North Atlantic cod recovery under climate change and exploitation pressure, a non-linear approach

Camilla Sguotti

Faculty of Mathematics, Informatics and Natural Sciences

Department of Biology, University of Hamburg

Institute for Marine Ecosystem and Fisheries Science

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Prof. Michele Casini, Swedish University of Agricultural Science

Prof. Myron Peck, University of Hamburg

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CONTENTS

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ABSTRACT

Deteriorated marine ecosystems are the results of the impact of a multitude of human pressures, such as fisheries exploitation and human-induced climate change, and have pushed the introduction of comprehensive policies to manage the resources. These policies are built on the ecosystem based management framework. Measures to recover depleted stocks in order to guarantee sustainable fisheries in the future and safe and productive fish populations have been introduced. However, after many years of management, many stocks such as Atlantic cod (*Gadus morhua)*, are still depleted and far from safe biological limits, suggesting the presence of complex stock dynamics, and posing doubts on their recovery potential.

Over my PhD, using data from 20 Atlantic cod stocks distributed all over the North Atlantic, I have evaluated the recovery potential of Atlantic cod stocks under climate change and exploitation pressure, and whether the recovery could be hindered by discontinuous dynamics. Applying a range of non-linear methods, I show that cod stocks present discontinuous and catastrophic dynamics hindering their recovery and resulting in lower productivity under climate change. Moreover, I uncover these dynamics not only in biomass but also in population processes such as recruitment.

I demonstrate that catastrophic transitions have occurred and that, most of the stocks present very low resilience and are currently in a low and unsafe biomass state far from historical levels. Temperature increase, a proxy for ecosystem changes, and unsustainable exploitation are the drivers of these shifts and therefore under climate change, the recovery of the stocks seems unlikely. Moreover, recruitment is highlighted as one of the fundamental processes to achieve a population rebounding, but it is also negatively (on average) influenced by climate change.

These results are fundamental from a management perspective because: i) they reveal non-linear discontinuous dynamics that are difficult to uncover but necessary to incorporate into management, ii) they highlight the role of climate change in limiting the productivity of Atlantic cod stocks, thus suggesting that new ecosystems structure might need to be expected in the future, and that recovery of the stocks might be unachievable in some areas, iii) they identify possible recovery mechanisms, thus giving the possibility to understand where the management action should be taken and what processes should be mainly managed and iv) they show how novel methods could be applied to Atlantic cod stocks management and also on other marine stocks (i.e. herring).

Thus, these results can help define new achievable stocks´ reference points considering changing ecosystems and especially climate change. The methods used here can improve future population predictions and can define stressors´ thresholds levels to avoid in order to guarantee resilient and healthy fish populations and thus sustainable fisheries in the future. Therefore, my thesis on Atlantic cod stocks recovery gives new perspectives and new starting points to develop a more efficient ecosystem based management in the face of discontinuous behaviours.

ZUSAMMENFASSUNG

Geschädigte Meeresökosysteme sind das Ergebnis einer Vielzahl anthropogener Belastungen, wie u.a. der Nutzung fischereilicher Ressourcen und dem vom Menschen verursachten Klimawandel. Zur Bewirtschaftung dieser Ressourcen wurde die Einführung umfassender Richtlinien, basierend auf dem ökosystemgestützten Managementansatz, stark vorangetrieben. Maßnahmen zur Wiederauffüllung erschöpfter Bestände wurden implementiert, um zukünftig eine nachhaltige Fischerei sowie sichere und produktive Fischbestände zu gewährleisten. Dennoch sind viele Bestände wie der Kabeljau (*Gadus morhua*) trotz jahrelangem Management immer noch erschöpft und weit entfernt von sicheren biologischen Grenzen. Dieses deutet auf eine komplexe Bestandsdynamik hin und stellt das Erholungspotenzial dieser Bestände in Frage.

Im Rahmen meiner Doktorarbeit nehme ich eine Bewertung des Erholungspotentials von Atlantik-Kabeljaubeständen unter dem Einfluss des Klimawandels sowie des Nutzungsdrucks vor. Ferner soll herausgefunden werden, ob eine Erholung der Bestände durch eine diskontinuierliche Dynamik behindert werden könnte. Um dieses Beurteilung vorzunehmen, verwende ich Daten von 20 Kabeljaubeständen, welche über den gesamten Nordatlantik verteilt sind. Mit einer Reihe nichtlinearer Methoden zeige ich, dass Kabeljaubestände unter dem Einfluss des Klimawandels eine diskontinuierliche und katastrophale Dynamik aufweisen, die u.a. ihre Erholung behindert und zu einer geringeren Produktivität führt. Darüber hinaus belege ich, dass diese Dynamiken nicht nur in der Biomasse, sondern auch in Populationsprozessen wie der Rekrutierung auftreten.

Ich zeige, dass katastrophale Übergänge bei nordatlantischen Kabeljau-Beständen stattgefunden haben. Zudem lege ich dar, dass eine Vielzahl dieser Bestände eine sehr geringe Widerstandsfähigkeit aufweist und sich derzeit in einem niedrigen sowie unsicheren Biomassezustand befindet, der weit vom historischen Niveau entfernt ist. Der Temperaturanstieg, welcher ein Indikator für Veränderungen von Ökosystemen darstellt, sowie eine nicht nachhaltige Bewirtschaftung sind die Treiber dieser Veränderungen. Daher ist die Erholung der Bestände angesichts des Klimawandels unwahrscheinlich. Darüber hinaus wird die Rekrutierung als einer der grundlegenden Prozesse für eine Erholung der Population hervorgehoben, ist jedoch auch (im Durchschnitt) negativ durch den Klimawandel beeinflusst.

Aus Sicht des Managements sind diese Ergebnisse von fundamentaler Bedeutung, weil: i) sie nichtlineare diskontinuierliche Dynamiken beleuchten, die schwer aufzudecken sind, jedoch in das Management integriert werden müssen, ii) sie die Rolle des Klimawandels bei der Begrenzung der Produktivität der Kabeljau-Bestände im Atlantik unterstreichen, was darauf hindeutet, dass in Zukunft möglicherweise neue Ökosystemstrukturen zu erwarten sind und dass eine Erholung der Bestände in einigen Gebieten möglicherweise nicht zu erreichen ist iii) sie mögliche Erholungsmechanismen darstellen und so die Möglichkeit bieten, zu verstehen, wo welche Managementmaßnahmen ergriffen werden müssen und welche Prozesse hauptsächlich gesteuert werden sollten und, iv) sie darlegen, wie neuartige Methoden auf die

Bewirtschaftung von atlantischem Kabeljau sowie auch auf andere marine Fischbestände (z. B. Hering) angewendet werden könnten.

In Bezug auf sich verändernde Ökosysteme und insbesondere den Klimawandel tragen diese Ergebnisse dazu bei neue Referenzpunkte für Bestände zu definieren. Zudem können die angewandten Methoden zu einer Verbesserung der Populationsvorhersagen führen sowie Schwellenwerte für Stressfaktoren festlegen, um somit eine resiliente und gesunde Fischpopulation zu erreichen. Eine nachhaltige Fischerei kann so zukünftig gewährleistet werden. Meine Thesis, die sich mit der Erholung der Kabeljau-Bestände im Nordatlantik befasst, könnte neue Perspektiven und Ansatzpunkte für die Entwicklung eines effizienteren ökosystemgestützten Managements, basierend auf diskontinuierlicher Verhaltensweisen, bieten.

"ἓν οἶδα ὅτι οὐδὲν οἶδα
I know I know nothing"
Socrate
                    Platone, Apology

PREFACE

"*The unexamined life is not worth living*" (Ὁ ἀνεξέταστος βίος οὐ βιωτὸς ἀνθρώπῳ, Plato, Apology) synthetizes how from ancient times humans have always tried to understand and explain the world that surrounds them. One of the language used by men kind, to try to put order in a world dominated by chaos, is Mathematics, with the application of models and equations. With Mathematics humans managed to explain the movement of planets, to understand the law governing the world and to explain ecological processes such as population dynamics. Today, our need to understand natural phenomena is linked especially with the necessity of using natural resources, such as forests, carbon, fish, and of maintaining them after centuries of over-exploitation. Among the fish resources there is one fish species, Atlantic cod (*Gadus morhua*), which can be defined as the species that changed the world. This fish shaped human migrations, cities, market routes, traditions, everywhere in the world, however at present it is hugely depleted and can mainly be found just in one area of the North Atlantic. Will this species manage to recover under global changes and in a non-linear world? My thesis will try to shed light into this important question, ecologically but also economically, culturally and socially relevant.

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*"Nothing in nature is random…a thing appears random
only through the incompleteness of our knowledge"*
Baruch Spinoza

INTRODUCTION

Cumulative pressures on a non-linear world

Anthropocene (Crutzen, 2002; Rockström *et al.*, 2009) defines the epoch starting at the end of the eighteenth century and lasted until now, when human activities started to deeply modify the geological and ecological cycles of the planet (Walther *et al.*, 2002; Steffen *et al.*, 2011; Zalasiewicz *et al.*, 2011). Indeed, with the offset of the industrial revolution, human population have constantly grown and with it, also the impact of human´s activities on the planet. The world human population is projected to reach quota 9.1 billion by 2050, with a consequent increasing need for food and energy sources (FAO, 2018a). This poses a huge challenge, since many resources, both non-renewable and renewable, are depleted. Indeed, even forests and marine resources which could theoretically be inexhaustible are at present overexploited, thus potentially jeopardizing global food security and livelihoods.

The oceans are among the most exploited and impacted systems. Multiple, cumulative stressors act on the different marine ecosystems, such as fishing activity, mineral extraction, pollution and climate change (Halpern *et al.*, 2008). At present 97.7% of the entire oceans are impacted by multiple, often synergistic stressors, and in the last 5 years the human impacts increased by 66% (Halpern *et al.*, 2015). Among the main stressors, overfishing and climate change are believed to be the most relevant and disruptive for the marine ecosystems and the marine species (Boonstra *et al.*, 2015; Halpern *et al.*, 2015). Marine species are fundamental to maintain not only from an ecological point of view, but also from a socio-economic side, as they represent a high proportion of human´s animal protein intake, and provide jobs through fishery and tourism (Thilsted *et al.*, 2014). However, synergistic human stressors, coupled with environmental variability put them at huge risk (Reynolds *et al.*, 2005; Khan & Neis, 2010).

Fishing is one of the biggest threats endangering marine ecosystems and populations directly or indirectly (i.e. habitat loss) (Jennings M.J. Kaiser *et al.*, 1998; Mullon *et al.*, 2005; Reynolds *et al.*, 2005; Anderson *et al.*, 2008; Halpern *et al.*, 2015). Fishing pressure on marine ecosystems increased steadily until the industrial revolution when an historic change happened (Jackson *et al.*, 2001). New boats, new fishing gears, new conservation methods allowed the expansion of fishing activity far outside national borders thus allowing the exploitation of almost all the marine stocks (Engelhard, 2009). Moreover, more efficient propulsion and detection systems lead quickly to the overexploitation of lots of marine resources and their subsequent collapses (Hutchings, 2000; Myers & Worm, 2003; Reynolds *et al.*, 2005). At present, 33% of all the

world marine stocks is overexploited, a trend steadily increasing over the last decades, while 60% of the stocks is exploited at the maximum sustainable levels. Just 7% of the stocks, compared to 40% in the 1975, is currently under-fished, indicating the profound expansion of fishing in the last decades (FAO, 2018b). Indeed, between 2012 and 2016, industrial fishing took place in more than 55% of the oceans area (Amoroso *et al.*, 2018; Kroodsma *et al.*, 2018a, 2018b).

Environmental drivers, such as climate variability or extreme events, can also strongly influence marine ecosystems (Lehodey *et al.*, 2006). In the last decades, anthropogenic climate change, and in particular warming and ocean acidification, hugely harmed the marine environment and the human communities using it (Boyd *et al.*, 2014; O'Leary *et al.*, 2017; Sainsbury *et al.*, 2018). These drivers can act on multiple levels of the marine ecosystems, from primary producers to top predators, directly (through physiological processes) or indirectly (Brander, 2010; Cheung *et al.*, 2010; Pörtner & Peck, 2010). The consequences of climatic stressors on marine populations can be species movement, recruitment failure, growth changes, predator-prey mismatch and thus can reinforce and exacerbate the effect of overfishing on marine resources, facilitating their collapses (Perry *et al.*, 2005; Rijnsdorp, 2009; Casini *et al.*, 2010; Hoegh-Guldberg & Bruno, 2010).

Collapses of marine populations often came as huge surprises, and in some cases produced unexpected outcomes (Myers & Worm, 2003, 2005; Pinsky *et al.*, 2011; Filbee-Dexter *et al.*, 2017). A text book example is the depletion of top predators, such as sharks, tunas, groundfishes, in many marine ecosystems (Myers & Worm, 2003; Frank *et al.*, 2005; Casini *et al.*, 2008a), which often has been attributed to a combination of unsustainable fishing pressure and unfavourable environmental conditions (Scheffer *et al.*, 2005; Perry *et al.*, 2010; Planque *et al.*, 2010; Frank *et al.*, 2016). In some areas, after the collapses and the consequent decrease of fishing pressure to low sustainable levels to allow the stocks of large predators to rebound, the stocks surprisingly did not show any sign of recovery. On the contrary, in some cases, the entire ecosystem completely changed its configuration (i.e. trophic cascade) hindering the increase of the top predators (Daskalov *et al.*, 2007; Casini *et al.*, 2008a; Estes *et al.*, 2011; Pershing *et al.*, 2015a). Similar examples of surprising outcomes can be described for coral reefs, kelp forests and a multitude of marine ecosystems (Steneck *et al.*, 2002, 2013; Mumby, 2009; Ling *et al.*, 2015).

These ecological surprises are characterized by the fact that they are induced by multiple cumulative factors, that they are often unpredictable and that they are usually very difficult, if not impossible, to revert (Doak *et al.*, 2008; Filbee-Dexter *et al.*, 2017). This kind of unexpected behaviours challenge the linear, predictable paradigm of natural sciences. Indeed, to explain the world and the laws and phenomena governing it, scientists had to create simplified models to overcome the world complexity. However, during the twentieth century, more and more scientific disciplines started to realize that natural patterns were often too complex and erratic to be explained with simple linear models and that most of the time nature was governed by chaotic and non-linear dynamics.

