize the services that can be provided by this newly transformed ecosystem.

2. Materials and Methods

2.1. Systematic review

We conducted a systematic review (September 2019) of the scientific literature related to regime shift dynamics in the North Sea ecosystem with special attention on how theory of critical transition is addressed. *Web of Science* and *Science Direct* were used as platforms to screen literature multiple databases using the following search criteria:

“TS = ("tipping point" OR "regime shift" OR "top-down" OR "bottom-up" OR "trophic cascade*") AND TS = ("North Sea") AND TS = ("complex dynamic system" OR "ecosystem" OR "natural system" OR "ecology" OR "economic" OR "socio ecological system")” (adapted for the two websites).*

The first part of the search string referred to the type of dynamics and change we were interested to analyze and detect, in particular abrupt changes of the system and system functioning. In the second part of the search string (after *AND*) the types of publications that we were targeting were addressed, ranging from just ecological studies to economic and socio-ecological. However, just one economic study was found and therefore was dropped from the main analyses. Identified publications were added to a reference organizer and checked for duplicates. We excluded papers not dealing with the North Sea or not investigating regime shifts in any of the North Sea ecosystem components from the analysis. Subsequently, we developed a protocol (see Table 4.1 and SI) to rigorously analyze each publication and the analysis was conducted by 10 co-authors. To avoid biases due to subjective interpretation, the protocol contained 6 fixed multiple choice answers, each of which followed by a descriptive explanation (Table 4.1, SI Text). The timing of regime shifts and the type of method used in the paper were all screened by the first author, who, at the end assembled all the data checking for mistakes. The data collected were then analyzed with respect to how scientific studies address regime shifts in the North Sea ecosystem.

Table 4.1. Coding to analyze the papers collected from the review. Each column represent one of the information that we wanted to collect from the papers. In the row the fixed multiple answer choices established to make the review stronger. More info about the coding protocol in SI Text.

Paper	**Field**	**Basin**	**Dynamics**	**Dependent variable**	**Year of the shift**
	Ecology	North Sea	Regime shift	Full ecosystem	
	Economy	Multiple	Change	Species	
	Sociology			Trophic Level	
	Inter-disciplinary			Assemblage	
				Multiple	
Drivers	**Control**	**Methods**	**Hysteresis**	**Resilience**	**Flags of regime shifts**
Environment	Bottom-up	Empirical	Mentioned	Mentioned	Multimodality
Fishing	Top-down	Theoretical	Quantified	Quantified	Bistability
Eutrophication	Wasp-waist	Descriptive			
Food-web	Multiple	Review			
Management		Experimental			
Multiple		Field-based			

2.2. Biological data

We assembled a multivariate dataset to re-analyze North Sea ecosystem dynamics with special emphasis on regime shifts (SI Tables 4.3, 4.4). Our dataset covered the period from 1985 until 2015 and represents several trophic levels from plankton to fish. Plankton data were provided by the Continuous Plankton Recorder (CPR) program (www.cprsurvey.org) and included aggregated phytoplankton biomass indicators for dinoflagellates and diatoms as well as the phytoplankton color index as a bulk biomass indicator (Maritorena et al. 2010). The zooplankton community is represented by aggregated indicators for small and large copepods together amounting for most of the biomass (Maritorena et al. 2010). The fish community of the North Sea is represented by time-series on abundance (catch per unit of fishing effort) derived from the International Bottom Trawl Survey (IBTS) program of ICES (http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx). The IBTS is an international survey which seasonally collects data on fish populations and communities. Each vessel deploys a standard otter trawl as sampling gear. The data collected are recorded as catch per unit of effort which means that they are standardized per unit of trawling time (ICES 2015). In order to assure standardized sampling, at least two hauls are always conducted for each North Sea spatial unit (i.e. statistical rectangle), which cover one degree longitude and 0.5 degree latitude (ICES 2015). Just data from Quarter 1 (January to March) were used in the analyses. The IBTS database contains data for more than 100 species. In order to numerically balance the dataset between fish and plankton we selected eight of the most important fish species as indicated in previous publications. The species chosen were also balanced between forage fish, groundfish and benthic fish (Engelhard et al. 2011; Lynam et al. 2017). In order to use comparable annual estimates, all the data were first aggregated per hauls, then averaged over statistical rectangle and finally summed over the entire North Sea.

2.3. External pressures

We analyzed North Sea regime shift dynamics in relation to fishing pressure and climate dynamics. Fishing effort data, representing the exploitation pressure on the system, were collected from Couce et al., 2019 (Couce et al. 2019). These data consisted of beam and otter trawl effort data (hours swept per year), collected and reconstructed for the period from 1985 to 2015. Data were summed over the entire North Sea in order to obtain estimates of the total annual fishing effort. Climate-related variables in our analysis were Sea Surface Temperature (SST), as a local variable, and two climate indices, i.e. the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO). We selected these two indices because they have been shown to affect North Sea community dynamics and to induce past regime shifts (Beaugrand 2004). SST was extracted from an oceanographic model developed by Nunez-Riboni & Akimova 2015 (Núñez-Riboni & Akimova 2015). NAO and AMO were collected from the Earth System Research Laboratory (NOAA, www.esrl.noaa.gov). NAO is a high frequency index (7-25 years) depending on the different pressure at sea level between Iceland and Azores, while AMO is a low frequency multidecadal index (60 years) representing climate-related SST changes in the Atlantic Ocean (Hurrell 1995). All the environmental data were averaged annually over the entire North Sea, apart from the NAO that was averaged just between December and March.

2.4. Principal Component and change point analysis

To identify a major long-term signal of the North Sea ecosystem, a Principal Component Analysis (PCA) was performed on the community dataset. This technique is particularly useful because it allows to simplify the dataset, extracting the main variability and understanding relationships between variables (Legendre & Gallagher 2001). Additionally, a cluster analysis was performed to detect differences in the community in different periods (Murtagh & Legendre 2014). The hierarchical clustering was performed firstly estimating Euclidean Distance between the years based on their projections on the PCA biplot, and subsequently estimating the number of significant clusters, based on Ward´s criterion, based on graphical interpretation of the dendogram (Murtagh & Legendre 2014). PC1 and PC2 were extracted as long-term signals of the community and to identify abrupt changes. PC1 and PC2 were extracted as long-term signals of the community and were analyzed using two different types of change point analysis, the Bayesian change point analysis and change in mean and variance, to detect the presence of abrupt changes (Erdman & Emerson 2007). The presence of abrupt changes in the community can indeed be a sign of regime-shift like dynamics, but cannot unequivocally confirm the presence of discontinuities and cannot highlight the effect of external drivers.

2.5. Stochastic cusp model

To detect the presence of true discontinuous dynamics and understand the synergistic effect of two drivers, one bottom-up, i.e. environment, and one top-down, i.e. fishing pressure, we applied the stochastic cusp model. This model comes from catastrophe theory and is based on the canonical form of the cusp, which describes abrupt changes of a state variable (z_t) depending on small changes of two control factors (α,β) (Dakos & Kéfi 2022; Diks & Wang 2016; Thom 1977). It is based on a cubic differential equation (Eq.1), reformulated as a stochastic differential equation adding a Wiener process (Eq.2) (Diks & Wang 2016; Grasman et al. 2009; Sguotti et al. 2019).

$$-\mathrm{V}(\mathrm{z_t}, \alpha, \beta) = -\frac{1}{4}\mathrm{z_t^4} + \frac{1}{2}\beta \mathrm{z_t^2} + \alpha \mathrm{z_t} \qquad (1)$$

where $V(z_t, \alpha, \beta)$ is a potential function whose slope represents the rate of change of the system (z_t), depending on the two control variables (α,β)

$$-\frac{\delta \mathrm{V}(\mathrm{z}, \alpha, \beta)}{\delta \mathrm{z}} = (-\mathrm{z_t^3} + \beta \mathrm{z_t} + \alpha)\mathrm{dt} + \sigma_\mathrm{z} \mathrm{dW_t} = 0 \qquad (2)$$

where the first part of the equation is the drift term, σ_z, is the diffusion parameter, and W_t represents the Wiener process.

The parameters, α and β, and the state variable (z^t) are modelled as linear function of one or more exogenous variables, using a likelihood approach (Eq.3 a-c). Here, the state variable was modelled as a linear function of the two long-term signals in the community (i.e. PC1 and PC2). Fishing effort was used as a linear predictor of α, the so-called asymmetry parameter, which controls changes in the community and can be managed (top-down) (Sguotti et al. 2019). Environmental drivers were used separately as linear predictors of β, the bifurcation parameter, that controls whether the relationship between the state variable and α is linear or discontinuous and thus allows the emergence of regime shift dynamics (Eq.3 a-c).

$$z_t = w_0 + w_1 PC1 \tag{3a}$$

$$\alpha = \alpha_0 + \alpha_1 FishingEffort \tag{3b}$$

$$\beta = \beta_0 + \beta_1 ClimateDriver \tag{3c}$$

where α_0,β_0,and w_0 are the intercepts and α_1,β_1,and $w_{1,2}$ the slopes of the models.

The best models were selected based on the Aikake Information Criterion (AIC) and the R². To detect the presence of multiple equilibria and therefore discontinuous dynamics it was necessary to solve Eq.4 and determine the Cardan´s discriminant (δ) (Diks & Wang 2016; Grasman et al. 2009).

$$\delta = 27\alpha^2 - 4\beta^3 \tag{4}$$

The system follows a discontinuous path and shows multiple equilibria if the Cardan´s discriminant is smaller or equal to 0, otherwise the system follows a continuous path (Grasman et al., 2009; Diks and Wang, 2016). This allows, to understand whether the community is close or far from tipping at every moment in time and to understand its dynamics, depending on the external control drivers. Therefore, the application of this model can help in detecting the presence of regime shifts and the synergistic effect of the drivers controlling the system.

All analyses were conducted in R Studio (version 3.6.1). The PCA was performed using the package ade4 (Dray & Dufour 2007), the Bayesian change point analysis using bcp (Erdman & Emerson 2007) while the stochastic cusp model with the package cusp (Grasman et al. 2009).

3. Results

3.1. Systematic literature review

North Sea ecosystem regime shifts have previously received significant empirical attention. Following our review protocol we identified 211 papers of which 55 were deemed relevant to understand how regime shifts were addressed in the North Sea literature. In total, 72 regime shifts were identified in various aspects of the ecosystem (SI Table 4.1, Fig. 4.1a). The majority of the detected regime shifts were reported for the 1980s and 1990s (19 and 9, respectively; Fig. 4.1a), but no regime shifts were reported after 2000. Studies varied in their statistical rigor; only 24 of the 55 studies applied statistical methods capable of clearly identifying abrupt changes in time series (Fig. 4.1b, SI Table 4.2). The remaining papers either showed changes qualitatively without statistical testing or were review papers. Despite abundant theory linking the concept of regime shifts to ecosystems switching between alternative stable states, only 9% of studies examined the concept of irreversibility. Moreover, none of the empirical studies rigorously explored aspects of stability in regimes, indicating a significant need to examine these concepts further in the context of sustainable management.

Our review also found that previous research on North Sea regime shifts was taxonomically biased, primarily examined dynamics of a single trophic level, and focused on single rather than cumulative human and environmental drivers of regime shifts. Most studies focused on plankton (mostly copepods), and 60% of the papers examined only a single trophic level (Fig. 4.1b, SI Table 4.1). Additionally, most studies solely considered climatic variables as drivers of ecosystem change, e.g., temperature, the North Atlantic Oscillation (NAO) or the Atlantic Multidecadal Oscillation (AMO), and often ignored the potential importance of consumer resource interactions (Fig. 4.1c). Moreover, only 16% of studies considered the effects of more than one pressure on the ecosystem at a time, despite that theory suggests discontinuous regime shift dynamics to emerge from the interaction of multiple drivers (SI Table 4.1). These gaps in previous research have limited our capacity to detect the typical properties of regime shifts: feedback mechanisms and cascading effects across trophic levels.

Probably the most important theoretical aspect of regime shifts is the potential of switching between true alternative states that are difficult or even impossible to return. Both hysteresis in recovery and especially irreversibility are key questions for ecosystem-based management of the oceans. However, we found only 5 of the 55 papers reviewed mentioning the concepts of hysteresis and irreversibility. Furthermore, none of the empirical studies rigorously explored aspects of stability in regimes, indicating a clear lack in the understanding of the dynamics of marine ecosystems crucially important for their sustainable management. In total, the results of our review revealed a clear mismatch between the theoretical concept of regime shifts and its application to empirical studies of marine ecosystem dynamics.

We argue here that the evident inconsistency between the theory of regime shifts and its consideration in empirical studies is due to methodological limitations. Standard statistical methods applied in the marine sciences are still largely limited to linear approaches that are unable to deal with non-linear and state-dependent phenomena like regime shifts. In the papers we reviewed for the North Sea ecosystem, statistical analysis was largely limited to the application of change point analysis to detect abrupt changes in time series which is not suitable to address hysteresis or irreversibility (SI Table 4.2). Furthermore, mostly linear correlation and regression approaches are used to understand the relationship between state variables and drivers.

Analysis of North Sea ecosystem regime shifts

We described the North Sea community using a dataset including a taxonomically diverse group of species, from plankton to predatory fish and covering the entire trophic structure, for the period from 1985 until 2020 (see methods, SI Table 4.3, SI Fig. 4.1). To describe the change in community structure through time, we used Principal Component Analysis (PCA) and extracted the main modes of variability in the data set (PC1 and PC2) (Fig. 4.2; for detailed results of the PCA analysis, SI Fig. 4.2-4.4). We then used hierarchical cluster analysis on the PCA results to demonstrate a shift in ecosystem states along the PC1 axis, which identified a clear distinction between community structures before and after 2002 (Fig. 4.2a, SI Fig. 4.5). At the beginning of the 2000s the North Sea was depleted from its demersal fish stocks, rich in small copepods, had an increasing number of pelagic fish, and was dominated by dinoflagellates. We here found a new until now unreported shift in 2003 after which the system was characterized by higher diatom biomass, and an increase in three fish species: saithe (*Pollachius virens*), plaice (*Pleuronectes platessa*) and sprat (*Sprattus sprattus*) (Fig. 4.2a). We applied statistical change point analysis to demonstrate that the shift between ecosystem states was abrupt (SI Fig. 4.6) and hence indicates a possible North Sea ecosystem regime shift at the beginning of the 2000s that was not described in the literature so far (Fig. 4.2b). Further variability in the ecosystem is represented by PC2, however without a clear and abrupt separation of states (SI Fig.

4.7). Is this new state after 2003 stable? Did the system undergo true discontinuous dynamics? Did warming and fishing pressure, dominant drivers of the previous shifts, cause also this new shift? To answer these urgent questions we used the stochastic cusp model (Box 1).

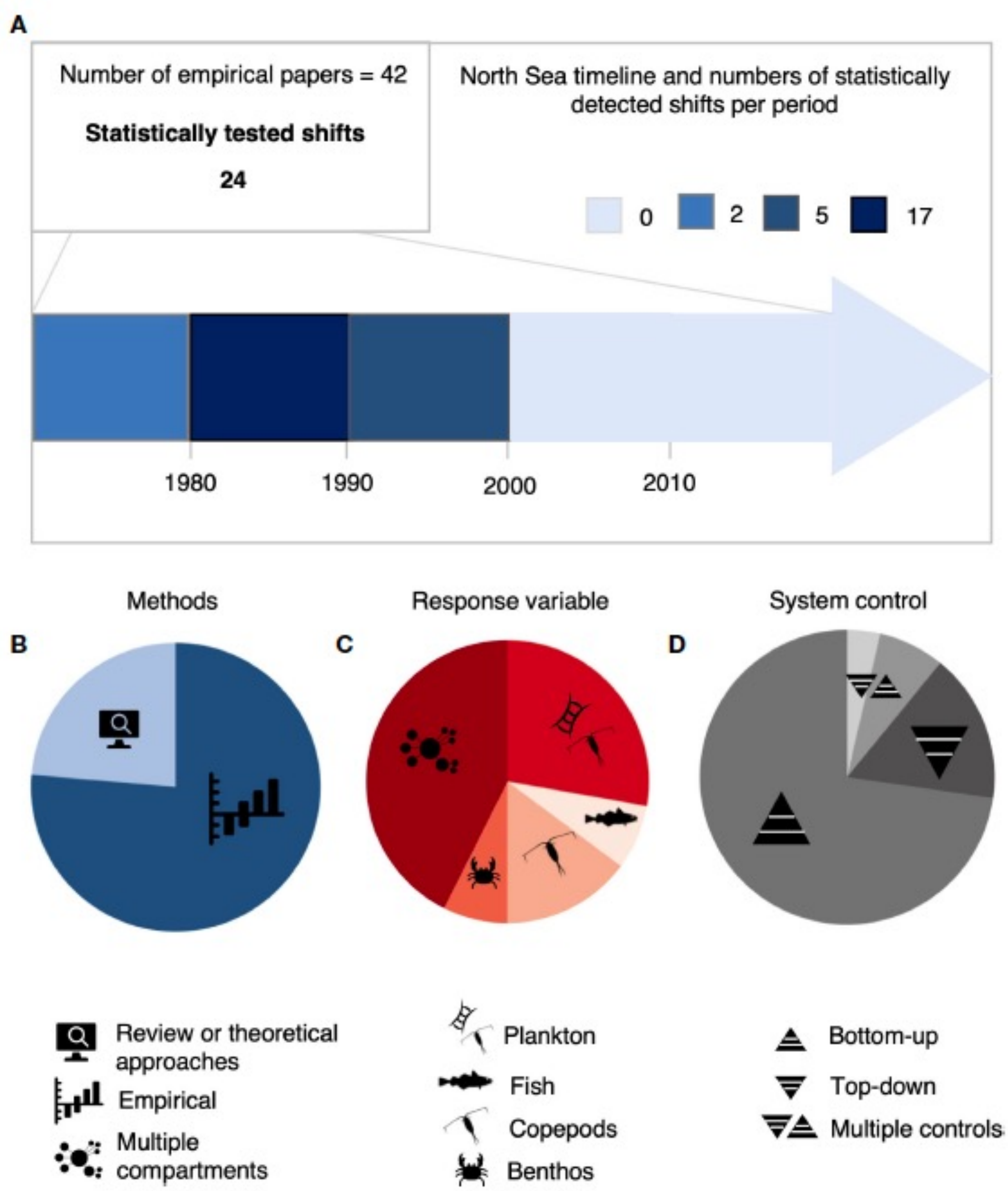


Figure 4.1. Results of the systematic literature review on regime shifts in the North Sea ecosystem. In total 55 papers dealt with regime shifts and 72 shifts were recorded. a, Decadal occurrence of reported statistically tested regime shifts. 42 papers used empirical methods but just 24 tested the abrupt shift. c-d, Percentage distribution of statistical methods applied, response variable and type of ecosystem control considered in reviewed studies. The percentages were calculated against the total number of papers (i.e. 55).

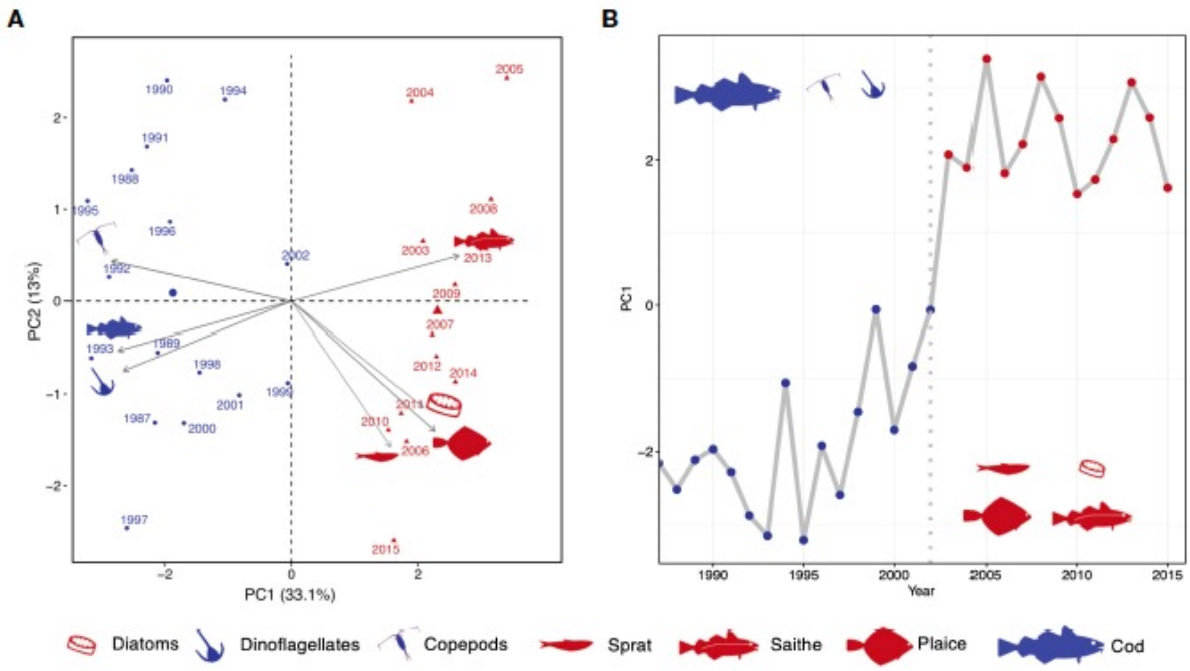
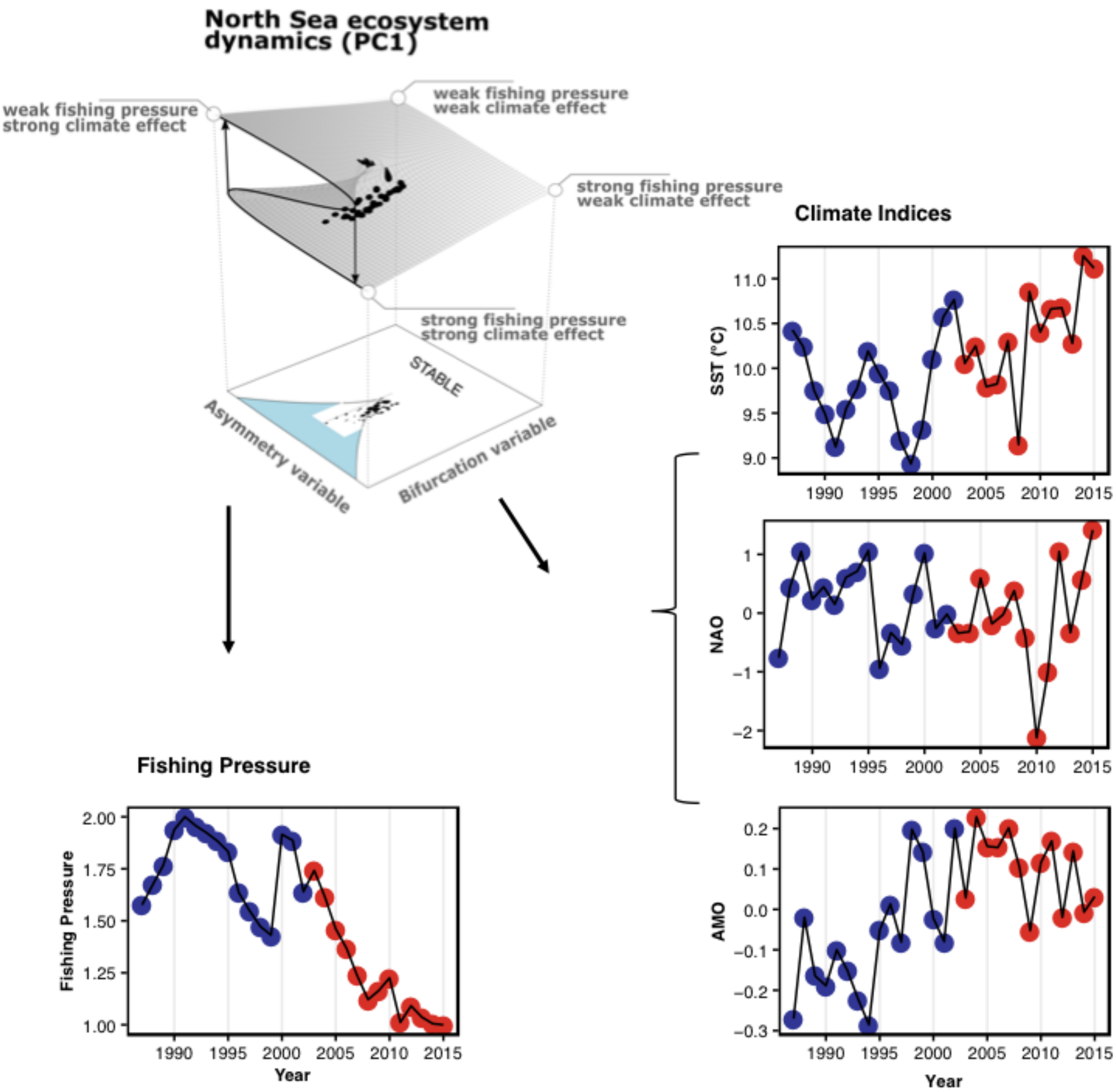


Figure 4.2. Regime shift in the North Sea ecosystem. a, Biplot of principal components PC1 and PC2 (explained variance in brackets) associating the periods of the two ecosystem regimes to dominating species/taxonomic groups; only species/taxonomic groups with the highest loadings in PC1 and which are emergent species in PC2 are shown; for full PCA output see SI Fig. 4.4. **b**, Abrupt shift in scores of PC1 evaluated by statistical change point analysis.

We used the main mode of variability in the ecosystem (i.e. PC1) to model the system´s response variable in three stochastic cusp models. Fishing pressure (approximated as total hours fished by beam trawls and bottom trawls) was used to fit the asymmetry variable that largely represents the top-down effect of fisheries management on the system. In each of the models we used one climate variable (i.e. SST, NAO and AMO, SI Table 4.4) as the bifurcation variable that affects the system from bottom-up and according to the assumption of the stochastic cusp model determines if the relationship between fishing pressure and the main community dynamics is linear continuous or non-linear discontinuous. We can infer stability patterns from the model results of the new regime by inspecting if the predicted PC1 loadings are outside (stable) or inside (bistable) the cusp area (lightblue in Fig. 4.3 and see also Box 4.1). A comprehensive model validation revealed that all three fitted stochastic cusp models are superior to alternative linear and logistic models, explained a large portion of the variability in the data and fulfilled additional criteria for this model type to be valid (SI Table 4.5).