Bifurcation theory and non-linearity

Erratic behaviours tend to be the rule more than the exception in nature, nevertheless they were often discarded or addressed as random noise by scientists, due to the difficulties in analysing them (May & Oster, 1976; Hastings *et al.*, 1993). During the twentieth century, scientists from different fields started to realize that these erratic dynamics of natural phenomena, such as climatic and weather fluctuations, geological coastline formations and ecological systems, needed to be described using different approaches (Lorenz, 1963; Mandelbrot, 1967; May, 1976a; Sugihara *et al.*, 1996). A scientific revolution started from physic and mathematic with the studies of Poincare on shapes and topology, which culminated in the creation of a new branch of mathematics, the bifurcation theory (Poincaré, 1890; Crawford, 1991). This theory recognizes multiple types of behaviour of dynamical systems such as chaotic dynamics and critical transitions (Andersen *et al.*, 2009).
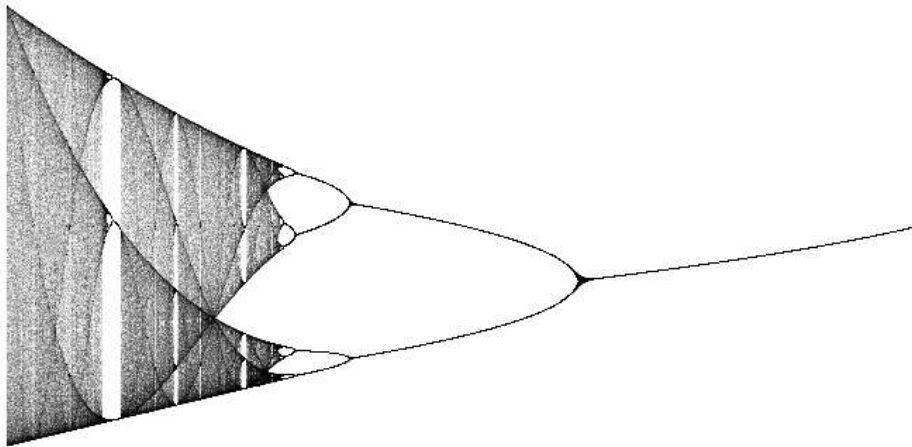

Figure 1: Systems dynamic with multiple equilibria formation. At the change of an external parameter the system can move towards very different states or equilibria.

Bifurcation theory is the study of changes in dynamical systems. A bifurcation occurs when a smooth change in a parameter leads to a sudden change in the system dynamics, thus moving the system away from an equilibrium point (Figure 1) (May, 1976a; Crawford, 1991; Beisner *et al.*, 2003). The theory, at the beginning more qualitative than quantitative, facilitated the development of catastrophe theory, from the French mathematician Thom, and chaos theory from the pioneer work of Lorentz (Lorenz, 1963; May, 1976a; May & Oster, 1976; Thom, 1977). While catastrophe theory is fully rooted in the bifurcation theory and studies the behaviour of a system influenced by external factors and moving between multiple equilibria, chaos theory focuses more on systems extremely sensitive to initial conditions which can move apparently randomly or again between equilibria (May, 1976a; Thom, 1977). These concepts of perturbation and equilibria lead to the formulation of another fundamental principle: *resilience*. The concept of resilience was introduced by Holling (Holling, 1973) and can be defined as the ability of system to absorb disturbances and still maintain the same internal structure and configuration, thus staying at the equilibrium point also called "state" or "attractor" (Beisner *et al.*, 2003). Repetitive disturbance can erode the system resilience thus moving the system away from the attractor to a new state or to "random" dynamics, following catastrophe or chaos theory (May, 1972; Holling, 1973; O'Leary *et al.*, 2017). Different types of models have developed from these two theories which are extremely useful to describe non-

linear and discontinuous dynamics of natural systems (Thom, 1977; Sugihara, 1994; Sugihara *et al.*, 2012).

The Empirical Dynamic Modelling framework was developed by Sugihara and collaborators, starting from Lorentz chaos-theory (Packard *et al.*, 1980; May *et al.*, 2008; Ye *et al.*, 2015; Deyle *et al.*, 2016; McGowan *et al.*, 2017). It is a data-driven approach that studies systems extremely sensitive to initial conditions (i.e. butterfly effect) and controlled by multiple external drivers (Sugihara, 1994). The past dynamics of a system can be reconstructed in state-space through the creation of an attractor manifold (Figure 2) (Sugihara *et al.*, 2012; Giron-Nava *et al.*, 2017). Every point in the space will correspond to the state of the system in a specific time step (Sugihara *et al.*, 2012; Ye *et al.*, 2015; Deyle *et al.*, 2018). The apparent random and erratic behaviour of the system can thus be reconstructed and then used to project the future system trajectories based on state-dependent dynamics (Sugihara *et al.*, 2012; Ye *et al.*, 2015). This method has been used in different disciplines (Sugihara *et al.*, 1996) and has found applications also in marine ecological systems, predator-prey interactions and marine management (Anderson *et al.*, 2008; Ye *et al.*, 2015; Deyle *et al.*, 2016, 2018).
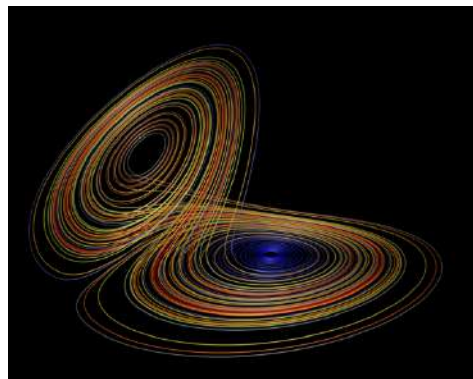
Figure 2: Reconstruction of a system dynamic in state-space. (source: www.medium.com)

The formulation of catastrophe theory and its mathematical approach (Zeeman, 1976; Thom, 1977; Arnol'd, 1992) was one of the first attempt to render the bifurcation theory more quantitative and more applicable to empirical data, and thus was acclaimed and quickly embraced by scientists in different fields (Figure 3) (Copes, 1970; Clark, 1976; Zahler & Sussmann, 1977). However, was soon also heavily criticized and its usefulness was questioned, due in particular to its earlier deterministic framework (Kolata, 1977; Sussmann & Zahler, 1978a, 1978b). Catastrophe theory studies systems undergoing abrupt transitions between multiple

Figure 3: Dali tribute to catastrophe theory, which he defined as "the most beautiful aesthetic theory in the world"

states and describes them through a differential equation that can have multiple solutions and thus can be at the equilibrium or not. It differentiates seven canonical forms, depending on the

number of parameters of the system, of which the FOLD and the CUSP catastrophe are the most commonly used (van der Maas *et al.*, 2003; Diks & Wang, 2016; Pe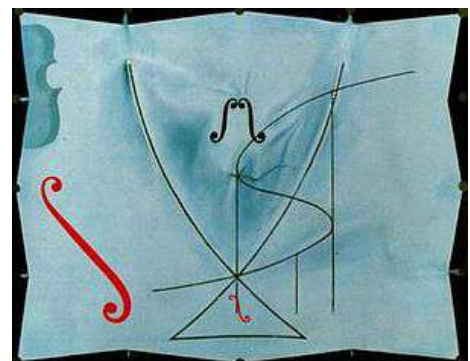traitis & Dudgeon, 2016). The FOLD describes the dynamic of a system influenced by one external parameter, while the CUSP describes the dynamic of the system influenced by two external parameters (Scheffer *et al.*, 2001; van der Maas *et al.*, 2003). Of these two, one determines the dimension of the system while the other determines whether the system follow a continuous or a discontinuous abrupt dynamic (Figure 4) (Grasman *et al.*, 2009; Diks & Wang, 2016). From this descriptive framework, the stochastic CUSP model took form. The model can explain in a stochastic way both linear and non-linear dynamics and thus can be really useful to apply to marine systems and populations. Although the stochastic CUSP model has been used a lot in a range of disciplines such as economics, social science and psychology (van der Maas *et al.*, 2003; Escartin *et al.*, 2013; Diks & Wang, 2016), its applications in ecology and the marine ecosystems are limited at an early stage, to model fishery dynamics and predator prey interactions (Jones & Walters, 1976; Jones, 1977). Afterwards the methods was "forgotten", due to the early deterministic framework, and replaced by a new theory, the regime shift theory (Scheffer *et al.*, 2001).
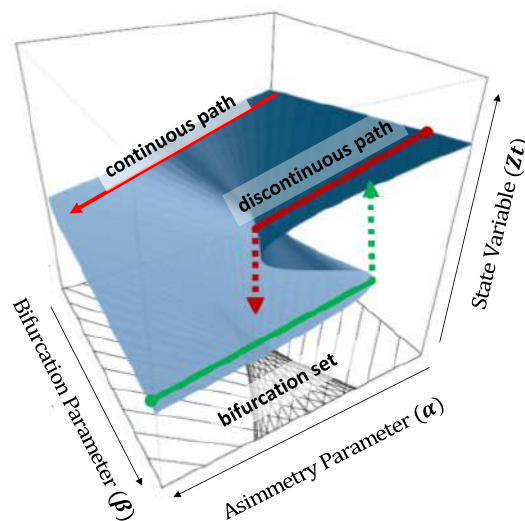
(Grasman et al., 2009)

Figure 4: Visual representation of the CUSP catastrophe theory. The State Variable (Z_t) is controlled by two control parameters, α and β. α controls the dimension of Z_t, thus whether it is in the upper or lower shield of the fold. β controls whether the state variable follows a continuous or discontinuous path. The fold is the so-called bifurcation set or instability area.

The regime shifts theory focuses on the FOLD catastrophe to explain the behaviour of a system depending on one external factor or condition (Scheffer *et al.*, 2001; Bestelmeyer *et al.*, 2011). The response of a system to the external driver can be classified in three ways: linear, non-linear but continuous, or folded-backwards, hence discontinuous (Figure5) (Scheffer *et al.*, 2001; Selkoe *et al.*, 2015). There are some disagreements about the meaning of regime shift, whether it just refers to the last type of behaviours (discontinuous) or to all the three. Here we use the term regime shift to indicate the dynamic of a system undergoing abrupt shifts and

showing discontinuous dynamics (see glossary, Chapter 1). In this case, the system presents two alternative states separated by one unstable equilibrium (Figure 5c) (Scheffer *et al.*, 2001; Andersen *et al.*, 2009). At the change of the external condition, the system, losing its resilience, crosses the threshold or tipping points and moves to the new attractor or stable state (Beisner *et al.*, 2003; Bestelmeyer *et al.*, 2011). Once in the new state, it has a new configuration and it is maintained by new feedback mechanisms. Therefore, the system is resilient and persistent in this new state, characteristic called hysteresis (Beisner *et al.*, 2003; Vasilakopoulos & Marshall, 2015; Folke, 2016). Hysteresis is very important to consider since it means that, even if the external condition goes back to its original level , the system would not be able to return to its previous state (Chapter 1 (Beisner *et al.*, 2003)). Hysteresis can have large repercussion for ecosystems and for the management of the natural resources (Levin & Möllmann, 2015).
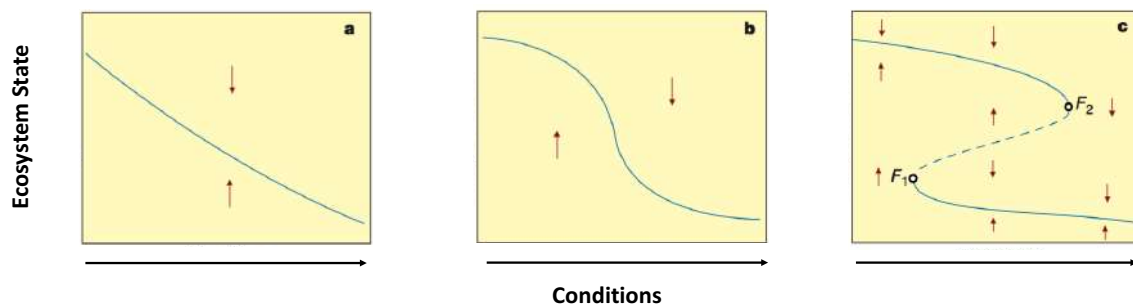

Figure 5: The range of responses of a system to external conditions, from Scheffer et al., 2001. a) a linear and continuous response. b) a non-linear but still continuous response. c) a typical folded-backward discontinuous response. Here two stable states are present. At the increase of the external condition the system will abruptly switch from one state to the other. When the condition will go back to its previous state, the system will not be able to return back (i.e. hysteresis).

The methods available to analyse regime shifts in empirical data are rather limited (Andersen *et al.*, 2009) and in particular are based on the analysis of the changes of the statistical properties of time series, such as mean and variance (Kéfi *et al.*, 2007; Dakos *et al.*, 2008, 2012, 2015). Among these for instance there are different types of change point analyses and early warning signals indicators. Additional analyses to understand single driver impact on the system are also available, like the integrated resilience assessment or the use of threshold generalized additive models which however might not explain the mechanisms of the driver's interaction (Bestelmeyer *et al.*, 2011; Vasilakopoulos & Marshall, 2015; Vasilakopoulos *et al.*, 2017). Thus, the empirical dynamic modelling and the stochastic CUSP models seem to be useful complementary analyses to understand the cumulative impacts of multiple drivers. Multiple regime shifts have been detected all over the world and especially in the marine realm, and effective methods are needed to fully understand them (deYoung *et al.*, 2008; Conversi *et al.*, 2015; Ling *et al.*, 2015).

Regime shifts are pervasive of complex systems influenced by multiple factors and in the marine realm can affect a population (Perretti *et al.*, 2015; Vasilakopoulos & Marshall,

2015a), a complete trophic level (Beaugrand *et al.*, 2002; Morse *et al.*, 2017) or even an entire large marine ecosystem (Hare & Mantua, 2000; Beaugrand, 2004; Casini *et al.*, 2008b, 2008a). Among the most famous examples there are transition of coral reefs to algal beds, of kelp forests to urchin barrens, and also trophic cascades, the passage from a predator-dominated system to a prey-dominated system, in many marine ecosystems (Mumby, 2009; Frank *et al.*, 2011; Steneck *et al.*, 2013; Graham *et al.*, 2015; Ling *et al.*, 2015). Detailed examples can be found in Chapter 1 of this thesis.

Regime shifts in the marine environment are particularly important because they can jeopardize the efficacy of the management measures and thus they can have important ecological but also socio-economic consequences, leading to failures in preserving the stocks (Blenckner *et al.*, 2015a, 2015b; King *et al.*, 2015; Levin & Möllmann, 2015; Rocha *et al.*, 2015). Indeed, these abrupt changes are usually very difficult to predict and sometimes they are not detectable even after decades from when they happened. Moreover, once the threshold is passed management intervention will fail to bring the system back to the desired state due to hysteresis (Beaugrand, 2004; Auber *et al.*, 2015). Therefore, more and more studies are trying to understand how to identify tipping points in advance and especially how to include these considerations into management, moving towards a more holistic management framework such as the ecosystem based management (see also Chapter 1) (Scheffer *et al.*, 2009; Lindegren *et al.*, 2012; Kefi *et al.*, 2013; King *et al.*, 2015). It is necessary to be able to identify these shifts and understand the cumulative effects of the multiple drivers acting on a system of interest, if we want to avoid unpleasant surprises. One example is the undesired outcomes, hugely debated in the literature, of the surprising collapse of all the Atlantic cod stocks (Hutchings & Myers, 1995; Frank *et al.*, 2016).

Atlantic cod

Figure 6: Atlantic cod (*Gadus morhua*)

Atlantic cod (*Gadus morhua*, Figure 6) is an iconic fish species from an ecological, economic but also social point of view (Myers *et al.*, 1997; Hutchings & Rangeley, 2011). The species comprises 22 assessed stocks distributed everywhere in the North Atlantic, from the east coast of USA and Canada, to the European waters (Figure 7). Cod is a demersal species, and a top predator of different marine ecosystems with a maximum length ranging from 81 to 167 cm (Wang *et al.*, 2014). This variation in life history traits depends on the vast range of latitudes in which the species can be found, presenting different environmental conditions, different trophic chain and thus leading to different patterns of genetic variation (Pörtner *et al.*, 2008; Wang *et al.*, 2014; Berg *et al.*, 2017). Nevertheless, some characteristics are typical from the species. Adult cod mainly preys on forage fishes and benthic animals and can be found until maximum

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600-meter depth, but generally around 200 meters in the continental shelf (Worm & Myers, 2003; Minto & Worm, 2012). Adults perform spawning aggregations; group spawning and homing towards spawning grounds have been recorded (Robichaud & Rose, 2001). The species has very high fecundity and one female can produce millions of eggs. The eggs and the larvae float in the upper layers of the water column, where they are transported by currents to feeding areas. They are influenced by multiple environmental drivers and can be predated by predators, often forage fishes (Walters & Kitchell, 2001; Beaugrand *et al.*, 2003; Brander & Mohn, 2004; Stige *et al.*, 2006). Cod larvae mainly prey on copepods and other plankton groups (Beaugrand *et al.*, 2003). Differences have been detected between northern and southern stocks but also between eastern and western ones, such as differences in thermal tolerance, life history traits, maturation, condition and also fisheries exploitation patterns (Rätz & Lloret, 2003; Pörtner *et al.*, 2008; Righton *et al.*, 2010; Köster *et al.*, 2013; Frank *et al.*, 2016). The latter lead to the collapse of the stocks across the North Atlantic (Myers *et al.*, 1997).

Atlantic Ocean

Figure 7: Map of the distribution of Atlantic cod over the North Atlantic. (Source: www.fao.org)

Atlantic cod fisheries trace back to the Medieval times, and after the 16th century a world market already existed for this species (Barrett *et al.*, 2008; Orton *et al.*, 2011). In European waters, the species became one of the most popular especially due to the easy way in which the meat could be preserved, either smoked or salted. Thus, it started to be exported everywhere, not only in northern Europe, where it was caught, but also in the south and the Mediterranean area. After the discoveries of America, new stocks were found in Canada and USA and this helped the

Figure 8: Example of the importance of cod in Canada.

colonization of these areas by European fishermen and the creation of a trans-oceanic and subsequently world market (Figure 8) (Kurlansky, 2009). Already in this period the stocks in both Europe and America were heavily exploited and, after the industrial revolution more and more pressure was exerted on them. The paucity of the European stocks, induced European fleets, in particular huge Spanish and Portuguese trawlers, to fish especially on Canadian stocks, while continuing to exploit what left in EU waters (Hutchings & Myers, 1995; Myers *et al.*, 1997). Around the mid-1960s, in Canada, the small-scale coastal fishermen noticed a decline of their catches. In the 1970s, the introduction of the Exclusive Economic Zone excluded European fleets from the fishery in USA and Canada (Hutchings & Myers, 1995; Myers *et al.*, 1997; Bundy, 2005). However, the fishing pressure was everywhere high and the populations started to be extremely vulnerable, thing that went unnoticed among scientists and large scale

fishermen. Around the 1980s-1990s almost synchronously the stocks collapsed, leading to one of the most unexpected and spectacular collapses of a fish species (Frank *et al.*, 2016).

All the Atlantic cod stocks, apart from the most northerly ones i.e. North-East Arctic and Iceland cod, collapsed or dramatically declined around the 1990s (Frank *et al.*, 2016). The reasons for the collapse are still debated, even though the main cause seems to be a combination of unsustainable fishing pressure and non-favourable environmental conditions (i.e. very cold waters especially in the Canadian areas) (Hutchings & Myers, 1995; Myers *et al.*, 1996, 1997; Bonanomi *et al.*, 2015; Frank *et al.*, 2016). The collapse was thus mainly driven by a decline of biomass and large fish, a high mortality of juvenile phases due to the colder temperature and a reproduction failure due to the selection of smaller adults in the population exerted by fisheries (Myers *et al.*, 1997; Brander, 2006; Kuparinen & Hutchings, 2012). These huge collapses lead to the complete closure of the fishery in Canada, and the establishment of strict quotas in the other areas, thus leading to important socio-economic repercussions (Gray *et al.*, 2008). The scientists and the managers were however confident that as the stocks collapsed quickly, they would have also recover relatively fast, if suitable management plans were set up.

Figure 9: Atlantic cod fished (picture by Heike Schwemer).

Recovery is difficult to define and can have multiple definitions depending on who is measuring it or why. In general, it can be defined as a return to a normal state, however the definition of "normal state" especially for ecosystems is difficult to give (Lotze *et al.*, 2011). This is mainly due to the fact that ecosystems were highly impacted by human activities since centuries and thus we do not know what is normal anymore (shifting baseline syndrome) (Pauly, 1995). Moreover, declines of some ecosystems parameters can completely change the ecosystem structure so that a recovery to the "normal state" would become impossible. Based on Lotze *et al.*, 2011, recovery can be defined as: a simple increase, an increase towards a specific target (such as MSY), an increase towards historical or pristine level (i.e. state before the collapse) or a recovery of structure and functions typical of the stocks (i.e. recruitment, growth). After more than 20 years of management measures, recovery of cod stocks towards their state before the collapse appears to be delayed. However, a comprehensive analysis of the recovery of Atlantic cod stocks has still to be done and should be done in the light of drivers and ecosystems changes.

After the collapse of the stocks, many features of the ecosystems and the socio-economic systems changed. The effects of climate change have become more and more severe and are particularly deleterious especially for cod in the lower distribution limit (Drinkwater, 2005; Stige *et al.*, 2006; Pörtner *et al.*, 2008; Pershing *et al.*, 2015b; Stiasny *et al.*, 2016). Temperature increase and ocean acidification can negatively affect recruitment and thus the entering of new adult in the population and growth directly but also indirectly through switch in predators and prey or mismatch (Beaugrand *et al.*, 2003; Swain & Benoit, 2015), hence potentially hindering recovery despite management measures in place. Changes in ecosystem structure and dominant species (i.e. trophic cascade) occurred in many ecosystems and could also play a role in hindering recovery of Atlantic cod stocks (Swain & Sinclair, 2000; Walters & Kitchell, 2001; Frank *et al.*, 2005; Estes *et al.*, 2011; Frank *et al.*, 2011; Swain & Mohn, 2012). Finally, the socio-economic systems relaying on these ecosystems also changed, introducing new management systems and switching to new resources exploitation, e.g. crustaceans (Shelton & Morgan, 2006; Steneck & Wahle, 2013). Thus, at present is still not clear whether Atlantic cod stocks will recover across the North Atlantic, which mechanisms are fundamental to favour the recovery and whether the recovery potential of the stocks is high or low.

MOTIVATION AND OUTLINE OF THE THESIS

This thesis aims to understand the recovery potential of Atlantic cod (*Gadus morhua*) under climate change and exploitation pressure. Two main questions were asked in this thesis:

1) **Do Atlantic cod stocks present non-linear dynamics hindering their recovery?**
2) **What is the recovery potential of the stocks under climate change?**

The motivation of this work takes root in the spectacular collapse of the majority of the 22 stocks of cod all over the North Atlantic and the subsequent delayed recovery. The reasons why recovery is failing in these stocks, even though the management measures in place are quite developed, is still controversial and is creating huge debate not only in the scientific community, but also among the stakeholders due to the impossibility of bringing the stocks back to high exploitable levels. Moreover, since the collapses happened quite abruptly and, in some cases were followed by ecosystems reorganization, non-linear and non-equilibrium dynamics might be the key to explain recovery of the stocks, but have rarely be considered.

In **Chapter 1,** my co-author and I **review non-linear, non-equilibrium dynamics (i.e. regime shifts) in the marine environment**, to understand how pervasive these phenomena are in marine ecosystems, why they are important from a socio-ecological point of view and the challenges of incorporating these concepts into management. We also briefly review the theory behind the regime shift concept and try to clarify some terms used throughout this manuscript.

In **Chapter 2**, after understanding how non-linear dynamics are pervasive of marine ecosystems, my co-authors and I investigate whether **Atlantic cod stocks recovery can be explained by discontinuous stocks dynamics**. Using stock assessment data from 19 cod stocks we firstly analyse stocks recovery 20 years after the collapses and the application of management measures. Subsequently we apply the stochastic CUSP model from catastrophe theory to understand if cod populations (i.e. biomass) follow catastrophic, discontinuous dynamics, which might be hindering the recovery. Moreover, we model the role of fishing pressure and climate change as drivers of cod populations to understand the stocks' recovery potential under climate change.

Chapter 2 was done at a stock level, thus in **Chapter 3** my co-authors and I move more into population mechanism level, investigating whether the **relationship between recruitment**

(number of fishes entering in the adult stock) and biomass in cod stocks is linear and continuous or transient, and if it can represent a mechanism of recovery. To do this we apply the wavelet decomposition and in particular the partial wavelet coherence to the recruitment and biomass of 17 cod stocks. The stock-recruitment relationship was analysed depending on stock status (e.g. healthy, collapsed, in hysteresis or recovering) in order to propose possible mechanisms of recovery for cod stocks.

Starting from the results of Chapter 3, in **Chapter 4** my co-authors and I then **evaluate the performance of different models in predicting cod stocks recruitment and the advantages of including environmental variables when predicting it.** These models could potentially be incorporated in management to account for non-linear dynamics in fish populations. We apply the standard continuous Ricker stock-recruitment model, the stochastic CUSP model and the empirical dynamic modelling framework to 20 cod stocks to reveal non-linear, state-dependent and catastrophic dynamics in cod stock-recruitment and to highlight the differences between stocks population dynamics.

Finally, in **Chapter 5**, we test whether **the stochastic CUSP model used for cod stocks could also be applied to other species presenting different life history traits**, like herring (*Clupea harengus*). Firstly, we analyse whether 15 herring stocks show linear or non-linear dynamics. Subsequently, we apply the model considering as drivers fishing pressure, climate change, but also cod, to unravel possible mechanisms of trophic cascade.

This thesis helps to better understand the recovery potential of Atlantic cod under climate change which is fundamental from a policy and also economic point of view. Moreover, it highlights how non-linear discontinuous dynamics need to be considered in management considerations and need to be investigated in fish populations, in order to apply efficient and effective management measures. Moving towards a comprehensive ecosystem based management it is necessary to unravel correctly stocks dynamics. Therefore, my study on Atlantic cod stocks recovery gives new perspectives and new starting points to develop a more efficient ecosystem based management in the face of discontinuous behaviours

"to speak of non-linear physics is like calling
zoology the study of non-elephant animals"

Stanislaw Ulam

STUDIES OF THIS THESIS

Fractals, going from broader to deeper

Chapter 1: Regime shifts in the marine environment

Regime shifts, a global challenge for the sustainable use of our marine resources

Camilla Sguotti[1], Xochitl Cormon[1]

Abstract

Over the last decades many marine systems have undergone drastic changes often resulting in new ecologically structured and sometimes economically less valuable states. In particular, the additive effects of anthropogenic stressors (e.g. fishing, climate change) seem to play a fundamental role in causing unexpected and sudden shifts between system states, generally termed regime shifts. Recently, many examples of regime shifts have been documented worldwide and their mechanisms and consequences have been vigorously discussed. Understanding causes and mechanisms of regime shifts is of great importance for the sustainable use of natural resources and their management, especially in marine ecosystems. Hence, we conducted a session entitled "Ecosystem dynamics in a changing world, regime shifts and resilience in marine communities" during the 8th YOUMARES conference (Kiel, 13-15th September 2017) to present regime shifts concepts and examples to a broad range of marine scientists (e.g. biologists and/or ecologists, physicists, climatologists, sociologists) and highlight their importance for the marine ecosystems worldwide.

In this chapter, we first provide examples of regime shifts which have occurred over the last decades in our oceans and discuss their potential implications for the sustainable use of marine resources; then we review regime shift theory and associated concepts. Finally, we review recent advances and future challenges to integrate regime shift theory into holistic marine ecosystem-based management approaches.

Author´s affiliations
[1]Institute for Marine Ecosystem and Fisheries Science, University of Hamburg, Germany

Introduction

Today, living marine resources represent a primary source of proteins for more than 2.6 billion people and support the livelihoods of about 11 percent of the world's population (FAO, 2014). Oceans worldwide concentrate dense and diversified human activities, e.g. fishing, tourism, shipping, offshore energy production, while experiencing a range of environmental pressures, e.g. increase of water temperature, acidification (Halpern *et al.*, 2008; Boyd *et al.*, 2014). Together anthropogenic and environmental pressures may threaten the integrity of marine systems and their sustainable use, altering their different components in many ways. These ecosystem changes may have great impacts for the social-ecological systems they are a part of, particularly when associated with changes in ecological keystone, cultural and/or commercial species (Garibaldi & Turner, 2004; Casini *et al.*, 2008b; Möllmann *et al.*, 2008; Llope *et al.*, 2011; Blenckner *et al.*, 2015b).

The World Summit on Sustainable Development in Johannesburg (2002) provided a legally binding framework to implement the Ecosystem Approach to Fisheries Management (EAFM). This holistic approach aims i) to conserve the structure, diversity and functioning of marine ecosystems and ii) to provide the economic benefits of a sustainable exploitation of marine ecosystems. Scientific activities supporting approaches such as the EAFM are hence highly encouraged (FAO, 2014). However, the insufficient knowledge on the diversity and entanglement of interactions between the ecological system components (deYoung *et al.*, 2008), as well as their vulnerability to increasing anthropogenic and environmental pressures, may hinder successful management.

Even if systems may react to stressors in a non-linear way shifting suddenly to a different state and losing important ecosystem services, management is indeed still more based on continuous dynamics (Scheffer *et al.*, 2001; Sugihara *et al.*, 2012; Glaser *et al.*, 2014; Travis *et al.*, 2014; Levin & Möllmann, 2015). Some ecosystems may be able to absorb stronger disturbances than others depending on their characteristics, but in general, marine ecosystems are known to be particularly vulnerable to drastic and unexpected shifts, referred in ecology as regime shifts (deYoung *et al.*, 2008). Because such non-linear dynamics may have serious and strong implications for the sustainable use of natural resources and their management, they should be taken into account and dealt with great precaution when taking environmental policy decisions (Holling, 1973; Carpenter, 2001; Scheffer *et al.*, 2009; Rocha *et al.*, 2014).

In this chapter, we first present some examples of marine ecosystems which have exhibited non-linear dynamics in response to external changes. These examples allow us to highlight different mechanisms potentially involved in regime shifts from an empirical point of view, as well as their potential implications for the sustainable use of marine resources. Secondly, we review the regime shift theory and associated concepts to finally consider recent advances and future challenges of integrating regime shift theory into holistic marine ecosystem-based management approaches.