Box 4.1- The stochastic cusp model and its application to North Sea ecosystem dynamics



The cusp model is based on catastrophe theory that differentiates seven elementary catastrophes of which the most known in ecology is the fold catastrophe often used to represent regime shifts in a two-dimensional space (Thom 1977; Grasman *et al.* 2009; Diks and Wang 2016). In contrast to the fold, the cusp catastrophe considers a three-dimensional system where a state variable depends on two interacting control variables. The *asymmetry variable* affects the dimension of the *state variable* determining its transition between system states. The *bifurcation variable* determines the form of the relationship between the state variable and the asymmetry variable along a continuum from linear and continuous to non-linear discontinuous. The cusp catastrophe is represented by a potential function that can be fit to data using the method of moments and maximum likelihood estimators, and the *state, asymmetry and bifurcation* are canonical variables fit using linear models of observed quantities (see methods). In our analysis of the North Sea we modelled the dynamics of the *state variabl*e as a function of PC1 representing the main mode of variability in the ecosystem. The *asymmetry* and *bifurcation variables* were fit to time-series of fishing pressure and climate indices, respectively. Fishing pressure is represented by the logarithmic value of annual total hours fished (by beam and bottom trawls) of the North Sea fisheries. We used three indices for climate change (colors according to regimes identified in PC1; see Fig. 4.1), i.e. sea surface temperature (SST) that represents the direct effect of climate on the water column, as well as the indices for the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO) that represent decadal and multidecadal climate dynamics, representatively. Our model setup bears the assumption that climate change can alter the relationship between fishing pressure and ecosystem state from linear to non-linear and vice versa. Importantly, using the stochastic cusp model we can distinguish between unstable (in fact bistable) and stable states in the dynamics of the system. Bistable dynamics exist under the folded curve where the state variable can flip between the upper and lower shield, called the *cusp area* (shaded in light blue) in the 2D representation of the model surface. Outside the cusp area the system is stable and present progressively higher hysteresis as we move away from the area.

Fitted stochastic cusp models revealed that the recent regime shift in the North Sea ecosystem occurred when the system resided in the cusp area indicating unstable dynamics where the system state can flip between two configurations (Fig. 4.3). All three models demonstrate that the regime shift in the food web of the North Sea is a response to a combination of climatic changes and a decrease in fishing pressure. SST and AMO models clearly show that the ecosystem is now in a significantly warmer state (Fig. 4.3a,b), and also decadal atmospheric changes indicated by the NAO are supporting the effect of ongoing climate change (Fig. 4.3c). Importantly, our empirical study shows that the new ecosystem state characterized by the dominance of diatoms as well as the fish species sprat, saithe and plaice is potentially irreversible. PC1 scores reflecting ecosystem dynamics in recent years are outside the unstable cusp area and are not likely to return to the previous state (Fig. 4.3).

4. Discussion

The North Sea is one of the best studied marine systems in the world ocean since for centuries it has been an hotspot of human pressures (Emeis et al. 2015). Our literature review revealed that regime shifts have been previously documented in the North Sea at the end of the past century and extensively studied (Beaugrand 2004). The most well-studied North Sea regime shift occurred at the end of the 1980s and involved in particular the plankton assemblage (Alheit et al. 2005; Beaugrand 2004).

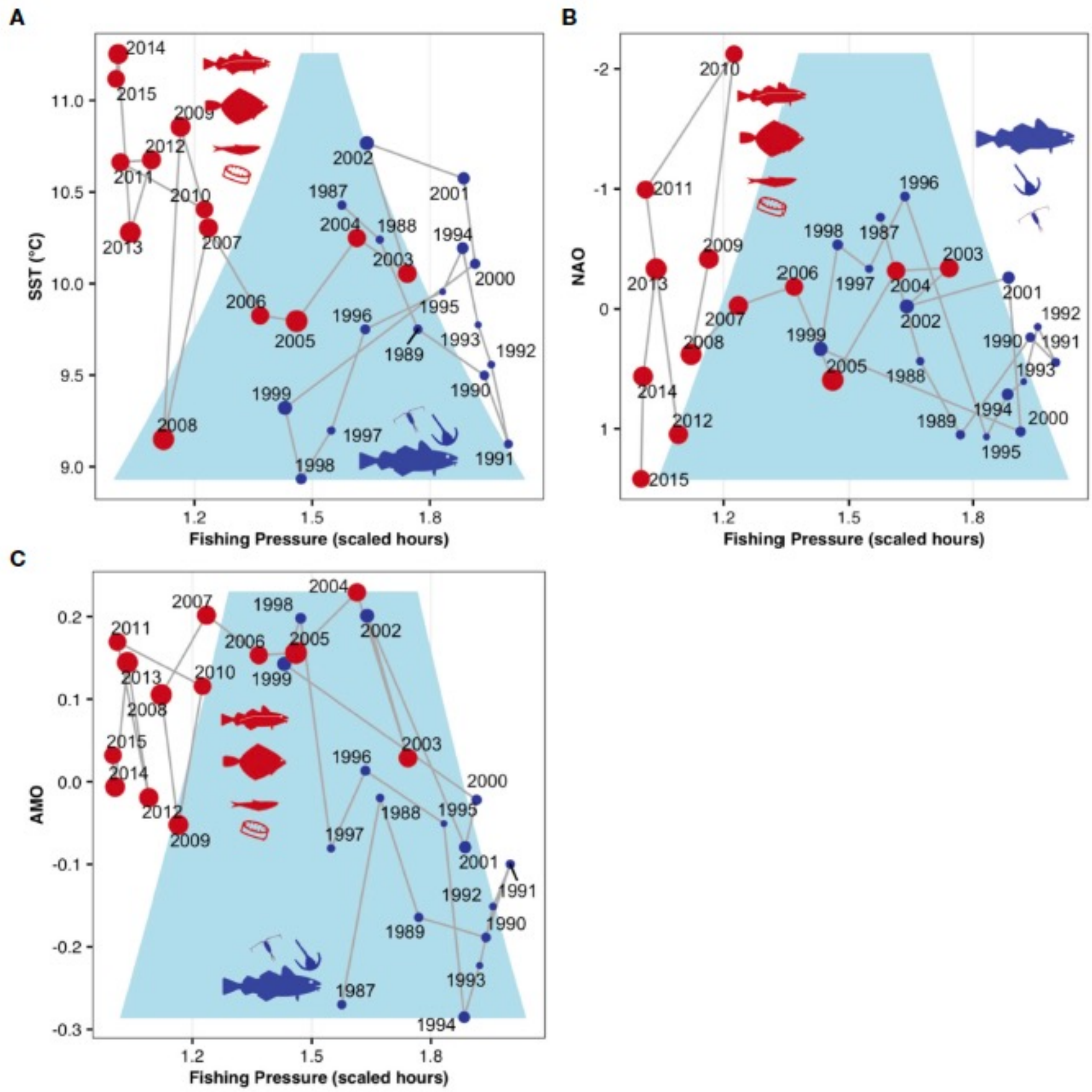


Figure 4.3. Potential irreversibility of a regime shift in the North Sea ecosystem. Results of stochastic cusp modelling showing predicted PC1 scores in relation to fishing pressure and **a**, sea surface temperature (SST) **b**, the index of the North Atlantic Oscillation (NAO), and **c**, the index of the Atlantic Multidecadal Oscillation (AMO). Points are scaled according to PC1 scores; colors and regimes-specific species/taxonomic groups according to Fig. 4.2; the light blue area represents the cusp area (below the fold) in which the system can exist in three states, two stable and one unstable and can therefore flip from a state to the other. Note that NAO values are on a reverse scale.

An increase of temperature led to a progressive increase in dinoflagellates, a reduction in diatoms, and a decrease in the size copepods (Alheit et al. 2005). Before 1980s demersal fish populations were abundant and the gadoids stocks in particular were at their highest level (Hislop 1996). However, continuously high fishing pressure coupled with the changes in the plankton community, led to a collapse of the entire demersal assemblage, particularly Atlantic cod (Beaugrand et al. 2003; Lynam et al. 2017). After the 1980s the North Sea underwent an ecosystem reorganization where demersal fish assemblages were depleted, Atlantic herring increased in abundance, and the plankton community underwent an additional shift in species composition. Another shift, even if less reported, occurred at the end of the 1990s and included another change in the phytoplankton assemblage, with a new diatom-dominance (Beaugrand & Ibanez 2004). At the brink of the 2000s, the North Sea presented a new structure and strong management measures have been implemented, in particular fishing restrictions with the goal to recover the depleted fish populations and to bring the system back to its previous flourished, before-1980s, period (Cardinale et al. 2013). Was this new state characterized by forage fish and diatom reversible? We solve this enigma by investigating whether there was hysteresis or not in the system, since no previous studies attempted this.

Hysteresis is very difficult to detect since standard statistical methods are often limited to linear approaches that are unable to deal with non-linear and state-dependent phenomena like regime shifts (Litzow & Hunsicker 2016). However, empirical methods that are able to model and represent regime shifts were developed already in mathematics, and one such method is the stochastic cusp model (see box1) (Thom 1977). The model is part of catastrophe theory and was developed in the 1970s by the mathematician Rene Thom, and applied to a range of disciplines such as economics (Diks & Wang 2016), behavioral and psychological studies (Cramer et al. 2016), and fisheries science (Jones 1977; Möllmann et al. 2021; Petraitis & Dudgeon 2015; Sguotti et al. 2019, 2020). The stochastic cusp model, simplifying the system, is able to detect discontinuous dynamics of a state variable depending on the interactive effects of two drivers (Dakos & Kéfi 2022). Moreover, it also mathematically identifies the combination of levels of the two drivers in which the system is unstable and in which it is resilient and therefore where strong hysteresis exists.

We showed for the first time that the North Sea underwent a true, irreversible regime shift and that the community completely restructured after 2003. The regime shift was due to fishing pressure and climate change, two of the most important drivers of marine ecosystems in the Anthropocene (Emeis et al. 2015). Even though fishing pressure has been decreased significantly over time the regime shift could not be reversed. This is due to the interaction between fishing and climate change that creates hysteresis on the system. Nevertheless, the reduction of fishing pressure has probably helped the recovery of different demersal stocks which are now abundant in the ecosystem (Beukhof et al. 2019). Warming, creating high hysteresis in the relationship between the ecosystem and fishing, is impeding the transition of the system towards the previous state and is expecting to continue. Indeed, warming will likely be impossible to reverse due to the limited mitigations that can decrease climate change, thus the new North Sea regime is likely irreversible (Fig. 4.3) (Heinze et al. 2021). Hence, our analysis provides the first evidence of irreversibility of an ecosystem regime shift in the North Sea and likely beyond, suggesting that in areas where regime shifts depend on fishing and warming, similar patterns could apply. It is important to note that hysteresis can be detected in the relationship between fishing and ecosystem and thus that the interaction between warming and fishing is hindering policies to recover the system.

Our analyses showed a new regime shift in the North Sea ecosystem in 2003. Inspecting comprehensively the evolution of the North Sea through time, it appears more as if a slow regime shift, from a state dominated by gadoids and copepods, to a new state dominated by new demersal species (saithe and plaice), different plankton communities and also pelagic species such as sprat, started at the end of the 1980s (Fig. 4.4) (Heinze et al. 2021; Hughes, Linares, et al. 2013a). Even though this transition is not strictly abrupt (in the sense it occurred relatively slowly, in few years), the model highlights how it followed discontinuous and non-linear dynamics depending on two interactive drivers, fishing and climate change (Fig. 4.3, 4.4). Thus, we can conclude that a regime shift occurred in the North Sea, affecting different elements of the trophic chain at different times, but eventually leading to a system reorganization, maintained by new feedbacks loop (Beukhof et al. 2019; Fauchald 2010).

More gradual regime shifts are typical of systems that present multiple scales (i.e. in space, but also trophic levels) and thus can present asynchronous responses to drivers, such as large marine ecosystems (Heinze et al. 2021; Hughes, Carpenter, et al. 2013; Hughes, Linares, et al. 2013b). Identifying this type of long and not abrupt regime shift is hard since their more gradual nature can let them go unnoticed (Hughes, Linares, et al. 2013b). However, from a management perspective they could also be easier to reverse since the window of opportunity of action is longer than the one of a sudden shift (Heinze et al. 2021; Hughes, Linares, et al. 2013b).

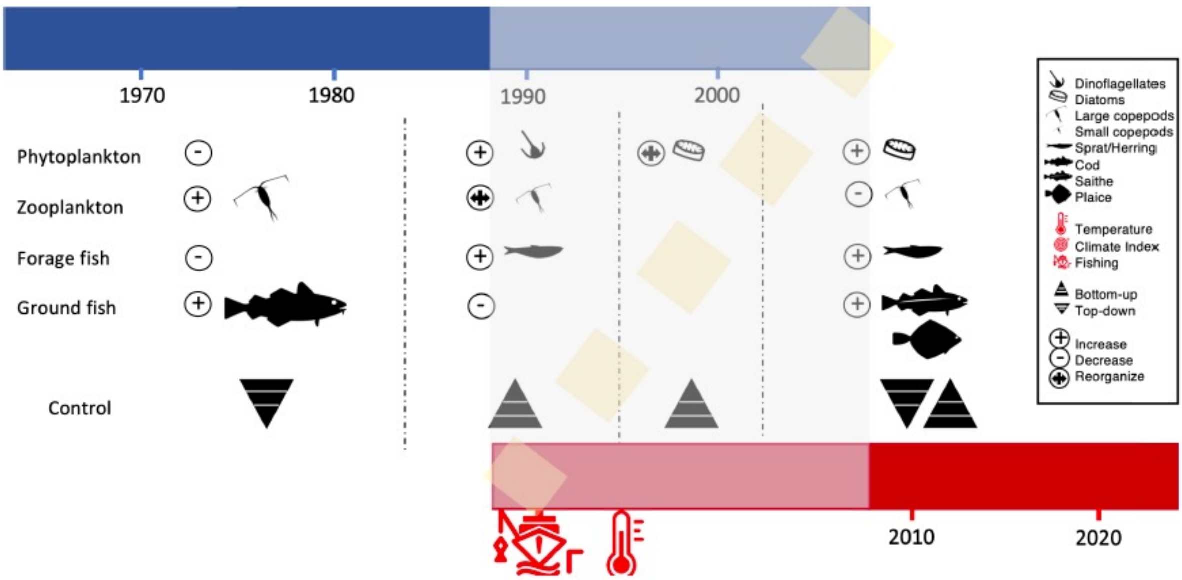


Figure 4.4. The North Sea regime shift. The 4 states of the North Sea community are indicated started from before the 1980s to after the 2003. In blue the first part of the time series which was stable and in red the new irreversible state of the system. The first 3 states are described in the literature, while the latter is for the first time detected in our comprehensive analyses. The two main drivers of the regime shift, fishing and climate change are indicated by the icons. The shaded area corresponds to the area of instability before a new stable state was reached, as indicated by our analysis. Icons in circles indicate whether a particular trophic level increased, declined or reorganized (in terms of relative species composition) in relation to a shift. Icons for organisms indicate regime-dominating species. Additionally, the food web control type (top-down or bottom-up) reported to be dominating during a specific regime is indicated.