Marine ecosystems regime shifts all over the world

Although the regime shift concept is still vigorously discussed, an increasing number of studies provide evidence for the potential of abrupt changes and surprises in marine ecosystems worldwide (Steneck *et al.*, 2002; Beaugrand, 2004; Mumby *et al.*, 2007; Möllmann *et al.*, 2008, 2009; Mumby, 2009; Bestelmeyer *et al.*, 2011; Frank *et al.*, 2011; Llope *et al.*, 2011 Auber *et al.*, 2015; Beaugrand *et al.*, 2015; Gårdmark *et al.*, 2015; Ling *et al.*, 2015; Vasilakopoulos & Marshall, 2015; Frank *et al.*, 2016). These studies, based on empirical observations, highlight mechanisms of regime shifts, firstly formulated by theoretical studies (Holling, 1973; May, 1977; Scheffer *et al.*, 2001).

The Atlantic cod trophic cascade

Surprises in natural systems are relatively common and can happen even in well-studied systems, due to different drivers. One driver of non-linear dynamics is the overfishing of top-predators. Top-predator overfishing may cause the depletion and collapse of their population resulting in unexpected ecosystem structure reorganisations through trophic cascades (Myers & Worm, 2005; Fauchald, 2010; Llope *et al.*, 2011; Möllmann & Diekmann, 2012; Steneck & Wahle, 2013). Atlantic cod (*Gadus morhua*) is an important top-predator fish species, which can regulate marine ecosystems through top-down control, and has supported entire human communities through fisheries for centuries (Haedrich *et al.*, 2000; Myers & Worm, 2005). After the industrial revolution and the increase of fishing power and capacity around the 1980's-90s, many cod stocks collapsed bringing high economic losses (Myers *et al.*, 1997; Frank *et al.*, 2016). Multiple analyses conducted in different basins such as in the Baltic Sea or in the Eastern Scotian Shelf, showed that the collapse of cod stocks was caused by a combination of increased fishing pressure and unfavourable climatic conditions (Frank *et al.*, 2005, 2016; Casini *et al.*, 2008a; Möllmann *et al.*, 2008, 2009). The high economic loss and social issues induced, led governments to adopt a range of management measures, such as drastic quota reductions and, in some cases, even fishing moratoria. Nevertheless, despite all the management measures and plans adopted, cod stocks failed to recover (Hutchings, 2000; Frank *et al.*, 2011; Hutchings & Rangeley, 2011).

One of the reasons advanced to explain these management failures is the undergoing non-linear dynamics known as trophic cascades (Casini *et al.*, 2008b; Star *et al.*, 2011). Indeed, the collapse of this top-predator resulted in a shift from a cod-dominated to a forage fishes-dominated system (Frank *et al.*, 2005; Gårdmark *et al.*, 2015). Before overfishing, adult cod biomass level was high and cod controlled forage fish populations through predation. This hindered the forage fish from negatively impacting younger cod (through predation and/or competition), thus enhancing its biologically sustainable biomass. However, when cod biomass became depleted, the consequently increased forage fish abundance caused a further decline of cod population by increasing their negative direct (predation) or indirect (competition) impacts on younger cod. This feedback loop is then very difficult to reverse (Walters & Kitchell, 2001; Möllmann *et al.*, 2009; Nyström *et al.*, 2012). Based on this example, it is clear how such systems can show two distinct configurations depending on their level of top-predator biomass. Of course, changes in mid-trophic levels will also reflect in lower ones, for instance high abundance of forage fishes will likely reduce plankton abundance. Under this new configuration with low cod biomass, a reduction in fishing pressure would likely lead to a very delayed or

even none cod recovery, since new mechanisms would keep its population in the new depleted state. To summarise, both Baltic Sea and Scotian Shelf regime shifts were caused by a combination of overfishing and climate variation, and characterized by a trophic cascade (top-down mechanism) due to the depletion of Atlantic cod stocks (Frank *et al.*, 2005; Casini *et al.*, 2008a; Llope *et al.*, 2011; Möllmann & Diekmann, 2012). This led to high social and economic losses on the short time and, subsequently, a fisheries reorganization in order to adapt to the new ecosystem configuration.

The North Sea regime shift
The North Sea regime shift involved different mechanisms that induced changes which started at the bottom of the trophic chain and propagated up to higher trophic levels (Reid *et al.*, 2001; Beaugrand, 2004; deYoung *et al.*, 2008; Conversi *et al.*, 2010; Lynam *et al.*, 2017). The North Sea regime shift occurred during the 1980s and was mainly induced by a combination of increased sea surface temperatures and changes in hydro-climatic forces (Beaugrand, 2004). Due to the increase of sea surface temperature and changes in the water inflows, phytoplankton biomass increased. As a consequence, the zooplankton assemblage, originally dominated by cold waters species, e.g. *Calanus finmarchicus*, shifted to an assemblage dominated by warmer water species, e.g. *Calanus helgolandicus* and gelatinous zooplankton such as jellyfish (Reid *et al.*, 2001; Beaugrand, 2004; Möllmann & Diekmann, 2012). These changes in the zooplankton community, combined with hydro-climatic changes, propagated to higher trophic levels. Changes in temperature and/or salinity led to an increase of flatfish biomass (Möllmann & Diekmann, 2012) while the decline of *C. finmarchicus,* which is the preferred prey of gadoids and especially of cod larvae, led to cod recruitment failures (Beaugrand *et al.*, 2003; Beaugrand, 2004) enhancing the negative sea warming effects. These changes in recruitment had a lagged impact on the adult gadoids biomass that, already stressed by overfishing, started to decline inexorably at the end of the 1980s (Hislop, 1996). The changes in fish biomass and composition, together with warmer temperatures, favoured the emergence of previously scarcely present species such as horse mackerel (*Trachurus trachurus*) and mackerel (*Scomber scombrus*), especially in the northern North Sea (Reid *et al.*, 2001; Beaugrand *et al.*, 2003; Beaugrand, 2004).

This regime shift, induced by bottom-up processes, was more qualitative than quantitative in the sense that changes in assemblage and not in total biomass of trophic levels occurred (Beaugrand, 2004). The dynamics of these changes highlighted different response time patterns depending on the organisms affected. Indeed, the phytoplankton and zooplankton communities, with their fast life cycles, responded to climatic changes faster than the fish community. Spatial patterns were also different: the coastal areas were less sensitive to change in hydrodynamic conditions, and the regime shift was stronger in the northern North Sea (Reid *et al.*, 2001; Beaugrand, 2004; Möllmann & Diekmann, 2012). This regime shift completely changed the structure of the North Sea fish community and led to the decline of various commercial species like cod, while the abundance of other species like flatfishes and mackerel increased, consequently having impacts on fisheries (Reid *et al.*, 2001).

Coral reefs and kelp forests transitions

Other examples of marine regime shifts are coral and kelps transitions (Rocha *et al.*, 2014). For instance, the Caribbean coral reefs were flourishing ecosystems providing many ecosystem services, sustaining large fish populations and associated human communities. The integrity of the reefs depended on the presence of sea urchins and grazing fishes, which, by eating the algae, maintained the coral reef structure. When the populations of grazing fish started to decrease due to overfishing, nothing seemed to change in the system. Indeed, sea urchins were still able to regulate algae population through predation, preserving the reef structure (Nyström, 2006; Standish *et al.*, 2014). However, the ability of the reef to absorb disturbances was already eroded by overfishing, when two concomitant and dramatic events occurred, leading to the total destruction of the reef (Mumby *et al.*, 2007). Sea-urchin populations quickly collapsed due to an illness outbreak, while more nutrients, discarded from the islands, were added to the system, causing rapid eutrophication. In a short time, coral reefs were substituted by algae beds which were not regulated by any top-down (sea urchin predation) or bottom-up (limitation of nutrients) processes. This algae-dominated system is now difficult to reverse due to the feedback mechanisms maintaining the system in its new status (i.e. the number of new algae growing every year can impede the reintroduction of corals, Mumby *et al.* 2007; Mumby 2009; Kates *et al.* 2012).

Similarly, kelp forests are highly diverse ecosystems which can maintain flourishing fish populations and offer many services for humans such as fisheries and cultural values (Steneck *et al.*, 2013; Ling *et al.*, 2015). Kelp forests are mainly maintained by fish predation on sea urchins, which controls sea urchin populations. In Australia, overharvesting of predatory fish, coupled with diseases weakening the kelp, led to a boom of the sea urchin population and a shift from high biodiversity kelp forest to poorer urchin's barren (Ling *et al.*, 2015). This state was then difficult to reverse due to various feedback mechanisms such as the increase of juvenile urchin abundance and facilitation of juvenile survival, but also because of the lack of efficient measures to recover the stocks of the sea urchin's predators (Ling *et al.*, 2015). In these two examples, the regime shifts were caused by multiple stressors which altered the regulation (top-down and/or bottom-up) of previously highly productive ecosystems and led to huge economic, social and ecological losses. Similarly to the Atlantic cod example, management measures failed to reverse these unexpected regime shifts due to feedback loop mechanisms (Steneck *et al.*, 2002; Ling *et al.*, 2015).

From examples to theory
From these four examples, several conclusions can be drawn. Stressors potentially inducing regime shifts may affect a system gradually, e.g. decline of top-predator due to fishing (Baltic Sea and Scotian Shelf regime shifts), or abrupt and exceptionally, e.g. disease outbreak (Caribbean coral reef destruction). The examples of the Atlantic cod stock collapse and the North Sea regime shift showed that climate change may play and important role in such mechanisms (Beaugrand, 2004; Conversi *et al.*, 2015; Yletyinen *et al.*, 2016). In addition, these examples showed the cumulative effects of different stressors and how they may act together in synergistic ways. The mechanisms and processes involved in regime shifts may be induced by top-down and/or bottom-up regulation (Holling, 1973; Beisner *et al.*, 2003a;

Conversi *et al.*, 2015a; Pershing *et al.*, 2015a). Finally, these examples highlight the importance and necessity to understand regime shifts mechanisms for a sustainable use of marine resources in order to provide ecosystem services and benefits for human communities (Doak *et al.*, 2008). Also, they uncovered some fundamental properties of regime shifts, e.g. the abruptness of changes and their lack or low reversibility (Scheffer *et al.*, 2001, 2015; Dakos *et al.*, 2012). However, due to the complexity and entanglement of the mechanisms involved, defining regime shifts based on empirical evidences is challenging. A review of the concepts associated with regime shifts, which are mostly theoretical (Levin & Möllmann, 2015), is essential to understand the non-linear mechanisms potentially involved in complex systems dynamics, particularly in a time of pronounced environmental changes.

The regime shift theory

Different mathematical frameworks lead to the development of the regime shift theory (Jones, 1975; Thom, 1975a; Jones, 1977; Crawford, 1991), describing how changes in some controlling factors can lead to huge and abrupt changes in various systems (e.g. biological, physical, behavioural; (Jones, 1975; Carpenter, 2001; Scheffer *et al.*, 2001)). Marine regime shifts can be defined as dramatic and abrupt changes in the system structure and function that are persistent in time, where the system can range from a single cell to a population or an ecosystem (Beisner *et al.*, 2003; Scheffer & Carpenter, 2003). Due to the high number of terminologies and definitions used in the literature, a glossary was added to this chapter in order to have consistent and clear definitions. All terms highlighted in italics in the following text can be found in the glossary section.
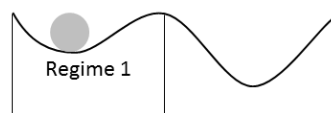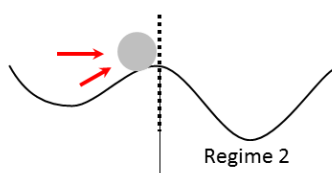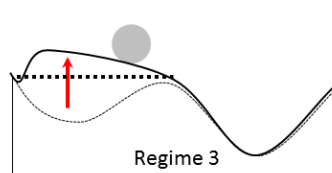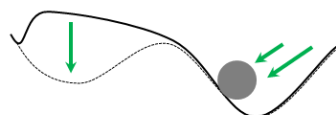
Figure 10.1 Regime shift theory represented by ball-in-cup diagrams (Crawford, 1991)**.** The ball represents the system and the cups (or valleys) the system states (see text for more information). The thick dotted lines represent the tipping points. The arrows represent disturbances, red for disturbances inducing a shift and green for reversed disturbances having no effects. (**a**) System in its original state. (**b**) Regime shift induced by changes in system state variables. (**c**) Regime shift induced by change in system parameter variables. (**d**) System in its new state showing hysteresis. Referring to our Caribbean example (Sect. 2.3) the light grey ball represents coral reef dominated system while the dark grey ball, the algae dominated system.

The easiest way to understand and visualize *regime shifts* is the example of the ball-in-cup or ball-in-valley (developed from the pioneer work of Poincare in the 1800's in Crawford 1991, Figure 1.1). The ball represents the study system, for instance the Caribbean coral reef. The system reef (our ball) has certain parameters such as coral abundance, coverage, and biodiversity. The system state is represented by the valley in which our ball (system) lies (regime 1 in Figure 1.1). The dimension of the valley (width and height in our two dimensions' figure) corresponds to the *resilience* of the system state. For instance, even when the Caribbean coral reef system was stressed by intensive fishing on grazing fishes, the system maintained its original state and did not shift because its resilience was high (i.e. the sea urchins were able to maintain top-down regulation on algae, Mumby *et al.,* 2007). Indeed, when the valley is large and deep, the ball/system remains in it, maintaining its structure, despite the disturbances. Repetitive disturbances such as overfishing and eutrophication did, however, reduce the system resilience (the valley became narrower and shallower) and when a strong disturbance occurred (here a disease outbreak), the system shifted abruptly to a new state (i.e. algae beds). This new state is now resilient, maintained by new *feedback mechanisms* that help its stabilisation, e.g. the higher survival of algae and the non-recovery of grazer fishes (Beisner *et al.*, 2003; Roe, 2009; Conversi *et al.*, 2015). Resilience is defined as the capacity of the system to absorb disturbances and reorganise, so as to still retain essentially the same functions, structure, identity and feedback mechanisms (Holling, 1973; Beisner *et al.*, 2003; Vasilakopoulos & Marshall, 2015; Folke, 2016).

Some perturbations may act either on the system state variables (pushing our ball from its valley into a new one, e.g. disease outbreak, Figure 1.1b) or on the system parameter variables (modifying the shape of the valley, hence affecting system resilience, e.g. overfishing and eutrophication, Figure 1.1c; Beisner *et al.*, 2003). As highlighted by the Caribbean coral reefs example, combination of multiple mechanisms generally cause a system to shift from a stable state to another (Biggs *et al.*, 2012). This shift of a system between two alternate stable states is the foundation of regime shift theory (Carpenter, 2001; Scheffer *et al.*, 2001). The separation point between two *regimes* (or alternate stable states) is the so-called *tipping point* (Selkoe *et al.*, 2015). Once crossed, the system will shift to a new regime with new characterising parameters. Clearly, once a tipping point is crossed, it is not easy to push the ball back in its original valley, since the new valley is deep and large, thus highly resilient, and/or the original valley might have disappeared. This can hinder a return of the system to the previous state even when disturbances stop (e.g. fishing ban, end of disease outbreak) or are reversed (Figure 1.1d and Figure 1.2, Beisner *et al.*, 2003). This property of regime shifts is called *hysteresis* and can be defined as the phenomenon for which the return path of a system from the altered to the original state can be drastically different from the one which have led to this altered state (Beisner *et al.*, 2003; Bestelmeyer *et al.*, 2011). Hysteresis is a typical feature of discontinuous regime shifts and can be detected when the relationship between the stressors and the system differs depending on the regime (stable state) of the system (Scheffer & Carpenter, 2003; Bestelmeyer *et al.*, 2011).

Another way to visualize the regime shift is the fold bifurcation curve (Figure 1.2, Scheffer *et al.,* 2001). The system reacts in a smooth way to condition changes until a tipping point (F1 or F2) is reached and the system jumps from one state to another. In the area of discontinuity (Figure 1.2, dashed blue line) the system can present three equilibria. As evidenced by this visualisation, systems that show such behaviour are difficult to reverse to previous state even when condition changes are reversed (hysteresis). Although some debates exist regarding the definition of regime shift we adopted the definition of Scheffer et al. (2001) and Selkoe et al. (2015) of an abrupt change over time with discontinuous dynamics exhibiting hysteresis. This is opposed to phase shifts *sensu* Selkoe *et al.,* (2015), where system state´s response to condition change is continuous, e.g. a logistic response, with two states but only one equilibrium.
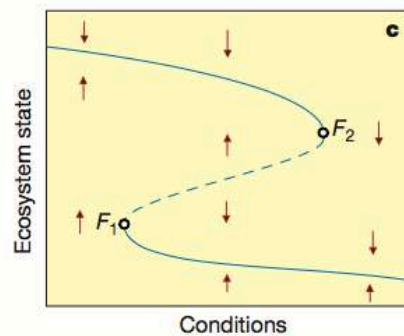
Figure 1.11 Fold bifurcation curve (reproduced from Scheffer et al. 2001). The dashed line represents the unstable equilibria and the border between the two alternate stable states represented by plain lines. F1 and F2 represent the tipping points

Resilience, feedback mechanisms, tipping points and hysteresis are important attributes of regime shifts (van der Maas *et al.*, 2003; Bestelmeyer *et al.*, 2011). These properties make regime shifts extremely important in the real world and have profound implications for management (Travis *et al.*, 2014; Selkoe *et al.*, 2015; Angeler *et al.*, 2016). Imagine having as system a fish population. When you start fishing, the population still manage to absorb the perturbation and might decline, but would remain in a state with high biomass, high recruitment, a certain growth rate, etc. At some point the fishing pressure, usually combined with other external stressors, increases so much that the population collapses and its internal mechanisms change. The exploited population is now in a new state at low abundance, possibly with different growth and mortality rates. Now suppose that we are the managers. We could assume that reducing the fishing pressure to pre-collapse levels would make the population quickly rebound. This could work in a context of linear dynamics but if the population has crossed a tipping point and it is now in a new alternate stable state, controlled by new mechanisms that cause hysteresis, recovery of the system may be slow and difficult, or even impossible. From this example, the importance of regime shift appears clear. In order to apply efficient and useful management measures, we should aim to detect regime shifts in advance or, at least, we should consider the possibility that an exploited system can show non-linear behaviours, and apply precautionary management approaches (Holling, 1973; Carpenter, 2001; Scheffer & Carpenter, 2003; deYoung *et al.*, 2008; Dakos *et al.*, 2012; Punt *et al.*, 2012; Levin & Möllmann, 2015). Many marine ecosystems have undergone drastic shifts often resulting in new ecologically structured and/or economically less valuable states (Conversi *et al.*, 2015b;

Möllmann *et al.*, 2015). These regimes shifts have brought catastrophic ecological and social consequences (Rocha *et al.*, 2015), such as economic losses, social issues and losses of ecosystem services (Casini *et al.*, 2008b; Möllmann *et al.*, 2008; Blenckner *et al.*, 2015b). Thus, since several processes at several levels of the ecosystem are often involved, it appears evident from these examples that an ecosystem approach to manage marine ecosystems prone to regime shifts is essential (Long *et al.*, 2015).

Challenges and implications of regime shifts for management purpose
To include the concept of regime shift into management perspectives, multiple *a priori* steps have to be made to first identify the mechanisms and the drivers involved (feedback loops, interactions, etc.), and then integrate this information into suitable and adapted policy. The documentation of a broad range of regime shift examples, involving different mechanisms applied to different ecosystems may be very useful to compare the various processes involved, to understand potential implications in a better way (Rocha *et al.*, 2015) and therefore to adapt management to local characteristics (deYoung *et al.*, 2008). In this context, the Regime Shift Database (Rocha *et al.*, 2014), based on a participatory approach, aims to review regime shifts of social-ecological systems worldwide with a particular focus on regime shifts having a potential large impact on human well-being and ecosystem services. This database, available online (www.regimeshifts.org), is an initiative led by the Stockholm Resilience Centre to increase general knowledge and understanding of regime shifts and associated concepts and to help managers and policy makers to take these concepts into account in their future decisions.

Knowledge of different mechanisms and local characteristics of regime shifts may facilitate their detection. Indeed, the first step and challenge to consider regime shifts in management, is to actually detect them (Carpenter, 2001; deYoung *et al.*, 2008; Rocha *et al.*, 2015). For instance, regime shifts in the North Sea and English Channel communities were only detected 10 years after they occurred (Beaugrand, 2004; Auber *et al.*, 2015). This late detection may partly be explained by the very large scale at which these shifts occurred and highlights the need of studying different spatial scales when wanting to understand ecosystems processes and dynamics. Similarly, temporal scales of changes might be different depending on the lifespan of the affected organisms and might lead to temporal lags in system responses to stressors (Holling, 1973; deYoung *et al.*, 2008) as it was the case in the North Sea. These differences in spatio-temporal patterns need to be addressed and disentangled as they might hinder or delay regime shift detection and exacerbate social and economic consequences (Levin, 1992; Scheffer & Carpenter, 2003; Kerkhoff & Enquist, 2007; Levin & Möllmann, 2015). It might also be necessary to disentangle regime shifts (*sensu* Selkoe *et al.,* 2015) from simple logistic dynamics and highlight hysteresis (which requires additional observations in time). For these reasons, regime shift detection requires long and extensive observation datasets of the system which is generally costly in time and money (Carpenter, 2001; Scheffer *et al.*, 2009; Levin & Möllmann, 2015). Moreover, the required time to obtain time series of suitable length might prove too long, particularly when such shifts may strongly impact ecosystems services and human well-being. For these reasons, experimental studies are necessary to enhance the understanding of systems responses to disturbances (Angeler *et al.*, 2016). Particularly, experiments may help to understand multi-causality and dual relationships between stressors and systems which

generally participate in hindering detection of regimes shifts (Scheffer & Carpenter, 2003; Conversi *et al.*, 2015; Levin & Möllmann, 2015).

When regime shift detection may be delayed, their unexpected and abrupt behaviour hinders even more regime shift prediction, which is necessary to ensure effective management measures. In addition, a post-regime shift detection may result in increased management challenges, particularly due to hysteresis, as described in the previous section for coral reefs (Mumby *et al.*, 2007; Mumby, 2009), kelp forests (Steneck *et al.*, 2002) and various fish stock shifts (Myers *et al.*, 1997; Hutchings, 2000; Myers & Worm, 2005; Hutchings & Rangeley, 2011). Challenges in prediction may be partly related to the common use of linear relationships to statistically describe natural processes which need to be overcome in favour of more realistic (thus more complex) models (Holling, 1973; Ludwig *et al.*, 1997; Scheffer & Carpenter, 2003). Indeed, the non-linear relationships between stressors and system variables need to be understood to be able to correctly predict system responses. Also, a new branch has been currently developing regime shift indicators, the so-called early-warning signals, to anticipate regimes shifts. These signals are generally based on the fact that the recovery of a highly-disturbed system to an equilibrium is slow, i.e. critically slowing down (Scheffer *et al.*, 2001, 2015; Dakos *et al.*, 2012; Lindegren *et al.*, 2012). Indeed, when systems are close to tipping points, their stability decreases, generally leading to an increased variability, and autocorrelation of the data describing them. These indicators work well with simulation models but still they have some limitations in predicting shifts using empirical data (Dakos *et al.*, 2008, 2017; Scheffer *et al.*, 2009; Dai *et al.*, 2013). They may be constrained by the length of the times series available and/or the limited amount of data, by methodological assumptions and/or sampling errors (deYoung *et al.*, 2008; Lindegren *et al.*, 2012). Moreover, they are not suitable to predict stochastically driven shifts. To overcome these limitations, Lade and Gross (2012) developed a new approach to detect early warning signals with reduced time-series. Lindegren *et al.*, (2012) recommended a multiple approach based on knowledge of the system and its local characteristics (key ecological thresholds, relationships with drivers), data availability, sensitivity and bias of the analysis carried out. Such advances need to be followed by the scientific community to develop more approaches overcoming these limitations. Alternative sources of data, e.g. public records and narratives, must be found and used, particularly when ecological data are not available, and systems must be monitored at an appropriate time scale to ensure shift detection as early as possible.

Because prediction of regime shifts is so challenging, and because the potential consequences for ecosystem services and human well-being may be abrupt and very difficult (or even impossible) to reverse, precautionary approaches are recommended (Holling, 1973; Carpenter, 2001; Scheffer & Carpenter, 2003; Selkoe *et al.*, 2015). When managing systems prone to regime shifts, risks and uncertainties must be assessed before any management action is taken (Levin & Möllmann, 2015; DePiper *et al.*, 2017). Risk assessment requires a clear definition of the system of interest, its potential tipping points, as well as suitable indicators. However, all the challenges already mentioned (multiple-causality, dual relationships to drivers, spatio-temporal different patterns, limitation of data, etc.) may impede the definition of appropriate indicators (Kelly *et al.*, 2015; Selkoe *et al.*, 2015). For instance, Vasilakopoulos and Marshall

(2015) showed that the spawning stock biomass (SSB) of Barents Sea cod did not suffice to detect a regime shift of this population, while SSB levels are generally the reference points used in current fishery management plans (single- or multi-species advices), and sometimes the only ones. These results evidence the need to base scientific advice to fishery managers on the monitoring of several ecosystem (community/population) parameters, particularly when suspecting potential impending shifts. Similarly, stressors effects may be unclear when studied individually, while their importance may appear only when combined with other stressors (Rocha *et al.*, 2015; Vasilakopoulos & Marshall, 2015). The factors undermining resilience (eutrophication, global warming, species invasion, etc.) should be of prior concern as small variations in stressors might lead to large changes in ecosystem structure and/or functioning when resilience is eroded (Ricker, 1963; Ludwig *et al.*, 1997; Scheffer *et al.*, 2001; Beisner *et al.*, 2003; Scheffer & Carpenter, 2003). The quantitative assessment of risk and associated resilience is difficult and challenging. Economic cost-benefit analysis might be useful when trying to quantify risks for ecosystem services (Carpenter, 2001), however, it might totally underestimate them when too narrow-focused, e.g. focusing on yield in fisheries while neglecting age-structure of the stock (deYoung *et al.*, 2008). Quantitative assessment of resilience may prove very useful but requires an extensive amount of data particularly in complex systems (Vasilakopoulos & Marshall, 2015). Therefore, qualitative analysis and/or conceptual models may be preferred (DePiper *et al.*, 2017), particularly when studying data-poor systems or when dealing with complex adaptive systems such as social-ecological ones.

Despite the increasing effort in scientific research, even when risk (or resilience) may be assessed, ecological uncertainties (about system evolution) and livelihood uncertainties (about impacts on human communities) related to regime shifts are high (Pindyck, 2000). When managing social-ecological systems (SES) prone to regime shifts, policy makers must face these uncertainties and different management strategies might emerge: reducing or limiting system stressors (mitigation), building up system resilience (adaptation) and/or reversing a shift (restoration, Kates et al. 2012; Angeler et al. 2013). These strategies might have different outcomes, benefits, costs and efficiency depending of goals and focus of management as well as the status of the system (Lade *et al.*, 2015; Selkoe *et al.*, 2015; Fenichel & Horan, 2016; Mathias *et al.*, 2017). For example, because of hysteresis, building up resilience might be more effective and less costly than restoration measures (Selkoe *et al.*, 2015). These measures might also require different levels of governance. For instance, the reduction of tuna fishing effort in the Pacific Ocean would require an international consortium for management to be efficient while similar measures applied to a coral reef fishery would be relevant at the local management scale. In addition, when mitigation generally requires international and global management (e.g. gas emissions reduction), building up systems resilience (adaptation) may succeed at local scales, countering global inaction (Rocha *et al.*, 2015). While decreasing variance of a system may seem a good idea, Carpenter et al. (2015) highlighted the adverse effects for system resilience management. Staying within a safe-operating space (Rockström *et al.*, 2009), including uncertainties around tipping points and using history as guideline (Fenichel & Horan, 2016; Liski & Salanié, 2016) might, however, prove effective and reduce risks of management failures. Adversely, managers might need to erode resilience of a system to tip it towards a preferable regime, e.g. more pristine or more valuable (Derissen *et al.*, 2011). This so-called

transformation would require intentional changes in the institutional framework in which the utilisation of marine systems (e.g. including switch to a novel management system), as well as a transparent and equitable redistribution of benefits across stakeholders takes place (Selkoe *et al.*, 2015). Uncertainties may as well increase immediate costs, and even if costs of inaction would be high in the future, they might hinder immediate decisions (Pindyck, 2000; Selkoe *et al.*, 2015).

Adaptive co-management might be ideal when cooperation between local and global stakeholders is possible (Plummer *et al.*, 2017). However, it might slow down management processes opposed to the potential flexibility and responsiveness of local stakeholders required for a good management of regime shift effects (deYoung *et al.*, 2008; Horan *et al.*, 2011; Blenckner *et al.*, 2015a; Rocha *et al.*, 2015; Valman *et al.*, 2016). Similarly, polycentric governance holds great potential at the international scale but is vulnerable to negative interactions between institutions and weak coordination (Galaz *et al.*, 2012; Mathias *et al.*, 2017). In both cases, the question of responsibility might be raised in case of management failures (Baumgärtner *et al.*, 2006; Fenichel & Horan, 2016). Local and/or global stakeholder cooperation, as well as responsiveness, may be improved by the knowledge of the stressors involved in regime shifts mechanisms, their shared interactions with the different components of the system, and the different scales at which they interact (Rocha *et al.*, 2015). Such knowledge may also help policy makers to set suitable management targets otherwise challenged when uncertainties are high.