In the case of the North Sea, the management applied was not sufficient to reverse the shift and the system was able to transit into a now irreversible state. Nevertheless, the reduction of fishing pressure has favored a healthier ecosystem in which some demersal species (even if different from the one of the 1980s) have been able to thrive. The new irreversible system offers different services compared to the previous system and favors different type of fisheries. Climate change and warming will continue, and, while we know that the system is irreversible, novel conditions could occur and the North Sea could continue to migrate towards completely novel and unexplored states (Ammar et al. 2021). Thus, adaptive management and a more flexible socio-economic sector, may help the human populations exploiting the North Sea to profit from the services the ecosystem provides (Biggs et al. 2012; Levin & Möllmann 2015; Selkoe et al. 2015).

5. Conclusions

Understanding if ecosystems can or tend to recover to historical states or rather develop into novel not yet anticipated configurations is crucially important to best adapt ecosystem-based management of these systems in the face of global climate change (Levin & Möllmann 2015). To do this, we need to extend our toolbox for empirically methods studying ecosystem regime shifts beyond change point analysis and linear correlative approaches, to whole ecosystem analysis that quantifies the stability of regime shifts and whether regime shifts can be reversed. Here, we combined multivariate analysis with stochastic cusp modeling, which allowed us to assess the interaction between climate and fishing in driving stable and potentially irreversible regimes in the North Sea ecosystem. This is one of a handful of promising new approaches such as Integrated Resilience Assessment (Vasilakopoulos et al. 2017), Early Warning Indicators of regime shifts (Scheffer et al. 2009) and Empirical Dynamic Modelling (EDM) (Ushio et al. 2018), which offer important and unique insights into ecosystem resilience, the drivers of ecosystem shifts, and the proximity of ecosystems to tipping points. While these tools are increasingly used in scientific studies, their application to management remains challenging. The stochastic cusp model can help management to understand the stability of the ecosystem under multiple drivers and thus to adjust policies to account for the stability of the system. Moreover, it could help identifying threshold in the effect of drivers that could induce tipping points favoring policies aiming at avoiding them. It is important to explore how to integrate this model and the others into management, to move a step forward towards a more resilient planet.

In conclusion, such an extended toolbox to empirically investigate regime shift dynamics will provide a more fundamental base for sustainably managing the ocean and the services it provides to humanity. Understanding whether a system can recover back to previous conditions or is resilient in the new state, is fundamental in a constantly changing world, to apply adaptive and efficient management measures that can sustain the livelihoods of the millions of people living in close contact with the sea (Selkoe et al. 2015).

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Supplementary Materials

Supplementary Text

Review protocol

<u>Search keys to collect papers about the topic</u>

<u>Web of Science</u>

“TS = ("tipping point" OR "regime shift*" OR "top-down" OR "bottom-up" OR "trophic cascade*") AND TS = ("North Sea") AND TS = ("complex dynamic system" OR "ecosystem" OR "natural system" OR "ecology" OR "economic" OR "socio ecological system")“

resulting in 202 papers.

<u>Science Direct</u>

“North Sea AND ("tipping point" OR "regime shift" OR "top-down" OR "bottom-up" OR "trophic cascade") AND ("complex dynamic system" OR "ecosystem" OR "natural system" OR "ecology" OR "economic" OR "socio ecological system")

resulting in 26 papers.

Adding all the papers and removing duplicates = 211 papers.
Of all these papers the first author has screened abstract and title to check for relevance. The relevant paper were in total = <u>118 papers, including papers describing regime shift and paper describing linear changes.</u>

<u>Information collected from the papers</u>

Paper
Name et al. date

Field

- Ecology → if it is mainly talking about ecological topics
- Economy → if it is talking about economy
- Interdisciplinary → if talks about both explicitly using a bio-economic model or just doing a review
- Sociology → if it has a social perspective

Basin

- North Sea
- multiple (if multiple basins)

Dynamics described

- Regime shift → if the word regime shift/tipping point is used.
- Change → if the paper describes dynamics without calling them regime shifts or tipping points (even if the description is of an abrupt systemic change but the term regime shift is never explicitly used).

If the paper did not talk about regime shift it was not considered relevant.

<u>Final number of relevant papers = 55 papers</u>

<u>Additional Information collected</u>

Dependent variable

The system analyzed. It can be the full ecosystem, one species, one trophic level, or multiple trophic levels.
If the full ecosystem is described → "full ecosystem"
If one species described → name of the species
If one trophic level described → name of the trophic level
If one group of organisms described (i.e. copepods) → name of the organisms or of the assemblage
If multiple trophic level described → "multiple"

If multiple regime shifts or changes are analyzed, for instance one in the 1980s and one in the 1990s, then use two rows to describe them separately. In this way we can look also at shifts and not just papers.

Year/period

Year or period of the shift (or regime shift if regime shift was mentioned). Again, if multiple period or regime shifts were mentioned in one paper they are separated.

Drivers of shift

Categories: "environment", "fishing", "eutrophication", "food-web", "management", "multiple".

Type of Control

Insert the type of control described as change in the system

- bottom up (from low trophic level to high trophic level)
- top down (from high trophic level to low)
- wasp waist (from the forage fish to high and low trophic levels)
- multiple → if multiple controls are discussed

Methods to detect shifts

- empirical
- theoretical
- descriptive
- review
- experimental
- field based

Detailed methods of shift

When the method was empirical the first author checked which methods was used

Hysteresis

Is hysteresis mentioned?

Hysteresis quantification

If yes, how is quantified?

Resilience mentioned

Is resilience mentioned?

Resilience quantification

If yes, how is it quantified?

Flags of RS (drop down menu)

Other flags of regime are described? (“multimodality” “bistability”)

Table S4.1 Summary of the main review results. The table show how many time a certain variable inside a category (i.e. Methods, Response Variable and System Control) appeared either out of the number of total shifts (N=72) or out of total papers (55).

	Variable	Number of regime shifts (total 72)	Number of papers (55)
Methods	Review	11	11
	Empirical	59	42
	Theoretical	2	2
Response variable	Multiple	25	23
	Phytoplankton	26	15
	Fish	4	4
	Economic	1	1
	Benthos	8	4
	Copepods	8	8
System Control	Bottom-up	56	40
	Top-down	5	4
	Multiple	9	11

Table S4.2. Summary of the statistical methods used to detect regime shift in the papers from the literature where statistical methods were used. The first column indicates the broad method category used to detect the shift. The methods are then specified in the second column together with the number of papers that applied them. In the last column the methods mostly used to detect correlation with drivers are indicated.

Methods shift	Detailed methods	Numbers	Methods drivers
Change Point	PCA + SMWB *+ CP ** clustering	21	gam
	Sliding correlation analysis		correlation analysis
	Multivariate SMWB		sliding correlation
	Niche		bayesian probabilistic classification
	Correlation		Models they used like AMOEBA or ECOSMO
	Changes in standard deviation		
	STARS***		
	wavelet		
	CUSUM****		
	differences between periods		
	stepwise change		
	Bcp*****		
Models	tgam *****	2	
	glm (not stat show shift)		
	Gaussian Linear state space model		
Early Warning Signals	Autocorrelation lag 1	1	

*SMWB = Sliding Moving Window Boundaries, **CP= Change Point Analysis *** STARS = Sequential t-test analysis of regime shifts **** CUSUM= Cumulative Sum ***** BCP= Bayesian Change Point Analysis ****** tgam = thresholds gam

Table S4.3. Index of variables used to represent the North Sea Community. The species or group of species is shown in the first column, followed by the species scientific name. In case of species grouping (i.e. plankton) the scientific name was left empty (/). The third column indicates the survey from which the data come from. The taxa of the species is indicated in the fourth column, to show the balance of the ecosystem. The last two columns show how the data were treated.

	Scientific name	**Survey**	**Taxa**	**Average**	**Time-span**
Phytoplankton Colour	/	Continuous Plankton Recorder	Phytoplankton	Annual	1985-2015
Dinoflagellates	/	Continuous Plankton Recorder	Phytoplankton	Annual	1985-2015
Diatoms	/	Continuous Plankton Recorder	Phytoplankton	Annual	1985-2015
Small copepods	/	Continuous Plankton Recorder	Zooplankton	Annual	1985-2015
Large copepods	/	Continuous Plankton Recorder	Zooplankton	Annual	1985-2015
Ammodytae	*Ammodytes sp.*	International Bottom Trawl Survey	Forage fish	Annual	1985-2015
Herring	*Clupea harengus*	International Bottom Trawl Survey	Forage fish	Annual	1985-2015
Sprat	*Sprattus sprattus*	International Bottom Trawl Survey	Forage fish	Annual	1985-2015
Norway Pout	*Trisopterus esmarchii*	International Bottom Trawl Survey	Forage fish	Annual	1985-2015
Cod	*Gadus morhua*	International Bottom Trawl Survey	Demersal fish	Annual	1985-2015
Haddock	*Melanogrammus aeglefinus*	International Bottom Trawl Survey	Demersal fish	Annual	1985-2015
Whiting	*Merlangius merlangus*	International Bottom Trawl Survey	Demersal fish	Annual	1985-2015
Saithe	*Pollachiuns vriens*	International Bottom Trawl Survey	Demersal fish	Annual	1985-2015
Plaice	*Pleuronectes platessa*	International Bottom Trawl Survey	Benthic fish	Annual	1985-2015
Sole	*Solea solea*	International Bottom Trawl Survey	Benthic fish	Annual	1985-2015

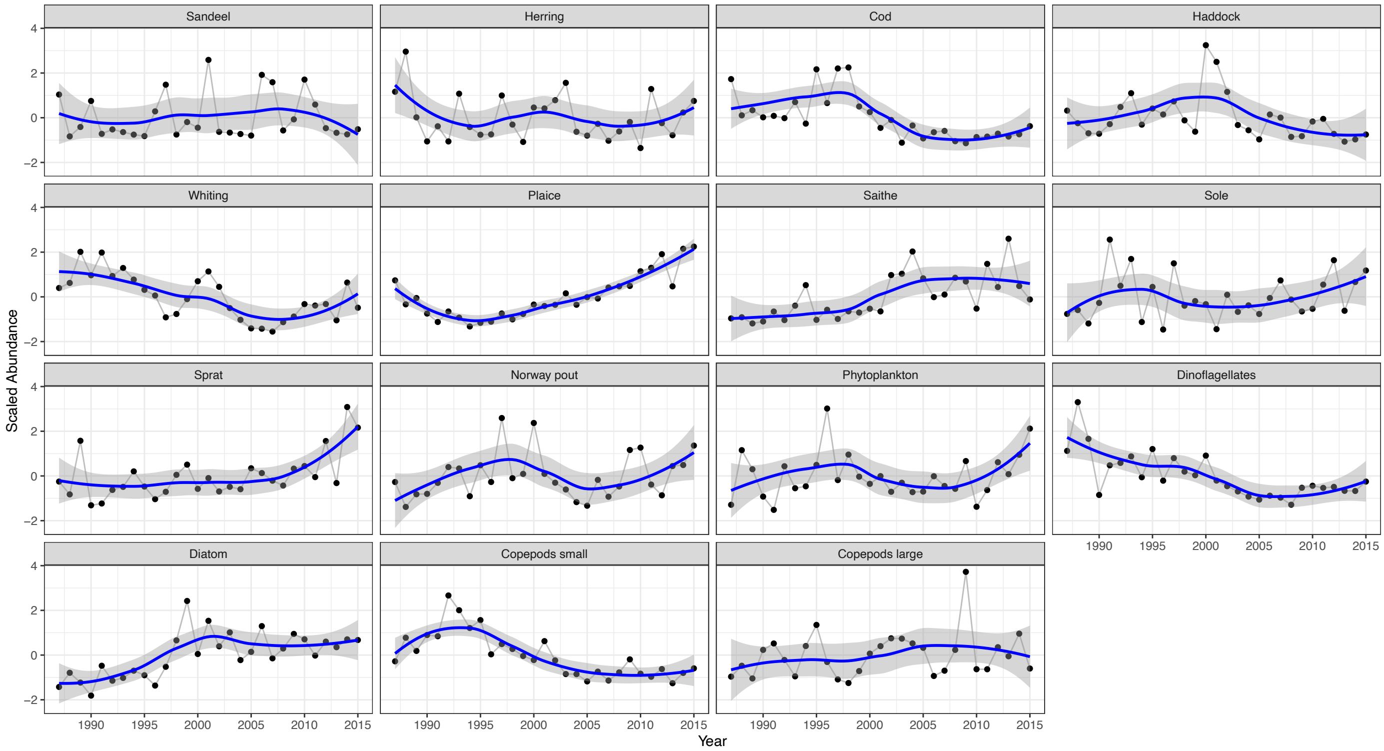

Figure S4.1. Time series of the scaled abundance (numbers or biomass) of the species used for the analyses. The blue line shows the smoothed trends of the time series, and the grey area represents the confidence intervals.