Finally, the integration of management and regime shift theory may prove quite complicated. The complex responses to stressors, the multiple, cross-disciplinary interactions between each system components, the high uncertainties and the different stakeholder perspectives and conflicts need to be understood and accounted for when considering regime shifts (and/or resilience) in social-ecological systems (SES) management decisions. This requires holistic and integrative approaches such as integrative ecosystem assessment (IEA, (Levin & Möllmann, 2015)). In this context, scientists have recently developed frameworks to conceptualize SES and assess their sustainability and uncertainties (Ostrom, 2009; Leslie *et al.*, 2015; Levin *et al.*, 2016). Particularly, these frameworks allow the combination of classic scientific information and local stakeholders' ecological, cultural and/or social knowledge of the system. These conceptual models may be used to promote interdisciplinary research, discussions between stakeholders, and allow a holistic management strategy evaluation after their operationalisation (Levin & Möllmann, 2015; Levin *et al.*, 2016; DePiper *et al.*, 2017).

Conclusions
Regime shifts are abrupt changes that can happen in complex systems worldwide at different temporal and spatial scales, depending on the resilience of the systems (Scheffer *et al.*, 2001; deYoung *et al.*, 2008). It is extremely important to study and understand these mechanisms since many regime shifts have led to catastrophic changes including ecological, social and economic losses worldwide (Mumby, 2009; Steneck & Wahle, 2013; Blenckner *et al.*, 2015b). Despite the fact that many studies and methods have focused on the detection of regime shifts, there is still a lot to be done to achieve marine ecosystem management integrating resilience

and regime shifts (Travis *et al.*, 2014; Selkoe *et al.*, 2015; Angeler *et al.*, 2016). New tools, such as early warning signals or new ways to assess the resilience of different systems, combined with an in-depth study of the mechanisms and stressors affecting natural systems are a good start to incorporate resilience and regime shift into policy-maker decisions (Carpenter & Brock, 2006; Scheffer *et al.*, 2009; Dakos *et al.*, 2012, 2017; Ling *et al.*, 2015; Vasilakopoulos & Marshall, 2015). Since regime shifts often affect many components of an ecosystem in different ways, ecosystem-based management (EBM) is necessary to include effectively regime shifts into management considerations (Blenckner *et al.*, 2015a; Levin & Möllmann, 2015; Long *et al.*, 2015; Rocha *et al.*, 2015). To make this holistic approach effective and to preserve the natural environment and ecosystems in a more integrative way, there is a real need to translate regime shift and resilience concepts from theory to applications (Punt *et al.*, 2012; Travis *et al.*, 2014; Selkoe *et al.*, 2015). Recently, the operationalisation of social-ecological systems (SES) conceptual models have shown promising improvements in this sense (Leslie *et al.*, 2015; DePiper *et al.*, 2017). Due to the different spatial and temporal scales at which regime shifts can act, i.e. from extremely local to global, and the high degree of associated uncertainties, innovative and flexible management options need to be developed at different levels of governance. For instance, Rockström et al. (2009) suggested a management at the planetary boundaries. Such management would require, in addition to adaptive management and polycentric governance, a societal shift in order to achieve a fair use of global resources, and a transformed economy (Hughes *et al.*, 2013; Lade *et al.*, 2013; O'Brien *et al.*, 2014). Finally, we can expect that the increasing awareness of the implications of regime shifts and associated concepts for human well-being worldwide will likely lead to more precautionary management approaches, while new tools and technics will be developed to achieve an integrative and efficient management of our natural resources.

Box 1

Glossary

Regime shift: dramatic and abrupt change in the structure and function of a system causing a shift between two alternate stable states following discontinuous non-linear dynamics and exhibiting three equilibria. There are some debates about the definition and *critical transition* or *phase shift* might be considered synonyms depending on the literature.

Resilience: capacity of the system to absorb disturbances and reorganise in a way that it retains the same functions, structure, identity and feedback mechanisms, potentially impeding a regime shift.

Regime: dynamic system maintaining certain structures and functions. It is also known as *stable state, basin of attraction* or *domain of attraction*.

Tipping point: threshold separating two dynamics regimes. It is also known as *critical threshold* or *bifurcation point.*

Feedback mechanism: ecological mechanisms stabilising a regime by amplifying (positive) or damping (negative) the response to a forcing. Positive feedbacks (reinforcing) move the system to an alternate stable state, out of equilibrium. Negative feedbacks (balancing) maintain the status of the system, close to the equilibrium dynamics.

Hysteresis: phenomenon for which the return path from regime B to regime A, is drastically different from the path that led from regime A to regime B.

Chapter 2: Discontinuous dynamics in Atlantic cod stocks

Catastrophic dynamics limit Atlantic cod recovery

Camilla Sguotti[1], Saskia A. Otto[1], Romain Frelat[1], Tom J. Langbehn[2], Marie Plambech Ryberg[3], Martin Lindegren[3], Joel M. Durant[4], Nils Chr. Stenseth[4], Christian Möllmann[1.]

Abstract

Collapses and regime changes are pervasive in complex systems governed by multiple stressors such as marine ecosystems. The demise of Atlantic cod (*Gadus morhua*) stocks constitutes a text book example of the consequences of overexploiting marine living resources, however the drivers of these nearly synchronous collapses are still debated. Moreover, it is still unclear why rebuilding of collapsed fish stocks such as cod is often slow or even absent. Here we apply the stochastic CUSP model which is based on catastrophe theory, and show that collapse and recovery of cod stocks are determined by the interaction of human exploitation pressure and environmental drivers, resolving earlier discussions on the relative importance of these two stressors. Our statistical modelling study demonstrates that for most of the cod stocks ocean warming induces a non-linear discontinuous relationship between fishing pressure and stock size, hence explaining hysteresis in their response to reduced exploitation pressure. Our study suggests that a continuing increase in ocean temperatures will likely limit productivity and hence future fishing opportunities for most cod stocks of the Atlantic Ocean. Moreover, it highlights the importance of considering discontinuous dynamics in holistic ecosystem-based management approaches, particularly under climate change.

Keywords: Catastrophe theory, stock collapse, *Atlantic cod*, stochastic CUSP modelling, population recovery.

Author´s affiliations
[1]Institute for Marine Ecosystem and Fisheries Science, University of Hamburg, Germany
[2]Department of Biological Sciences, University of Bergen, Norway
[3]National Institute of Aquatic Resources, Technical University of Denmark (DTU Aqua)
[4]Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, Norway

Introduction

Collapses and regime changes are pervasive in complex systems such as marine ecosystems (deYoung *et al.*, 2008; Conversi *et al.*, 2015; Möllmann *et al.*, 2015) and comprise fish populations (Vert-pre *et al.*, 2013; Perretti *et al.*, 2017), trophic level communities (Beaugrand *et al.*, 2002; Kortsch *et al.*, 2012; Morse *et al.*, 2017) and entire large marine ecosystems (Hare & Mantua, 2000; Cury & Shannon, 2004; Weijerman *et al.*, 2005; Möllmann *et al.*, 2009; Möllmann & Diekmann, 2012). Typically, such events are characterized by multiple external drivers that interact in causing abrupt changes, and show hysteresis effects to restoration and recovery efforts (Conversi *et al.*, 2015). Anticipating and considering regime shifts is hence a crucial challenge for marine ecosystem-based management that has the goal of a sustainable exploitation of the oceans (Dakos *et al.*, 2015; King *et al.*, 2015; Levin & Möllmann, 2015).

The demise of Atlantic cod (*Gadus morhua*) stocks constitutes a text book example of the consequences of overexploiting marine living resources (Figure S2.1) (Hutchings & Myers, 1995; Cook *et al.*, 1997; Myers *et al.*, 1997). Nevertheless, it is still debated whether these near synchronous collapses occurred due to overfishing, were caused by concurrent climatic changes across the entire North Atlantic, or a combination of both (Myers *et al.*, 1996; Frank *et al.*, 2016). Given the dire ecological and socio-economic consequences of these collapses (Haedrich *et al.*, 2000), a wide range of management measures has been implemented in the attempt to promote the recovery of cod on both sides of the North Atlantic (Gray *et al.*, 2008). Unfortunately, most of these recovery measures have proved inefficient. We here analysed trends of 19 collapsed cod stocks (Table S2.1-S2.2, Figure S2.1) and found only two stocks fully recovered, and six in the process of recovering (Supplementary Methods, Figure S2.2-S2.3). Eleven cod stocks can still be considered depleted, causing a great deal of controversy regarding the underlying processes of failed recovery both in the scientific literature (Frank *et al.*, 2016) but also in popular media (Gray *et al.*, 2008). Here, we address the question of how fishing pressure and climatic changes (represented by sea surface temperature) interact to cause patterns of collapse and recovery of Atlantic cod stocks applying an approach based on catastrophe theory.

Catastrophe theory and the CUSP model.

Catastrophe theory is a branch of bifurcation theory in the field of nonlinear dynamical systems that studies and classifies phenomena characterized by sudden shifts in behavior derived from small changes in external conditions (Barkley Rosser Jr *et al.*, 2007). The theory experienced an unrivaled intellectual bubble in the history of science. Developed by the French mathematician René Thom in the 1960s (Thom, 1972) and popularized by Christopher Zeeman in the 1970s (Zeeman, 1976), catastrophe theory became somewhat an intellectual fad (Barkley Rosser Jr *et al.*, 2007). The theory was believed to be applicable to every branch of science and hence was quickly embraced by scientists in diverse fields. Examples of applications in marine ecology and resource management questions included models of fishery dynamics (Copes, 1970; Clark, 1976; Jones & Walters, 1976) and predator-prey interactions of Great Lakes trout (Walters, 1986). But as quickly as it became popular, the theory started to be heavily criticized (Kolata, 1977; Zahler & Sussmann, 1977; Sussmann & Zahler, 1978b, 1978a) which resulted

in a major debate on its usefulness and potential misuse (responses appeared in Science and Nature in 1977, (Guckenheimer, 1977; Guastello, 1981; Arnol'd, 1992)). This debate gradually undermined the support for using catastrophe theory and led to a widespread disregard until the 2000s (Barkley Rosser Jr *et al.*, 2007).

Standard catastrophe theory differentiates seven elementary catastrophes (canonical forms) that can describe systems characterized by abrupt shifts with up to six dimensions in control and state variables (Thom, 1972). Most of the applications of catastrophe theory use the two simplest forms, the FOLD and the CUSP. The FOLD catastrophe describes sudden changes of a dynamic system in response to a single pressure variable and has been widely used in ecology to discuss concepts such as resilience and hysteresis (Scheffer *et al.*, 2001; Scheffer & Carpenter, 2003). The CUSP catastrophe, in contrast to the FOLD, considers a 3-dimensional system (Figure2.1) where a second external variable acts as splitting factor that can modify the system´s response to the principal external driver from linear and continuous to non-linear discontinuous. The CUSP catastrophe is hence an ideal model to evaluate the effect of two interacting drivers such as fishing pressure and environmental drivers on ecological systems, a potential that has not been exploited yet (but see (Petraitis & Dudgeon, 2016)).

Stochastic CUSP modelling.
A major criticism of early studies applying the deterministic catastrophe theory was their descriptive nature due to the lack of a stochastic framework (Grasman *et al.*, 2009). The recent development of such a framework to CUSP modelling has revived interest in the concept with an increasing number of publications in disciplines such as economy (Diks & Wang, 2016), sociology and behavioral science (Grasman *et al.*, 2009). However, despite the CUSP catastrophe may be ideal for explaining abrupt changes in ecological systems which are often due to the interaction of multiple external drivers (Conversi *et al.*, 2015; Möllmann *et al.*, 2015) the model is still rarely considered (Petraitis & Dudgeon, 2016). Here, we applied the stochastic CUSP model to 19 Atlantic cod stocks to understand i) whether cod stocks dynamics follow a continuous or discontinuous path, and ii) to understand the role of fishing and environmental drivers in their collapses and recovery potential.

Material and methods
Data.
In order to represent the population dynamics across all Atlantic cod stocks we collected time-series of comparable spawner biomass (i.e., biomass of mature fish in tonnes) and fishing mortality estimates derived from stock assessments. Data were provided by the International Council for the Exploration of the Sea (ICES), the National Oceanic and Atmospheric Administration of the USA (NOAA), the Northwest Atlantic Fisheries Organization (NAFO) and the Department of Fisheries and Ocean in Canada (DFO) (Table S2.1-S2.2). A few recent stock assessments (i.e., the Kattegat, the Western Baltic and the Norwegian coastal cod) comprised only reduced assessment periods. Where possible, we prolonged the spawner biomass and fishing mortality time-series by combining them with comparable estimates from previous assessments after performing consistency checks (Figure S2.6). To represent changes in environmental conditions experienced by each stock we collected time-series of sea surface

temperature (SST in °C). Although SST does not fully reflect the thermal habitat of cod, a predominately demersal (bottom-dwelling) species, SST has previously been shown to be a strong predictor influencing cod stock dynamics, including reproduction and growth (Drinkwater, 2005; Brander, 2010). SST data were collated from the NOAA Extended Reconstructed Sea Surface Temperature dataset (ERSST, www.ncdc.noaa.gov) version 4. The dataset represents a reconstruction of SST from 1854 to the present and represents monthly anomalies computed with respect to the period 1971-2000, resolved in a 2°x 2° grid of spatial coverage. For every stock, we calculated mean annual SST values averaged over the management area (Table S2.2). Since the Eastern Baltic cod stock is not strongly influenced by temperature but rather affected by oxygen, the annual extents of anoxic areas (in km^2) (Carstensen *et al.*, 2014) were used as environmental covariate for this particular stock.

Stochastic CUSP modelling.
We tested if a statistical approach to catastrophe theory can explain collapse and recovery patterns of Atlantic cod stocks. Catastrophe theory provides a mathematical framework to model both continuous and discontinuous changes in a system´s dynamics (Thom, 1972; Diks & Wang, 2016; Petraitis & Dudgeon, 2016). In particular, it is effective in describing abrupt changes in the system state variable as a result of small and continuous changes in control variables (Thom, 1972; Grasman *et al.*, 2009). This theory is based on a non-linear dynamic system which follows the following differential equation:

$$dy_t = -\frac{\partial V(y_t; \theta)}{\partial y_t} dt$$

where y_t represents the state of the system and $V(y_t; \theta)$ is a potential function determined by a control parameter θ influencing the specific structure of the system. When the equation is equal to zero the system is in equilibrium, otherwise it will become unstable and, eventually, shift to an alternative state. Hence this model allows the system to create bifurcation points and experience multimodality.
One finding of catastrophe theory is that the behaviour of a system around the equilibrium can be characterized by seven canonical forms, among which the CUSP catastrophe is the most commonly used (Thom, 1972; Grasman *et al.*, 2009). The CUSP catastrophe describes sudden and discontinuous transitions in the equilibrium state of a state variable Z_t (in our case a linear function of spawner biomass, see below) depending on two control parameters α and β.

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

In stochastic CUSP modelling, a stochastic differential equation was developed allowing the estimation of parameters α and β as linear functions of exogenous ($X_1 \ldots X_y$) variables, and the canonical dependent state variable as a linear function of one more observable dependent state variables ($Y_1 \ldots Y_y$) using a likelihood approach (Grasman *et al.*, 2009; Diks & Wang, 2016):

$$\alpha = \alpha_0 + \alpha_1 X_1 + \cdots + \alpha_y X_y$$
$$\beta = \beta_0 + \beta_1 X_1 + \cdots + \beta_y X_y$$
$$z = w_0 + w_1 y_1 + \cdots + w_y y$$

with $w_0, w_1, \ldots w_y$ being coefficients.

The control parameters α and β are respectively called asymmetry and bifurcation variables (Grasman *et al.*, 2009; Diks & Wang, 2016). We here applied the stochastic CUSP model to Atlantic cod stocks dynamics, where the status of the stocks Z_t, in our case spawner biomass, is modelled depending on two control variables (Figure2.1). An asymmetry variable (α) regulates the dimension of Z_t and is a linear function of fishing mortality, set by fisheries management and commonly assumed to be linearly related to population size (Anderson *et al.*, 2008). A bifurcation variable (the splitting factor, β) determines whether the state variable follows a continuous or discontinuous path, and in our case, is a linear function of sea surface temperature (SST). We used SST as an accepted proxy for environmental conditions affecting biological processes such as recruitment (Planque *et al.*, 1999; O'Brien *et al.*, 2000) and growth in Atlantic cod (Brander, 1995), and as an indicator for climate change effects (Drinkwater, 2005; Stige *et al.*, 2006).

Equilibria of the system corresponding to the solution of the cubic equation are as follows:

$$-\frac{\partial V(z; \alpha, \beta)}{\partial z} = -z^3 + \beta z + \alpha = 0$$

From this equation, a Cardan´s discriminant (δ) is derived, that allows us to distinguish if the system is in a state with only one ($\delta > 0$) or three equilibria ($\delta < 0$):

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

Our CUSP modelling approach can be visualized as a 3D landscape where the trajectory of cod stock size in response to changing fishing mortality can be continuous (i.e. linear, with one state) or discontinuous (i.e. folded, with two alternative states), depending on SST. As an example, Figure 2.1 presents the collapse of North Sea cod, indicated by the drop in spawner biomass from the upper to the lower fold of the phase plane due to high fishing pressure (Figure2.1). After the collapse, and with increasing temperatures, spawner biomass values progressively move below the discontinuous fold into the bifurcation area where three alternative states (2 stable and one unstable) are possible. Thus, critical thresholds are readily breached by relatively minor changes in fishing mortality (see Methods), causing stocks to potentially fluctuate between the two alternative states along the discontinuous path. Stocks following a discontinuous path, and thus staying close to the bifurcation area, are prone to tipping points. A projection on the 2D plane allows to follow the stock dynamics of North Sea cod and understand why its recovery may be limited (Figure 2.1). Stock size decreased in response to increasing fishing mortality, moving in and out the bifurcation area (indicated in light blue). Eventually, the stock collapsed to a very low biomass state and remained in the unpredictable zone of the CUSP. During the last 10 years, exploitation pressure of North Sea cod has been drastically reduced, however spawner biomass levels remained significantly lower compared to the beginning of the study period, when fishing mortality was similar. This hysteresis in response to decreased exploitation pressure is related to an increase in SST that is detrimental for North Sea cod (O'Brien *et al.*, 2000). Therefore, the CUSP model can also explain the slow recovery of the state variable (i.e. spawner biomass of Atlantic cod stocks), i.e. hysteresis. Recovery of a collapsed fish population can either occur when SST changes in a way that fishing mortality again has a linear effect on spawner biomass, or, within the bifurcation area, when chance events, e.g. high reproductive success, occur.
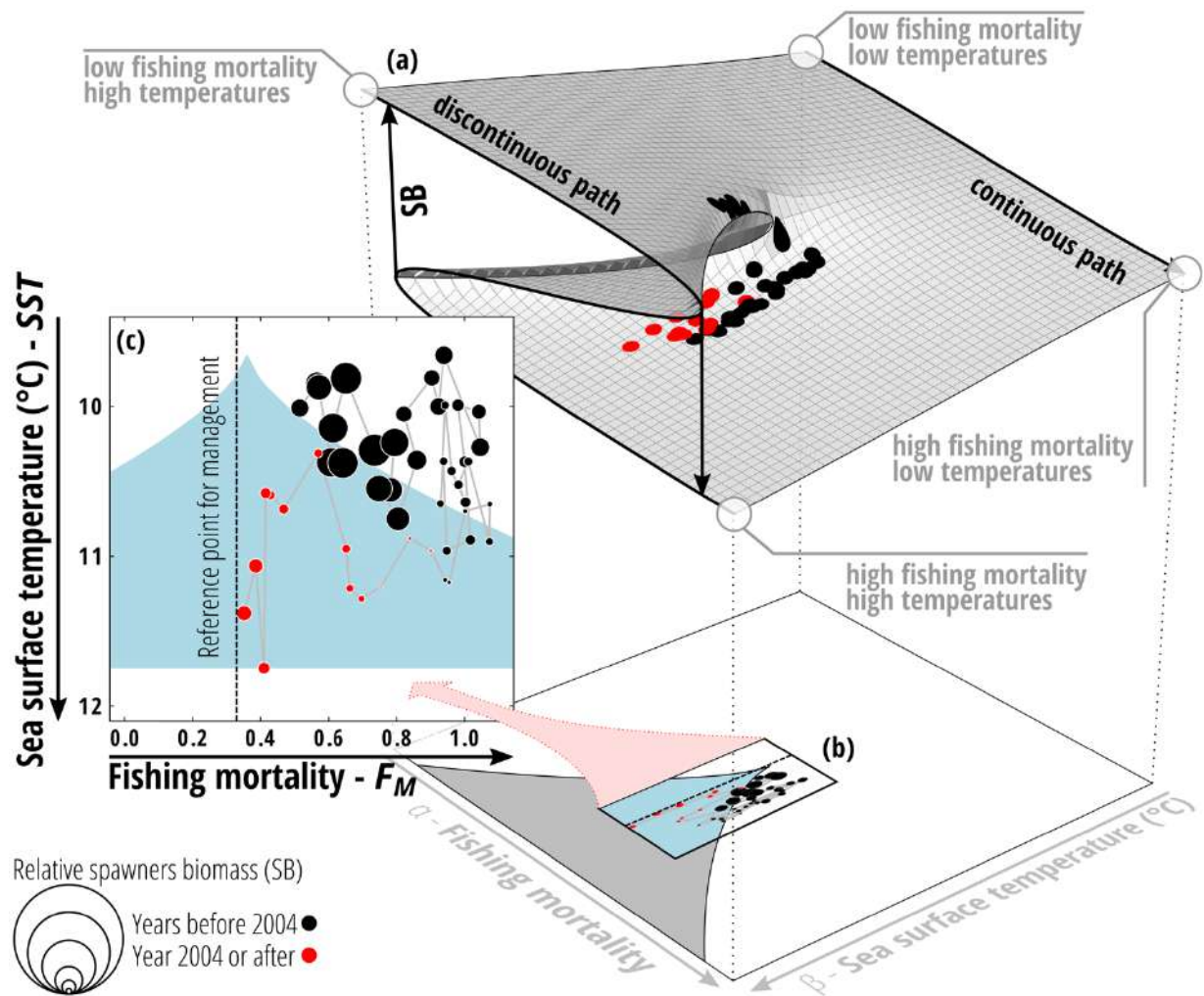
Figure 2.1 | The *stochastic CUSP model* – from 3D to 2D representation. *a)* The typical 3D representation of the CUSP model where North Atlantic cod spawner biomass (SB) dynamics depend on two controlling variables α (fishing mortality – F_M) set by fisheries management and β (sea surface temperature – SST) controlling whether SB follows a continuous or discontinuous path. *b,c)* 2D projection of the bifurcation area under the folded 3D phase plane shaded in grey and light blue (only the data range). Filled dots in b) and c) represent SB with the radius scaling relative to stock size.

To our knowledge, our study is one of the few to apply this methodology to empirical data from an ecological system. We applied the stochastic CUSP model to investigate how the interaction of fishing pressure and environmental conditions affects patterns of collapse and recovery of 19 Atlantic cod stocks. We compared the fitted CUSP models to alternative linear and logistic regression models using an information theoretic approach based on AIC. We further validated the fitted CUSP models by exploring the significance of the canonical state variable z, bimodality of the state variable in the bifurcation area as well as the percentage of observations in the bifurcation area (>10% being the benchmark) (Table S2.4).

Software.

All analyses were conducted in the statistical programming environment R (version 3.0) with Rstudio using R packages ggplot2, bcp, mgcv, ade4 and cusp.

Results and Discussion

Table 2.1 | Results of the valid stochastic CUSP models. Given are signifcant levels (p values) for alpha (fishing mortality) and beta (se surface temperature), explained variance (R^2) and AIC_c values that compare the CUSP models with alternative linear and logistic models (lower AIC values indicate a better model fit).

Stock No.	Stock	p(α)	p(β)	R^2	AICc (CUSP)	AIC_c (linear)	AIC_c (logistic)
(1)	Baltic E	0.152	0.041	0.77	107	1271	1252
(2)	Baltic W	0.878	0.311	0.69	137	1016	1015
(3)	Kattegat	0.02	<0.001	0.75	93	923	921
(4)	North	0.01	< 0.001	0.38	124	1335	1327
(5)	Scotland	0.187	< 0.001	0.64	67	751	745
(6)	Irish	0.194	< 0.001	0.59	108	975	971
(8)	Coastal	0.567	< 0.001	0.77	59	810	797
(9)	Arctic	< 0.001	< 0.001	0.78	53	1978	NA
(11)	Iceland	< 0.001	0.02	0.77	70	1649	1637
(12)	Northern	0.01	0.824	0.94	20	922	899
(13)	Lawrence N	0.807	0.001	0.85	72	1024	1021
(14)	Lawrence S	0.109	< 0.001	0.65	92	1128	1106
(15)	Scotian E	0.07	0.014	0.80	96	1003	974
(16)	Grand	0.006	0.196	0.62	138	1316	1302
(17)	Flemish	0.132	< 0.001	0.69	108	912	923
(18)	Georges	0.006	0.048	0.76	75	837	830

We applied stochastic CUSP modelling to 19 cod stocks from both sides of the North Atlantic. Generally, the CUSP model provided better statistical fits to the data than alternative linear and logistic models for all Atlantic cod stocks (Table 2.1). A further evaluation exploring the percentage and bimodality of the observations in the bifurcation area (Grasman *et al.*, 2009) revealed 16 out of the 19 CUSP models to be valid (Table S2.4-S2.5, Figure S2.4). Importantly, the model results indicate that in 13 out of the 16 valid CUSP models, SST is a significant predictor of cod spawner biomass dynamics. Additionally, fishing mortality was a significant predictor in five cases, and the only significant predictor in two cases (Table 2.1, Table S2.5). These results show that Atlantic cod stock dynamics are best described by discontinuous, catastrophic behaviors as reflected by the CUSP model.
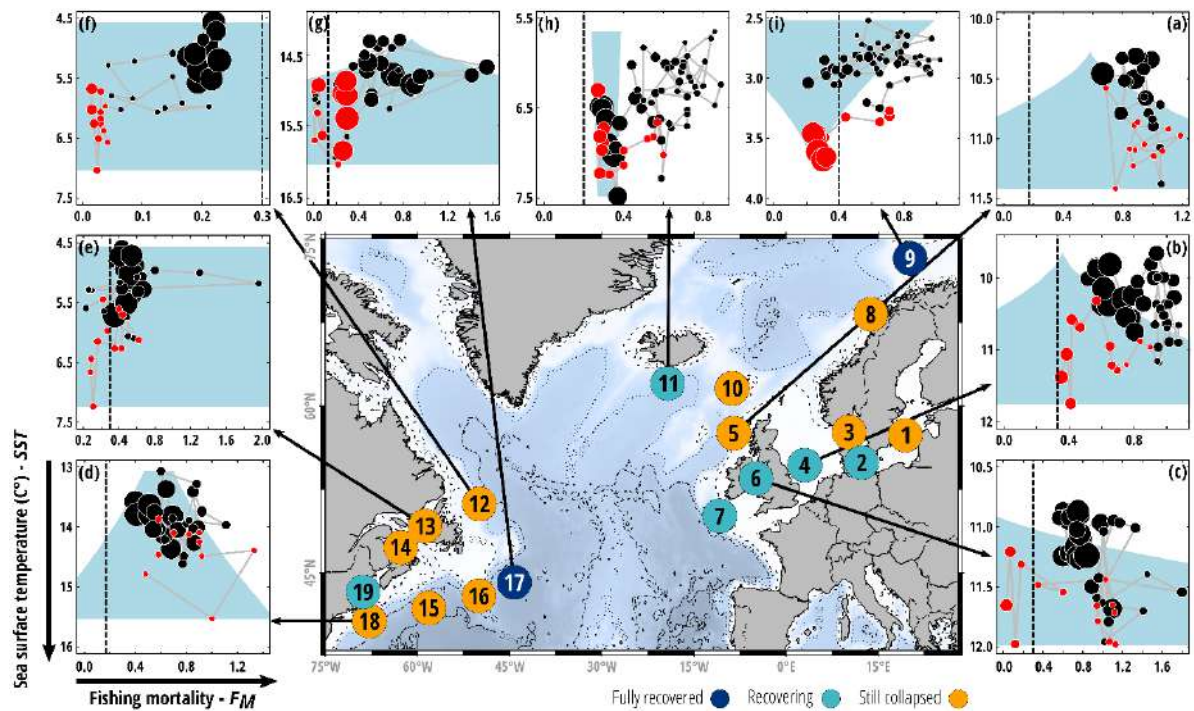
Figure 2.2 | 2D bifurcation plots of the *stochastic CUSP model*. Map indicating 19 North Atlantic cod stocks (number according to Table S1) and their recovery status. Panels show *CUSP model* results for 9 stocks (a -West of Scotland, b-North Sea, c-Irish Sea, d-Georges Bank, e-Northern Lawrence, f-Northern cod, g-Flemish Cap, h-Iceland, i-North East Arctic); other stocks see Supplementary Information. Dots represent spawner biomass scaled to stock size; years > 2004 in red. The *bifurcation area* is shaded in blue and vertical dashed lines indicate stock specific management reference points of F_M (Table S3).

Our results provide, for the first time, an explanation of the interplay between oceanic temperature conditions and fishing pressure, both strongly debated to be single dominant drivers for Atlantic cod stock collapses (Myers *et al.*, 1996; Frank *et al.*, 2016). According to our CUSP models the importance of SST is grounded in its ability to modify the relationship between fishing mortality and the state variable (spawner biomass) from linear to non-linear and discontinuous. Eastern Atlantic cod stocks best demonstrate this catastrophic behavior, as also seen for North Sea cod (Figure 2.1), where an increase in SST moves the stock trajectory towards the discontinuous region (i.e. down the y-axis) and into the bifurcation area (Figure2.2 a-c; Figure S2.5). Here, even minute changes of fishing mortality are sufficient to drive the stock to collapse. Similar dynamics are observed for Western Atlantic stocks (Figure2.2 d-f; Figure S2.5) where most of the spawner biomass observations are found within the bifurcation area. Having a large proportion of data points in the unstable region indicates a generally high degree of instability and vulnerability to fishing (Wang *et al.*, 2014), a pattern also found for cod stocks in the Baltic Sea and at the Norwegian coast (Figure S2.5).