PRINCIPAL COMPONENT ANALYSIS

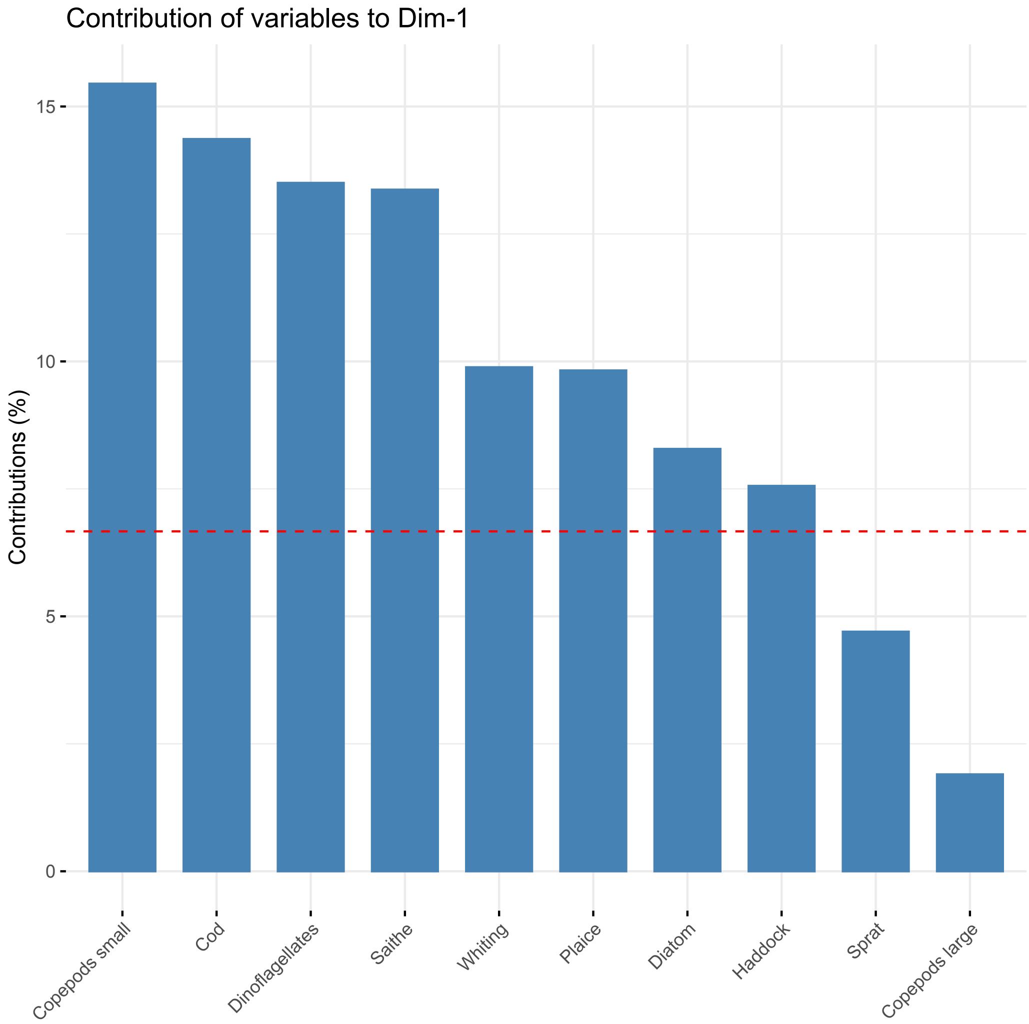

Figure S4.2. Percentage of contributions to the variation of PC1explained by the first most relevant 10 variables. The variables above the dotted red lines are significant in explaining variations in PC1.

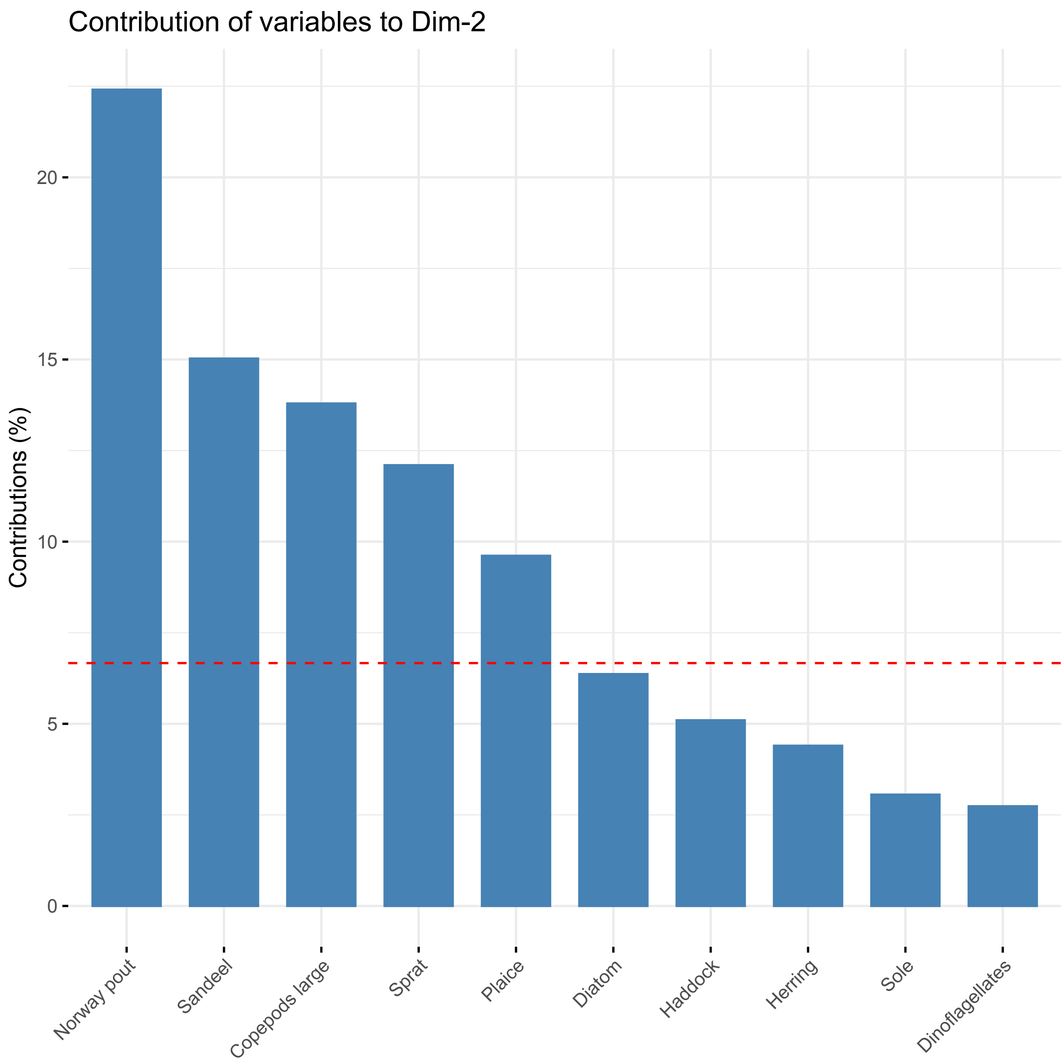

Figure S4.3. Percentage of contributions to the variation of PC2 explained by the first most relevant 10 variables. The variables above the dotted red lines are significant in explaining variations in PC1.

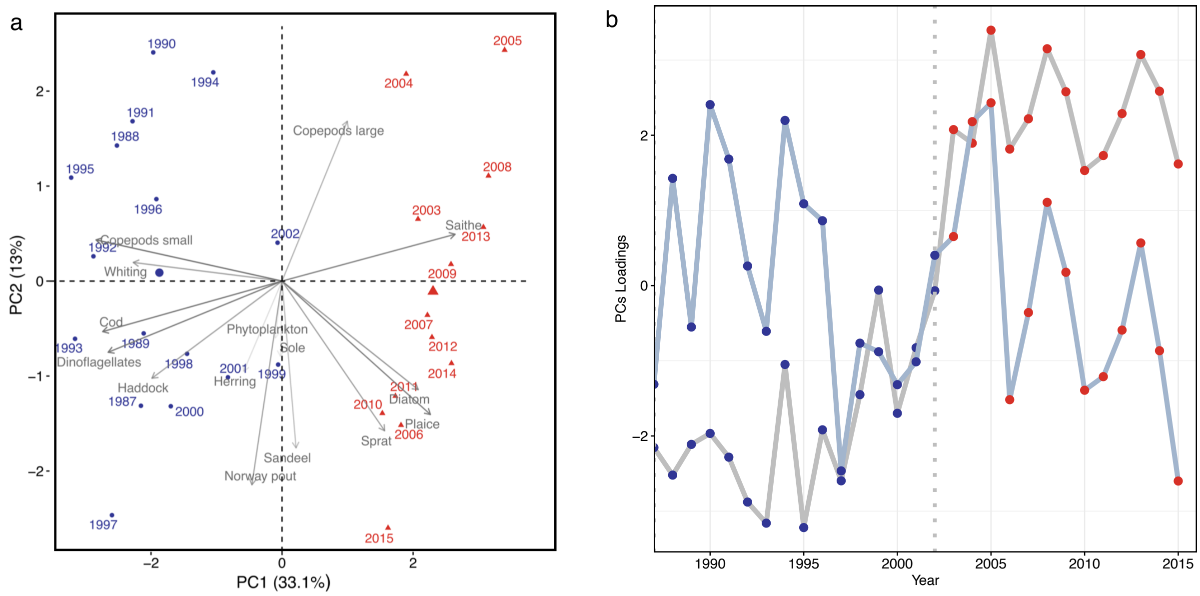

Figure S4.4. PCA Results. a, Biplot of principal components PC1 and PC2 (explained variance in brackets) associating the periods of the two ecosystem regimes to the species or taxonomic groups. **b**, PC1 (grey) and PC2 (blue) loadings against time. The dots represent the ecosystem regime. The dotted grey line indicates the abrupt change of PC1 in 2003.

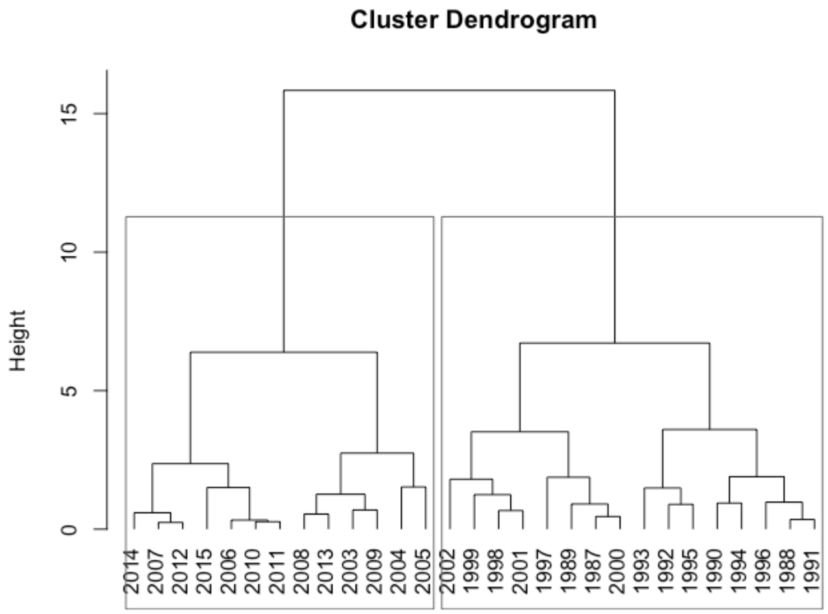

Figure S4.5. Cluster Analysis of the years in the PCA. Two clusters were identified following Ward´s algorithm. The distance between years was computed with Euclidean Distance based on the scores of the years on the PCA biplot.

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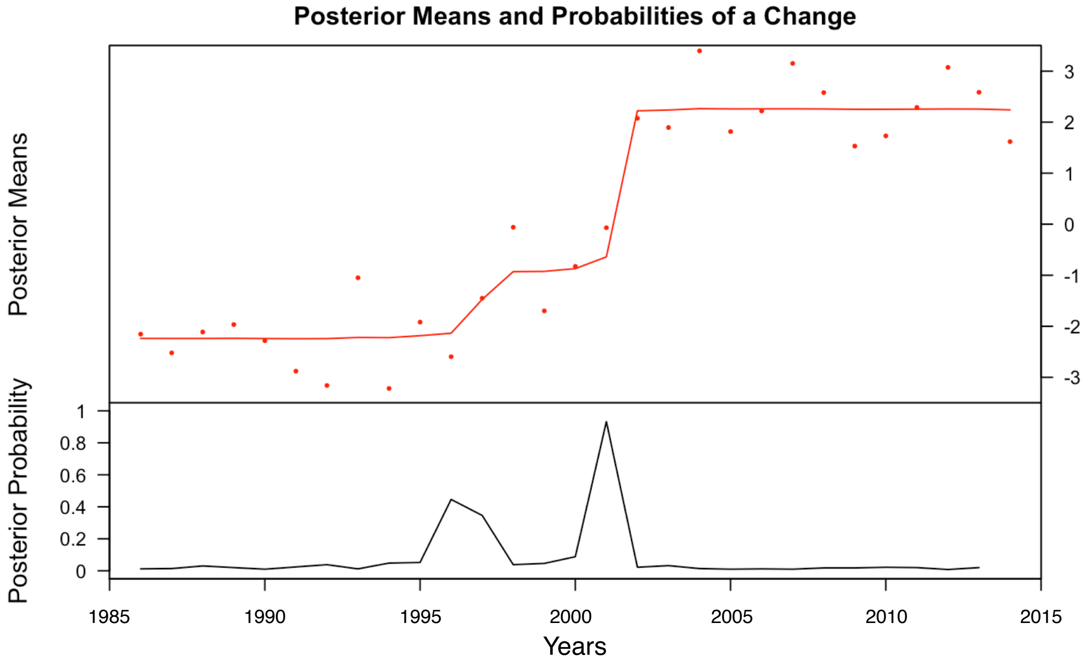

Figure S4.6. Results of the Bayesian Change Point Analysis performed on PC1 loadings. In the upper plot the Posterior Mean (red line) of the loadings against the real values (red dots) is shown. Above the probability of change at every time step of the time series. In general change points are identified when the probability of change is higher than 0.6 (60%), as in this case in the year 2003. The results of the Bayesian Change Point Analysis were validated also with a different algorithm from the Change Point package.

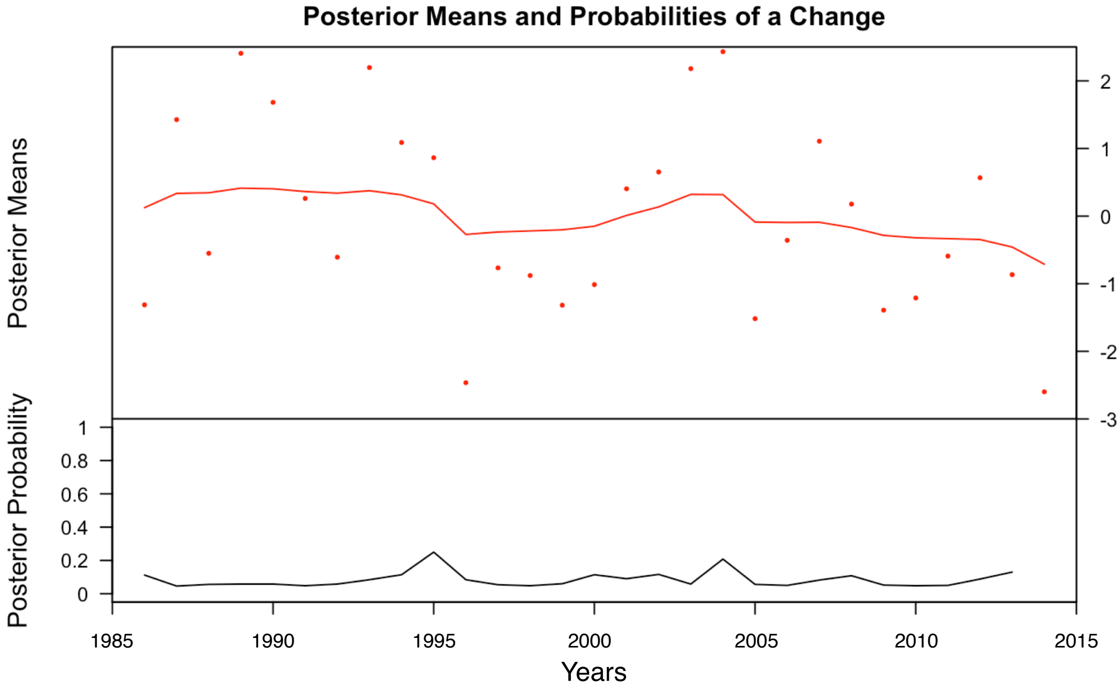

Figure S4.7. Results of the Bayesian Change Point Analysis performed on PC2 loadings. In the upper plot the Posterior Mean (red line) of the loadings against the real values (red dots) is shown. Above the Probability of change at every time step of the time series. In general change points are identified when the probability of change is higher than 0.6 (60%). In this case no change point was identified and the results were validated with a second algorithm from the Change Point package.

Table S4.4. Variables used to model community changes in the North Sea. The second column shows the sources from which the variables were collected. The third column shows what type of stressor is linked with the variable. The way the variables were treated and the time span are shown in the last two columns.

Explanatory variable	Data origin	Type of stressor	Average	Time-span
Atlantic Multidecadal Oscillation	NOAA	Global Climate	Annual	1985-2015
North Atlantic Oscillation	NOAA	Global Climate	December to March	1985-2015
Sea Surface Temperature	Nunoz-Riboni & Akimova 2015	Local Climate	Annual	1985-2015
Reconstructed Effort	Couce et al., 2019	Fishing Pressure	Annual	1985-2015

STOCHASTIC CUSP MODEL

Table S4.5. Results of the stochastic cusp model performed with the loadings of PC1 as state variable. The three columns show the model results for the three different climatic variables used as bifurcation variable. Alpha, beta and w are the intercept (0) or the slope (1) coefficient of respectively the asymmetry variable (effort), the bifurcation variable (one of the climatic variables) and the state variable (PC1 loadings). The AICc show the comparison of performance between the cusp model, a simple linear model and a logistic model. The modified R squared shows the model fit. The three further validation criteria to select the stochastic cusp model as the best, are shown in the last 3 rows. All the models passed the evaluation criteria (more than 10% points in the bifurcation area, a significant w1 and a high R squared).

	SST	**AMO**	**NAO**
α0	-0.02	0.01	-0.04
α1 (Effort)	-1.33**	-1.09**	-1.09**
β0	12.52**	2.05***	2.03***
β1	-1.05	-2.05	0.39
w0	-0.11	-0.08	-0.03
w1 (PC1)	0.66***	0.66***	0.67***
AICc_linear	110	106	110
AICc_logistic	105	101	105
AICc_cusp	46	49	49
Rsquared	0.88	0.85	0.84
Validation			
% points	41%	62%	65%
Significance Y	yes	yes	yes
Criteria passed	yes	yes	yes

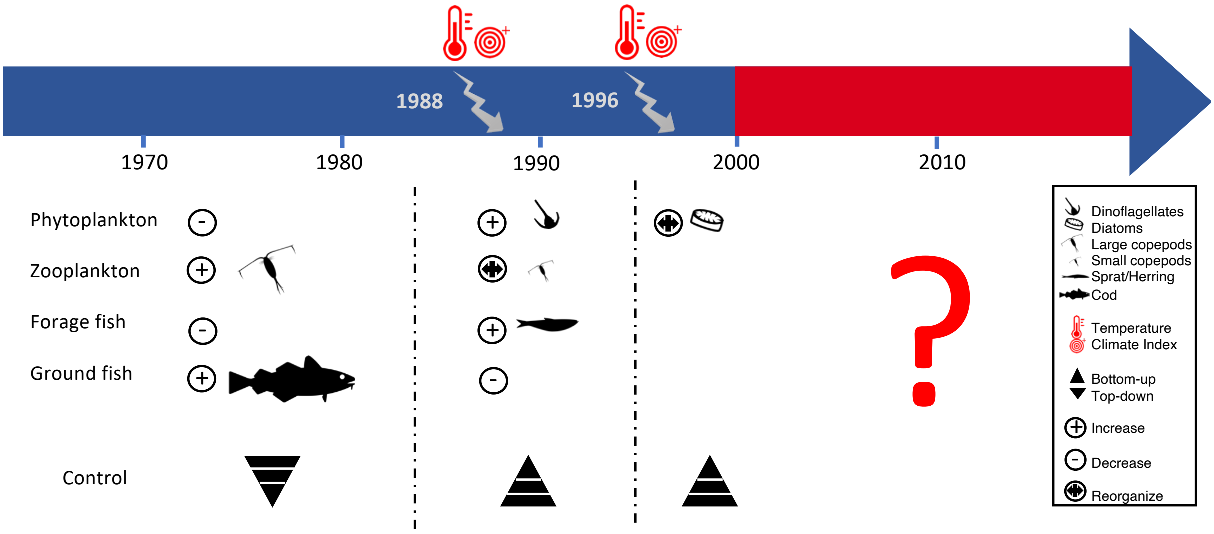

Figure S4.8. Summary of the North Sea regime shifts from the literature review. The schematic summarizes the regime shift reported in the literature (blue part of the timeline arrow). The reported years of the regime shifts are indicated by grey flashes. Red icons show dominant external drivers of the regime changes according to the literature. Icons in circles indicate whether a particular trophic level increased, declined or reorganized (in terms of relative species composition) in relation to a regime shift. Icons for organisms indicate regime-dominating species. Additionally, the food web control type (top-down or bottom-up) reported to be dominating during a specific regime is indicated. In red the part of the time series where the developments are still unclear.

3. DISCUSSION

Understanding how the regime shift concept is perceived, contextualized and framed by multiple stakeholders as well as how it is applied in ecology is crucial to i) identify the recovery potential of marine fish stocks, ii) determine the effectiveness of management measures, and iii) examine effects on the socio-ecological fisheries system. In this thesis, I studied differing conceptual perceptions of regime shifts among various stakeholders associated with North Sea cod (*Gadus morhua*) and regime shifts in their work (groups: management, fisheries, science, environmental NGOs), and identified regime shifts of the North Sea fish community under fishing pressure and climate change. To do so, I applied qualitative (e.g., semi-structured interviews) (Chapter I) and quantitative methods (e.g., change point analyses, stochastic cusp model) to identify respective tipping points and shifts implying discontinuous dynamics and hysteresis (Chapters II, III, IV). The knowledge about regime shifts in the North Sea and a common understanding of the regime shift concept among stakeholders support sustainable fisheries management preventing marine resource depletion.

Regime shift – an elusive concept

A concept is defined as “an idea or a principle that is connected with something abstract” (Oxford Learner’s Dictionaries 2022b), with ‘abstract’ meaning “based on general ideas and not on any particular real person, thing or situation” (Oxford Learner’s Dictionaries 2022a). A concept can be described as a “technique […] for making something understood, in other words for conceptualizing something so that it can be discussed” (Warder 1971: 184). This definition is halfway true for the regime shift concept, which describes an abrupt change from one system state to another due to drivers (Scheffer et al. 2001). Whereas at first sight, there seems to be a common understanding on the concept and its application to particular situations within the scientific context (Chapters II, III, IV) (Möllmann et al. 2015, 2021; Sguotti et al. 2019), it becomes rather elusive when looking closer at its perception among stakeholders and its application in science (Chapters I, IV). Nowadays, the regime shift concept is applied widely to real life situations in ecosystems, as for instance lakes switching from oligotrophic to eutrophic or woodlands changing to grasslands (Möllmann & Diekmann

2012; Scheffer et al. 2001; Stockholm Resilience Centre 2022). Also in the marine realm, the concept is increasingly used (Arif et al. 2022; Möllmann et al. 2021; Sguotti et al. 2019, 2020). Here, shifts are studied on different scales, ranging from single populations to communities, and even affecting several trophic levels (Alheit et al. 2005; Beaugrand et al. 2003). Also the species considered vary greatly, and can be either mobile or stationary, such as fish (Möllmann et al. 2021; Sguotti et al. 2019, 2020), plankton (Beaugrand 2004), or coral reefs (Arif et al. 2022). Given the diversity of biotic (e.g., species, communities, food webs) and abiotic (e.g., temperature, wind, pH) ecosystem aspects, several regime shifts can take place even within the same area at different times at different trophic levels. The North Sea, being a paradigmatic example for the study of regime shifts, experienced such shifts on the phytoplankton level in the 1980s (Beaugrand 2004; Beaugrand & Reid 2003; Lynam et al. 2017), on the fish level in the 1990s and 2010s (Chapters II, III) (Sguotti et al. 2019, 2020), and on the fish community level in the 2000s (Chapter IV).

A strong tool for understanding a concept in detail is to investigate *how* it is actually used in practice (Goguen 2005). The qualitative analysis of the conceptual framings revealed that the amount of details used to define the regime shift concept varies among stakeholders (Chapter I). Not only vary the types of knowledge in detail from non-knowledge, to general and detailed knowledge, but also timing aspects, the concept's application and drivers differ. In this way, a specific event like the gadoid outburst in the North Sea (1960s) can either be described as a regime shift or not, depending on individual perceptions of the concept. It shows from existing scientific literature that scientists develop individual definitions of regime shifts, thus making the concept applicable to their specific studies (Chapter I) (Mathias et al. 2020; Milkoreit et al. 2018; Möllmann et al. 2015). Also the application of the concept to real cases differs strongly among studies (Chapter IV), since there is no common agreement on the definition (Conversi et al. 2015; Steele 2004). Regime shifts are indicated by abrupt changes in a time series of a system (e.g., fish spawning stock biomass), but statistical methodologies to discover these changes are only used little (Chapter IV). Abrupt changes are rather shown using qualitative approaches or simply mentioned in review papers (Chapter IV). As for the different types of knowledges defined from the stakeholder interviews (Chapter I), the theoretical application reveals differences in the details of the concept. Only few studies consider the regime shift aspects hysteresis and irreversibility, and none focus in detail on potential stability of regimes (Chapter IV). If a system experiences hysteresis, reversibility of the system to a former state can be impossible. Both, hysteresis and irreversibility, are driven by feedback loops in the new regime which stabilize the new state (Beisner et al. 2003).

The elusiveness of the regime shift concept complicates its use in two ways: i) its *conceptual use*, and ii) its *scientific use* (Fig. 6, p.192).

i) *Conceptual use*

The application of a single concept, here the regime shift concept, which entails various aspects and framings, to diverse events complicates its use for communication. Stakeholders assume talking about the same issues, whereas in reality they do not (Fig. 6a, p.192) (Goguen 2005). People frame their perceptions based on differences in social norms, values, believes, knowledge, politics or education (Sterling et al. 2017). The believe of a common understanding and similarity might hide significant differences in values and patterns of use and might conceal the diverse thoughts about non-linearity (Goguen 2005; Milkoreit et al. 2018). A concept implies several properties, features and attributes (Gleitman et al. 1983). In this case for example, “a regime shift” is an ‘approach’, that implies ‘tipping points’, defines ‘discontinuous dynamics’, entails ‘hysteresis’ and ‘reversibility’, and describes a switch between ‘states’. These features can vary among stakeholders and cause severe misunderstandings between stakeholders, without them noticing it (Goguen 2005). Therefore, communicating results among scientists within the same discipline (disciplinary), but also across disciplines (interdisciplinary) and stakeholder groups (transdisciplinary) becomes difficult (Chapter I). If results are communicated for policy and management purposes, an agreement on a commonly shared understanding is essential. Hence, a multi-level management is required (Westley et al. 2011), where decision-makers know and understand a clear definition for regime shifts and for its related aspects. A better understanding of the regime shift concept can enhance communication and mutual respect for differences in perception. In this way, the acceptance of management measures among stakeholders and the success of management can be increased (Schwermer et al. 2021; Sterling et al. 2017).

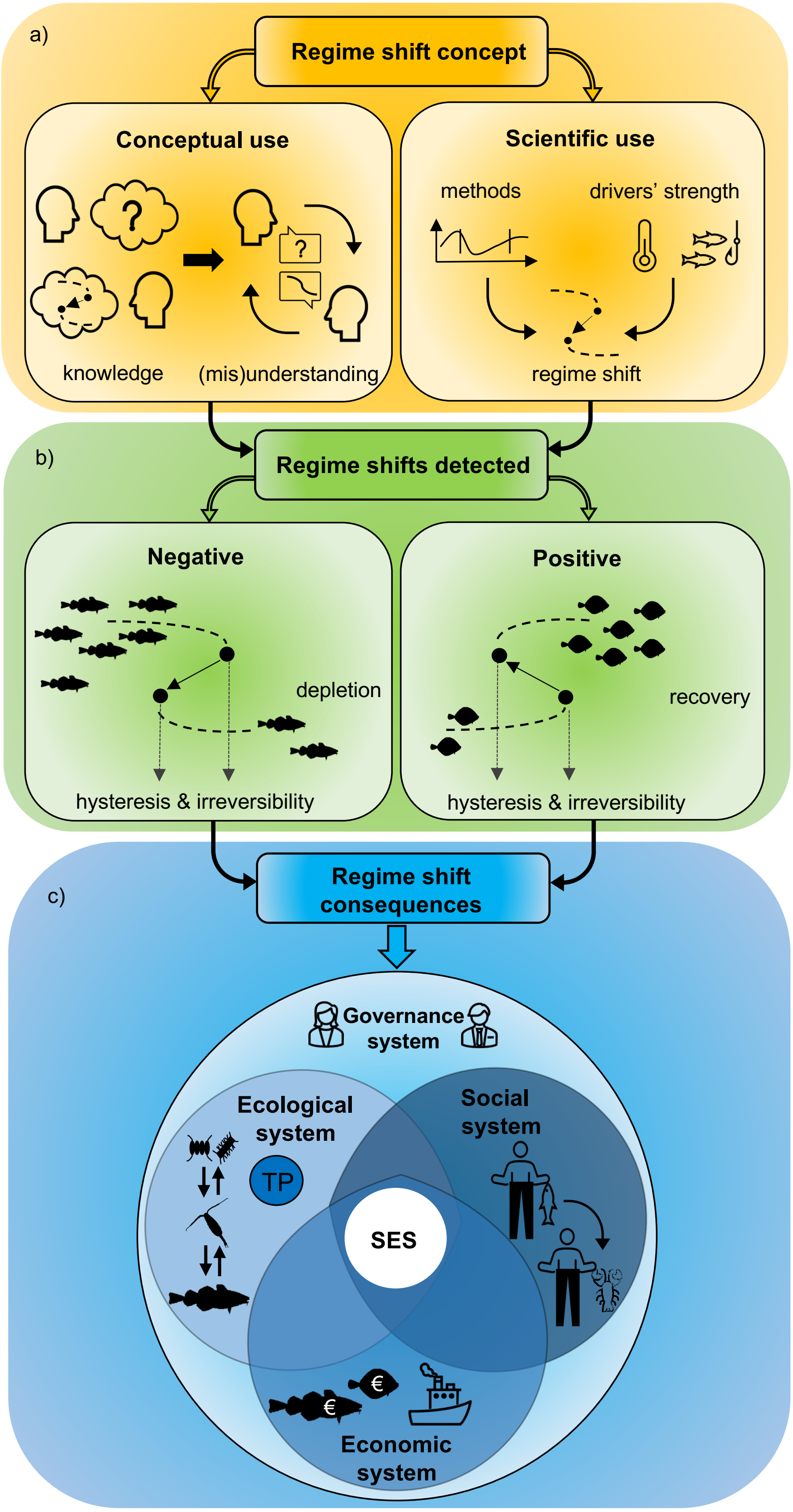

Figure 6. Schematic representation of a) the regime shift concept perception, b) regime shift detection and c) regime shift consequences. TP = Tipping point in ecological dimension, SES = socio-ecological system.

Not only the concept's details are understood differently by stakeholders, but also its application to real life events. Considering scientific literature (Sguotti et al. 2019, 2020), the North Sea cod experienced a regime shift implying hysteresis during the 1990s towards a depleted state due to overfishing and climate change (Chapter III). The qualitative interview analysis however shows that interviewees disagree on this event (Chapter I). On the one hand, interviewees from science and management identify the decline of the cod stock as a regime shift, taking the prestige high stock levels at the beginning of stock assessment data records (1963) as the reference state. On the other hand, two interviewees, one each from science and management, rather consider the gadoid outburst as the regime shift, stressing the strong increase in North Sea cod. The respective interviewees set the time before the outburst as the reference state and consider the decline as the return path of reaching former lower levels. Hence, based on the assumptions made for the reference state chosen, a system can depict regime shifts at different times with different outcomes (Scheffer et al. 2001).

ii) *Scientific use*

The regime shift concept is applied to diverse ecological contexts like different trophic levels within the ecosystem with distinct temporal and spatial aspects (Beaugrand 2004; Engelhard et al. 2011; Möllmann et al. 2021; Sguotti et al. 2019). There is no common framework of how to assess a regime shift quantitatively, wherefore methods vary strongly from simple abrupt change detection in a time series via change point analyses to the identification of hysteresis using the stochastic cusp model (Fig. 6a, p.192) (Chapters II, III, IV). These differences in assumptions about regime shift detection highlight, just as the interview analyses show (Chapter I), that scientists' opinions differ in the details of what a regime shift entails. Whereas for one scientist a change point analysis might detect a regime shift for a certain time frame, another scientist needs more details about the timing, the presence of discontinuous dynamics and herewith hysteresis and irreversibility (Chapters I, IV).

Another aspect of the scientific application is to look at the drivers included in quantitative regime shift detection methods. Not only whether drivers should be distinguished between internal (e.g., recruitment, changes in trophic levels) (Alheit et al. 2005; Beaugrand et al. 2003) and external dynamics (e.g., sea temperature increase, fishing), also the strength of drivers included should be considered (Chapters I, II, III, IV). Taking the North Sea cod as an example highlights the issue that several studies have identified various drivers such as climate-induced increases in sea temperatures, changes in lower trophic levels affecting the North Sea cod larvae, and fishing pressure causing the regime shift (Chapters II, III) (Alheit et al. 2005; Beaugrand et al. 2003; Sguotti et al. 2019, 2020). Scientific regime shift analyses however should not stop at the use of multiple drivers, because deeper insight is needed. Simultaneously occurring drivers shall be put into context to be evaluated for their weight; which driver has the strongest impact? In the cases of Atlantic cod stocks in the North Sea, Baltic Sea and Gulf of Maine, both, fishing pressure and climate change have caused the stocks to decline and remain at low levels (Brander 2018; Möllmann et al. 2021; Sguotti et al. 2019). However, exaggerating the impact of one driver over another driver can have consequences for the management and the system studied. Giving climate change the major weight causing the declines might, for instance, give reason to weaken the enforcement of sustainable fisheries management measures. Recovery plans or fishing pressure reductions to sustainable reference levels may become less relevant in protecting and enhancing recovery of fish stocks (Brander 2018).

The elusiveness and discrepancies of how to apply the regime shift concept conceptually in terms of communication and reference states, and scientifically in terms of methods and drivers show the fragility of the concept. Different versions of a concept can exist simultaneously, and discussions about which perception is appropriate and correct can arise. However, pushing a concept (e.g., regime shift concept) beyond its original intention can be problematic and demands the development of further concepts (e.g., tipping points, hysteresis, irreversibility) to sustain the first (Goguen 2005). One might discuss if the current state of the art of the regime shift concept is sufficient to consider it a mutually agreed concept. In contrast to the definition of a concept itself (Oxford Learner’s Dictionaries 2022b, 2022a), a concept applied to real life situations neglects its ‘abstract’ character and lays a foundation for discussion (Warder 1971).

The two faces of regime shifts – the good, the bad

William Shakespeare (1564-1616) once said “There is nothing either good or bad, but thinking makes it so.” A regime shift can have enormous consequences for the ecosystem (Alheit et al. 2005; Beaugrand 2004) and, across ecological boundaries, for the whole socio-ecological system (SES) (Ostrom 2007). If a shift is considered good or bad is, however, in the eye of the beholder. The two faces of a regime shift are distinguished in the concept’s tipping point aspect; the point at which a regime shift takes place and two distinct system states are separated (Sguotti & Cormon 2018). These tipping points can either be seen as i) *negative* or ii) *positive* (Fig. 6b, p.192) (Chapter II) (David Tàbara et al. 2018; Lenton 2020). A negative tipping point is seen as the switch to a undesired system state, causing degradations within the social and ecological systems. In contrast, a positive tipping point is seen as the transition to a desired system state, which initiates reinforcing improvements for the social and ecological systems (Marten 2005).

i) *Negative tipping points*

In scientific literature, regime shifts in marine ecosystems and their tipping points are mostly connotated *negatively* (Möllmann et al. 2021; Scheffer et al. 2001; Sguotti et al. 2019). This implies shifts from a positive, desired system state to a negative, undesired state (Marten 2005). The depletion of the North Sea and the Western Baltic cod stocks are major examples of negative tipping points (Fig. 6b, p.192) (Chapters II, III) (Möllmann et al. 2021; Sguotti et al. 2019), as well as the climate change induced coral bleaching (Arif et al. 2022). Also, regime shifts within communities (Chapter IV) and spatial shifts of species in the North Sea, such as the northward shift of cod (Engelhard et al. 2014) and the introduction of subtropical species from the south due to climate change (Baudron et al. 2020; Beare et al. 2004; Petitgas et al. 2012), can be perceived as negative changes. These examples of negative tipping points are often emphasized by the occurrence of the regime shifts aspects hysteresis and irreversibility (Chapters II, III, IV) (Scheffer et al. 2001). Both these aspects hinder the potential of reaching former levels of a desired system state, for example high levels of fish stocks or the preferred species composition for fisheries (Chapters II, III, IV). Irreversible regime shifts induce changes in established services, the system structure and functioning (Scheffer et al. 2009), and ask for adaptations in management (Chapter IV) (Carpenter et al. 1999).

ii) *Positive tipping points*

The research about p*ositive* tipping points is, in contrast to negative tipping points, still in its infancy and less promoted (David Tàbara et al. 2018; Lenton 2020; Lenton et al. 2022). In the urgent need for adapting a sustainable way of life through meeting climate goals and therefore reducing climate change impacts, the necessity for intentional abrupt changes towards a positive system state became apparent (David Tàbara et al. 2018; Lenton et al. 2022). Hence, positive tipping points are considered as a switch from an undesired to a desired system state with the aim of “greater sustainability” (Marten 2005: 77). Therefore, positive tipping points provide a floor of hope, where climate change and ecological urgency can be averted (Lenton et al. 2022). Positive tipping points find their application mainly in social sciences, and imply so-called positive social tipping dynamics in systems with social and technological components (Otto et al. 2020). They are also found in SESs, where a management measure is considered as a positive tipping point and herewith increases the sustainability of the ecological system (Lenton et al. 2022; Marten 2005). In this context, a positive tipping point is considered in the marine ecological system. It is represented by the implementation of a small marine sanctuary at Apo Island in the Philippines, leading to positive feedback loops and therefore to an ecosystem switch from an overfished area to a healthy marine ecosystem due to the spillover effect (Marten 2005). Even though the positive consequences (e.g., more fish) are within the ecological system, the tipping point is mentioned from a management point of view; the sanctuary implementation itself is rather seen as the tipping point, leading to increases in fish. In an ecological context, an example for a positive tipping point is the recovery of a fish stock, which can increase the ecological system’s sustainability (Fig. 6b, p.192). An example of such a positive tipping point in the marine realm is the recovery of the plaice (*Pleuronectes platessa*) and hake (*Merluccius merluccius*) stocks in the North Sea (Chapter II). Here, a fisheries management related decrease of fishing pressure induced positive feedbacks in the population. Despite the similarity of an increase in fish due to a management measure in both examples, the tipping point is seen from different points of view: in plaice and hake it is seen within the fish population system and, in contrast to the Apo Island example, not in the management system. Therefore, to enhance desired positive tipping points for marine ecosystems, a clear system understanding is required to determine accurate management measures. Critical features and variables of the system, e.g., fishing pressure, need to be identified and controlled (Lenton et al. 2022).

Even though a regime shift's tipping point can either be positive or negative, one cannot derive the good or bad from these results. Whether a regime shift outcome itself is considered good or bad requires more than only looking holistically at what happened. A detailed analysis at who (ecologically, socially, economically) is affected by the shift is required (Lenton et al. 2022). Taking Atlantic cod as a negative tipping point example, the depletion of Atlantic cod in the North Sea and Baltic Sea is negative due to the cod's high relevance as a top predator in the ecosystem from a scientific, biological point of view. Its loss has severe consequences in the food web (Frank et al. 2005). However, the loss of Atlantic cod in the Gulf on Maine can be considered positive from a social point of view: Atlantic cod in the Gulf of Maine preys on American lobster (*Homarus americanus*), wherefore the decline in cod led to higher abundance of lobster since 1985. Nowadays, the lobster fishery is the most valuable fishery in Canada and the United States, improving the social system (Marten 2005) by supporting fishers' livelihoods (Le Bris et al. 2018). Looking at North Sea plaice and hake as positive tipping point example, the increase of both stocks represents a shift to a desired state for fishermen (social system), who can increase catches. However, these shifts are spatially explicit events and therefore increase efforts in the management point of view demanding new implications for the fisheries (Chapter II) (Baudron & Fernandes 2015; Engelhard et al. 2011). Generally, sustainability for marine systems can only be obtained if the potential of tipping points towards a desired state is fully understood (Lenton et al. 2022). This involves stakeholder participation to cross scientific boundaries and to determine what is desired by whom and why. Local knowledge by, for instance, fishers can be incorporated (Schwermer et al. 2021) to analyze relations and feedback loops, as well as for data acquisition and modelling to predict possible tipping points and investigate their consequences (Lenton et al. 2022).

Consequences for the socio-ecological system (SES)

Consequences of regime shifts can cross the boundaries of the system experiencing the shift. A system is embedded within a SES, and a regime shift and its consequences can either propagate into the different components of the SES or occur in multiple components simultaneously (Lauerburg et al. 2020; Ostrom 2007). A SES consists of ecological, social and economic components, which in more detail can further be distinguished into system units (e.g. fish), system users (e.g. fishers), and the governance system (e.g. fisheries management) (Ostrom 2009). Even though these components can be analyzed and treated separately, they interact and produce feedback processes over different spatial and temporal scales (Ostrom 2007, 2009). Hence, the regime shifts identified in the North Sea, varying from recovered and depleted fish stocks to changes on community level, are of the propagating type and have consequences for each SES component (Chapters II, III, IV). Here, especially the loss of the Atlantic cod causes feedbacks for the *ecological*, *social*, and *economic* component (Fig. 6c, p.192).

i) *Ecological component*

The regime shift of the North Sea cod to depletion in the 1990s brings along strong effects for the ecological system (Chapters I, III) (Sguotti et al. 2019, 2020). Due to the interaction of bottom-up processes causing a prey mismatch (Beaugrand et al. 2003), top-down fishing effects, climate change induced increases in temperature (Sguotti et al. 2019) and internal non-stationarity stock dynamics implying low recruitment, the chances for recovery are limited (Chapter III). The loss of Atlantic cod as a top predator (Link & Sherwood 2019; Lynam et al. 2017) can result in ecosystem restructuring through trophic cascades (Frank et al. 2005). Alternative system states can appear and lead to new dominances within the assembled community (Möllmann & Diekmann 2012). On the Scotian Shelf of Canada, for example, overfishing caused the collapse of Atlantic cod in the 1990s and led to a switch from a cod dominated state to a forage fish and macroinvertebrate dominated state. Until now, this system has not reversed back to its initial state (Frank et al. 2011). In the Baltic Sea, the interaction of overfishing and hydrographic changes led to the decline of cod during the late 1980s, which caused a switch from a cod dominance to a sprat (*Sprattus sprattus*) dominance

(Möllmann et al. 2009). Indeed, the North Sea community experienced a similar phenomenon. The loss of North Sea cod resulted in an irreversible shift from a gadoid dominated state to a demersal (plaice and saithe (*Pollachius virens*)) dominated state in 2000 (Chapter IV). The removal of top predators can lead to trophic downgrading due to a strong top-down control of the stability of prey, hence reducing stability of lower trophic levels (Britten et al. 2014). Higher abundances of species with a greater variety in life histories occur at lower trophic levels (Britten et al. 2014) and the community structure is changed (Estes et al. 2011). In this way, a food web can contain a greater variety in species and become less homogeneous (Ellingsen et al. 2015, 2020), causing a fish community to be less stable, and therefore less resistant and resilient (Britten et al. 2014). The instability could be averted if the loss of North Sea cod opens a new niche for another top predator. In the Gulf of Maine, a similar situation is occurring between the depleted Atlantic cod and the Spiny dogfish (*Squalus acanthias*), which have overlapping niches (Morgan & Sulikowski 2015). The respective species can replace cod and therefore stabilize the system functioning and structure and, hence, the system's resilience.

ii) *Socio-economic components*

For the longest time, Atlantic cod has been an economically highly relevant species across the whole Atlantic Ocean, providing livelihoods through fishing and tourism and therefore a source for protein intake (Kurlansky 1997; Möllmann et al. 2021; Sguotti et al. 2019). The decline of Atlantic cod stocks had an enormous effect on the socio-economic system, especially on fishers that depended on this marine resource of high value (Kurlansky 1997). Given the decrease of catches in Newfoundland for example, thousands of fishers lost their jobs due to the abrupt collapse (Kurlansky 1997; Rice 2018). Fishers do not have a fixed monthly income and their salary depends on the amount of fish caught (Kube 2013). Therefore, quick adaptations to the loss of a target species are only manageable if savings are available. In the North Sea, the cod recovery plan was implemented to hinder further cod decline in the 1990s (ICES 2012, 2020). Fishers themselves showed a high participation in complying with the recovery plan and limiting cod catches. They decided to avoid fishing in areas with a high cod density. If too much cod was caught, fishers left these areas despite originally targeting a different species. Furthermore, fishers applied more selective gear types (technical decoupling) and fished below 200-300m to avoid the usual depth distribution of cod (spatial decoupling) (Kraak et al. 2013). Still, cod recovery was not successful and the stock remained depleted (Chapters II, III) (Sguotti et al. 2019). Fishers reported that the total allowable catches (TACs) were not sufficient and they had to discard cod larger than the minimum landing size. Hence, only avoiding areas where cod accumulated was not sufficient (Kraak et al. 2013). Regulating fisheries inappropriately can reduce their profitability and efficiency (Holt & Raicevich 2018). Hence, to avoid the loss of livelihoods, fishers should be included as agents to incorporate their knowledge in the development of management plans (Kraak et al. 2013; Schwermer et al. 2021). These plans should include the protection of both, fishers and fish, in the sense of social assets (Holt & Raicevich 2018; Nesbit 1943).

To deal appropriately with regime shifts and their consequences for the SES, a common understanding of processes and feedbacks within and between the SES components is required. This analysis requires the inter- and transdisciplinary cooperation of different disciplines (Sterk et al. 2017), which use different concepts and methods to describe SES complexity (Ostrom 2009). Therefore, a common framework to assess the sustainability of a SES should be applied including the division into the resource system, resource unit, users and governance system (Ostrom 2007, 2009). Breaking down the complexity of a SES to these sub-units and assigning attributes provides a mutual understanding of which interactions and outcomes take place on a temporal and spatial scale (Ostrom 2007; Sterk et al. 2017) The sustainable development of a SES is closely linked to the SES resilience (Sterk et al. 2017), and the SES affinity to tipping points and regime shifts; its so-called vulnerability (Lauerburg et al. 2020). To enhance a SES' resilience, the principles of involving the maintenance of biodiversity, management of connectivity and feedbacks, and supporting stakeholder engagement are only a few examples (Sterk et al. 2017; Sterling et al. 2017). The SES vulnerability can only be assessed by determining the vulnerability of each SES component (social, ecological, economic) (Lauerburg et al. 2020). So far, management advice and actions to support the SES vulnerability lack detailed guidance and instructions. They focus on general political support and on a stronger collaboration between agencies (Lauerburg et al. 2020).

The management of a SES, or even of only a single SES component, that experiences tipping points and regime shifts involves complex decision making. The North Sea cod example shows different approaches on EU level with the implementation of the Common Fisheries Policy (CFP) (EU 2013) or the cod recovery plan (ICES 2012, 2020), neither being successful for cod recovery (Chapters II, III). The lack of

i) common understandings and perceptions of definitions and concepts (Chapter I),
ii) including stakeholders in management plan decision making (Kraak et al. 2013; Schwermer et al. 2021),
iii) incorporation of non-linear regime shift dynamics in fisheries management (Chapters II, III, IV),
iv) detail in management measures (Lauerburg et al. 2020), and
v) understanding and determining the reversibility of drivers (Chapter IV)

complicate and hinder a successful implementation of management.

This thesis contributes to i) and ii) by stressing the necessity of a common definition of the regime shift concept to facilitate its application and clarify its consequences. It is expected that such a development can strongly benefit the mutually shared understanding between stakeholders to prevent miscommunication and, consequently, enable improvements in compliance, mutual recognition, and acceptance of management measures (Chapter I). Also, this thesis addresses iii) and iv) by showing that discontinuous regime shift dynamics can hinder a positive effect (i.e., a population increase) despite reducing fishing pressure (Chapters II, III). With regard to v), this thesis highlights the necessity for fully grasping the irreversibility of regime shifts in fish communities to adapt proper management approaches (Chapter IV). An adaptive governance approach, like ecosystem-based management, can target these issues. It combines management approaches and connects abruptly changing ecosystem dynamics with "individuals, networks, organizations, agencies, and institutions" (Westley et al. 2011: 769). Decision-making processes need to be transparent to sustain adaptive governance in times of social and ecological surprises (Schwermer et al. 2021; Westley et al. 2011).

4. CONCLUSION

The regime shift concept is widely applied in marine science, even though conceptually perceived differently among stakeholders. Regime shifts are found in socio-ecological systems, where they alter established relations and functioning. The North Sea, as a paradigmatic example, underwent regime shifts at different trophic levels, varying from phytoplankton to fish communities. These shifts caused changes not only in the ecological, but also in the socio-economic component of the North Sea.

In this thesis, the focus lies on stakeholders' perceptions of the regime shift concept, as well as on the regime shift detection in the North Sea fish community – highlighting Atlantic cod as a major example. My co-authors and I applied various methods such as a qualitative analysis via stakeholder interviews and quantitative modelling approaches to show how variable the knowledge around the regime shift concept is, and how regime shifts can cause different system state outcomes. We found that the regime shift concept is differently perceived and no strict definition exists, neither among stakeholders nor in the scientific methodological application. Resulting misunderstandings between stakeholders diminish fisheries management success (Chapter I). Also, we have shown that the success of the Common Fisheries Policy to achieve sustainable fish stock targets via fishing pressure reduction can be hindered by regime shift dynamics (Chapter II). Non-linear stock dynamics and low recruitment, in combination with hysteresis, changes in lower trophic levels and temperature increase maintain especially Atlantic cod at a depleted state (Chapter III). Nonetheless, recovery can be successful if species have stable stock dynamics and are not strongly affected by regime shift dynamics and temperatures (Chapter II). Furthermore, we showed that it is important to analyze a system's irreversibility to understand the recovery potential to former states (Chapter IV). An adaptive ecosystem-based management approach can incorporate regime shift dynamics in fisheries management, helping decision-makers to determine a system's stability. Knowing in which state a system is and under which drivers it might shift into a certain direction, allows for the right adjustments of policies. Including the knowledge and opinions of stakeholders in decision-making can enhance finding measures to promote positive tipping points to desired system states in the point of all stakeholders' view, supporting the whole socio-ecological system.

Still, to fully understand which implications a regime shift has for species, further research is needed to include regime shift effects on life history traits and to assess new spatial distributions. The significance of species distribution shifts and the introduction of new species into the North Sea from the south due to climate warming needs to be studied in more detail. Existing communities, fishers and the fisheries management will have to adapt. Hence, a detailed analysis of regime shift consequences for the SES is needed. To analyze the socio-economic consequences of the North Sea regime shifts in detail, more research is required to fully understand which adaptations (e.g. livelihood diversification) fishers, but also fisheries (e.g. fleets, gear), and fish markets (e.g. price competition) require to sustain themselves. Further social-cultural analyses can provide insight into stakeholders believes, values, and their background to fully grasp how they perceive a regime shift, how communication is taking place, and how their knowledge can be incorporated in sustainable management strategies.

The North Sea is increasingly impacted by anthropogenic use and climate change, resulting in ongoing transformations. The agreement on a definition of the regime shift concept and on its detection is crucial to define significant drivers to be controlled. Understanding the potential of fish recovery and new community compositions is key for sustainable adaptations within the SES. Successful fisheries management depends on common understanding among stakeholders, their engagement in decision-making processes, and the task for all stakeholders to define a common goal of how the North Sea SES should look like in the future.

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Presentations

Blöcker, A.M., Sguotti, C., Möllmann, C.. 2019. Abrupt collapses and resilience in North Sea cod stocks. ICYMARE 2019, 24-27 September 2019. Bremen, Germany

Blöcker, A.M., Sguotti, C., Möllmann, C.. 2021. Effects of Atlantic cod collapse on the vulnerability of the North Sea socio-ecological system". ICES Annual Science Conference 2021, 6-10 September 2021. Online (COVID-19 pandemic)

Blöcker, A.M., Gutte, H.M., Bender, R.L., Otto, S., Sguotti, C., Möllmann, C.. 2022. "The effect of fisheries management, internal dynamics and climate change on the recovery of North Sea fish stocks". ICES Annual Science Conference 2022, 19-22 September 2022. Dublin, Ireland

AUTHOR CONTRIBUTION

Chapter I Framing the Regime Shift Concept. An Epistemological Analysis of a Central Biological Notion in the Context of the North Sea Cod Crisis

All authors defined the research question. **AB** defined the study, wrote the interview guide, held all interviews. **AB**, HS, and MD analyzed and interpreted the data. **AB,** HS and MD prepared the original draft. CM reviewed and edited the manuscript. All authors reviewed and comment on the manuscript.

Chapter II Regime shift dynamics, tipping points and the success of fisheries management

All authors defined the study and the research question. **AB** and HG contributed equally to this work. **AB**, HG, RB, and SO performed the statistical analyses. **AB**, HG and RB prepared the figures. **AB** wrote the main manuscript. CS and CM contributed to the writing of the manuscript. All authors reviewed and comment on the manuscript.

Chapter III Discontinuous dynamics in North Sea cod (*Gadus morhua*) caused by ecosystem change

All authors defined the study and the research question. **AB** performed the statistical analyses and prepared the figures. **AB** wrote the main manuscript. CS and CM contributed to the writing of the manuscript. All authors interpreted the results.

Chapter IV Irreversibility of regime shifts in the North S**ea**

CS, CM defined the study and the research question. CS performed the statistical analyses. CS, CM, AS interpret the results and wrote the manuscript. CS, **AB**, LF, BB, RC, RD, JL HR, NS, VS perform the literature review and help writing the literature review results. All the authors comment on the manuscript.

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Signature

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EIDESSTATTLICHE VERSICHERUNG

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

Alexandra M. Blöcker

Hamburg, den 10.11.2022