Our study shows that all stocks, except the highly vulnerable Norwegian coastal and Northern cod (where most of the data points are in the bifurcation area), collapsed at a fishing mortality well above sustainable levels, i.e. F_{MSY} (Figure 2.2; Figure S2.5, Table S2.3), indicating the paramount importance of fishing pressure for cod stock dynamics (Brander, 2018). Specifically, fishing below or around F_{MSY} would have maintained larger stock sizes and reduced the vulnerability of these stocks to SST changes, as indicated by stocks falling outside the

bifurcation area (see especially North Sea and West of Scotland cod; Figure 2.2a,b). Recent management efforts have often reduced fishing mortality to near or far below F_{MSY} such as in North and Irish Sea cod (Figure 2.2a,c). While these stocks can be considered recovering (Supplementary Methods, Figure S2.2-S2.2), spawner biomass remains in most cases far below historical levels at similar or higher exploitation pressure. This hysteresis effect is due to the non-linear relationship between spawner biomass and fishing mortality caused by increased SST, and implies that recovery may only occur after a prolonged period of very low fishing mortality. Extreme cases of hysteresis are presented by some of the Western Atlantic stocks (e.g. Southern Gulf of St. Lawrence) (Figure S2.5) that presently reside in a depleted state in the unstable bifurcation area. Hence, sudden increases in spawner biomass are theoretically possible as demonstrated by the recently recovered Flemish Cap cod (Figure 2.2g). Still, a long-term reduction in fishing mortality is necessary to increase survival and year-class strength and eventually initiate a positive feedback leading to Atlantic cod stocks more resilient to the largely negative effects of ocean warming.

Climate change will lead to a considerably warmer Atlantic Ocean (Boyd *et al.*, 2014) and our results show that increasing SST will have negative repercussions for most of the Atlantic cod stocks that already live at their upper thermal tolerance limits (Pörtner *et al.*, 2008; Mantzouni *et al.*, 2010). However, the few stocks residing at or close to their lower thermal tolerance limits benefit from warming (Figure 2.2i-h). Warming and reduced fishing pressure initiated the recovery of the Icelandic cod stock, which could be even more pronounced if fishing mortality would be reduced to below F_{MSY}. To date, North-East Arctic cod is benefiting the most from ocean warming (Butzin & Pörtner, 2016). According to our CUSP model, North-East Arctic cod resides in (or is on the verge of) a high spawner biomass stable state (recent high spawner biomass values are outside or at the tip of the bifurcation area; Figure 2.2i), a development supported by effective management (Kjesbu *et al.*, 2014).

Our results demonstrate how ocean warming induces a non-linear and discontinuous relationship between stock size and fishing pressure for most of the Atlantic cod stocks, limiting their recovery. Our study has limitations resulting from uncertainties in the stock assessment data used, but also due to the methodological confines of the stochastic CUSP modelling approach, such as deficiencies in accounting for autocorrelation in time-series (Diks & Wang, 2016) and uncertainties when comparing the CUSP model fit to alternative models (Chow *et al.*, 2015). Furthermore, we acknowledge that a detailed understanding of the effect of temperature on biological processes such as growth (Morgan *et al.*, 2018; Tu *et al.*, 2018) and recruitment (Pershing *et al.*, 2015b; Koenigstein *et al.*, 2018) is needed to better explain our statistical model results. However, as the CUSP models are superior to alternative models, we believe our modelling results are valid in resolving a long-lasting debate about the relative importance of ocean temperature and fishing in regulating cod stocks dynamics.

Conclusions

Here, we contribute a novel assessment of the vulnerability of Atlantic cod stocks to climate change, explicitly accounting for the potential of non-linear and state-dependent dynamics that will be useful for ecosystem-based management of other fish species as well. Other resource

species may follow similar catastrophic dynamics as we have here demonstrated for Atlantic cod, and as such we suggest that a precautionary approach accounting for environmental change is warranted for the sustainable management of living resources under the expected future climate change (Levin & Möllmann, 2015). Eventually, we demonstrated the usefulness of the stochastic CUSP modelling approach to explain abrupt changes in ecological systems which hopefully will spur application as seen in other scientific disciplines.

Supplementary Information Chapter 2

Supplementary Information Text

Recovery analyses

Atlantic cod stocks have shown synchronous collapses and very little recovery in many areas of the North Atlantic. In order to confirm these results and back up our analyses on the non-linearity of cod stocks behaviour, we performed analyses on collapse and recovery. Collapse was investigated using statistical change point and trend analyses on long-term time-series of Spawner Biomass (SB). We applied *Bayesian Change Point Analysis* (bcp(Erdman & Emerson, 2007)), which returns a posterior probability of a change to occur at each year of the time series. In order to identify a breakpoint in time indicating a major shift, we validated the bcp results with a trend analysis. The trend analysis estimates the second derivative of the SB time-series smoothed by fitting a Generalized Additive Model (GAM) to time (Fewster *et al.*, 2000) and allow to detect years with increases in the rate of change in the SB time-series. Combining the two approaches allowed us to identify for each cod stock the year in which a major change point occurred and to better understand the trends in SB (FigureS2.1). A high frequency of collapses occurred during the early 1990s with 15 of the stocks declining to below 50% of pre-collapse SB. Only North-East Arctic cod collapsed already before the 1960s and afterwards SB increased abruptly, while the stocks in the Celtic Sea, on the Faroe Plateau and in the Gulf of Maine exhibited oscillating trajectories and a very recent stock depletion.

In order to compare biomass trajectories across cod stocks we used Principal Component Analysis (PCA) using SB data from 1983 to 2016. Missing values at the end of the time-series (i.e. when the time-series did not include 2016 or before) were substituted with the last value to allow for a PCA with all stocks. The main mode of variability across stocks (PC1, 58%) shows constantly declining SB since the early 1990s (Figure S2.2a) to which 16 of the 19 cod stocks were positively correlated (Figure S2.2b). A second mode (PC2, 20%) indicates partial recovery since the mid-2000s, a temporal pattern highly positively correlated to the North-East Arctic, Icelandic and Flemish Cap, as well as North Sea cod (Figure S2.2c).

Finally, we calculated a *Recovery Index* (RI) for all Atlantic cod stocks by comparing the average of the SB over the last 5 years (SB_{mean}) to the pre-collapse SB ($SB_{pre-collapse}$):

$$RI = (SB_{mean}/SB_{pre-collapse}) \times 100$$

Afterwords we classified all cod stocks into three recovery classes: (i) *collapsed* – RI ≤ 20%, (ii) *recovering* – RI >20 and ≤50%, and (iii) *recovered* – R >50%. We found only two stocks *recovered*, i.e. North-East Arctic and Flemish Cap cod, and six stocks *recovering*. 11 of the 19 stocks can still be considered *collapsed* (Figure S3.3).

Supplementary Information Plots
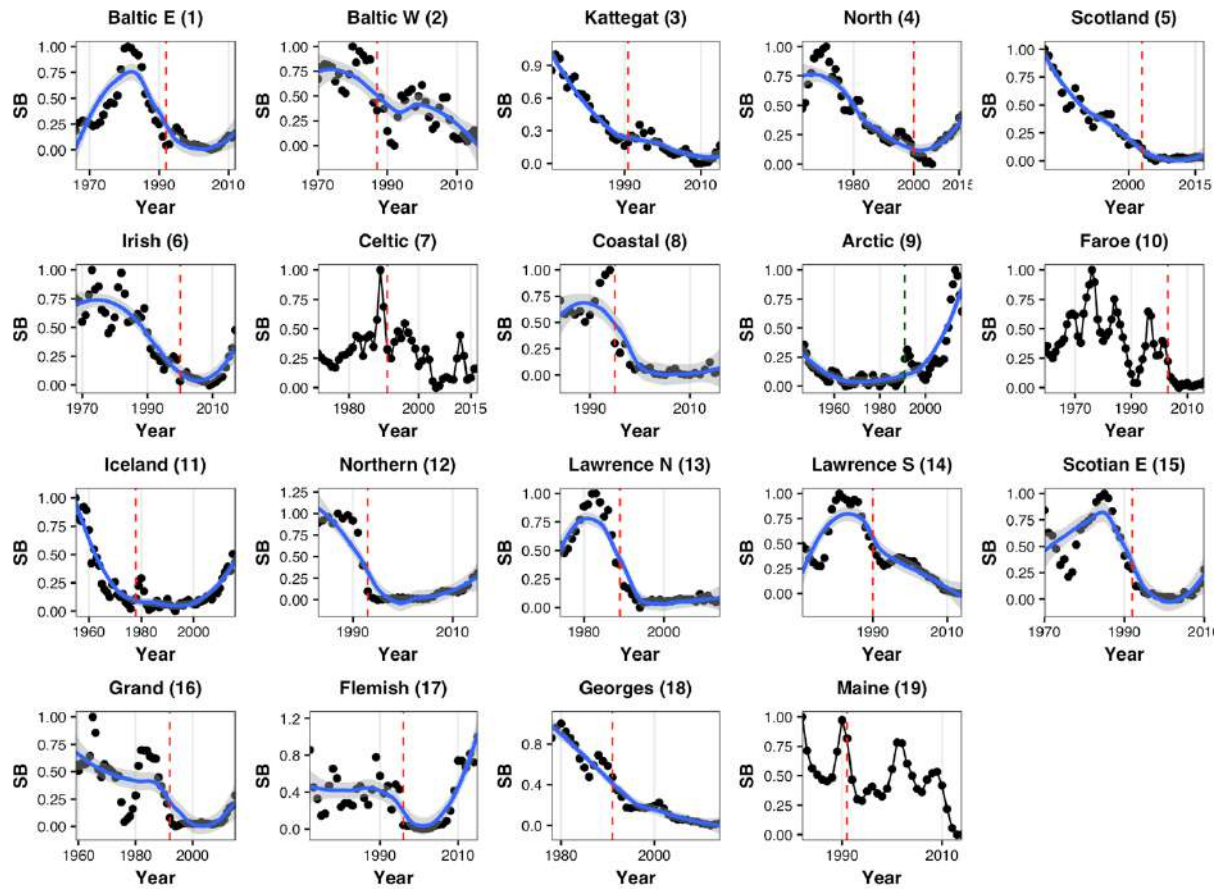
Figure S2.1. Spawner biomass trends and changepoints.
Scaled (between 0 and 1, SB-min(SB)/max(SB)-min(SB)) Spawners Biomass (SB) time-series of Atlantic cod stocks. Blue smoother lines indicate time trends and were fitted using Generalized Additive Modelling (no smoother was fitted to stocks that mainly oscillate). Dotted vertical lines represent the major change points in the time series (red lines indicated negative, green lines positive change points) derived by Bayesian Change Point and Trend Analysis. Stock names and numbers according to Table S3.2.1.
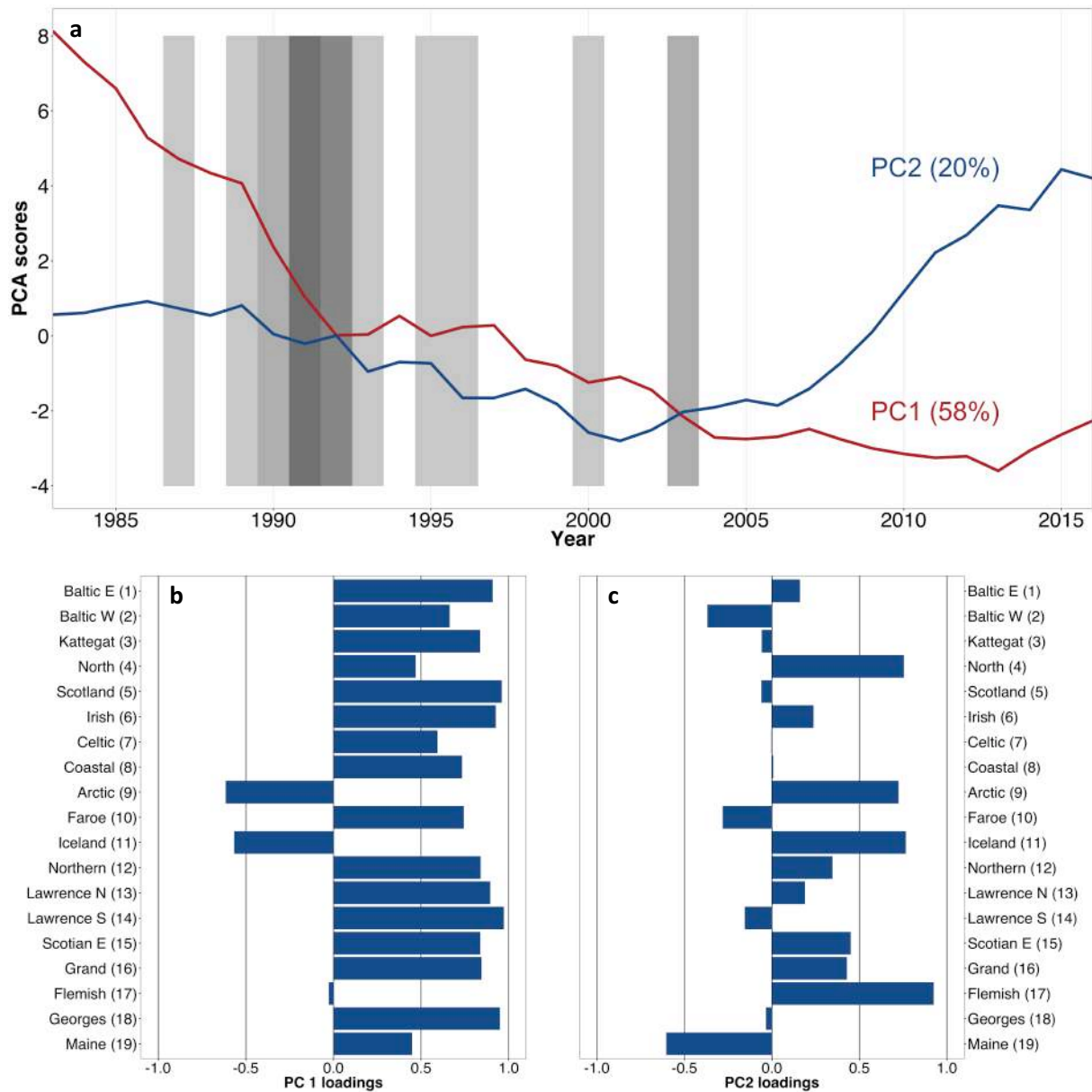
Figure S2.2. Collapse and recovery modes.
a, Dominant modes of Atlantic cod stock collapse and recovery revealed by PCA. PC1 (red line) indicates that most of the stocks are still in a *collapsed* state, PC2 (blue line) indicates a *recovery* pattern. Grey vertical bars indicate the number of stocks showing a significant change in any given year (light grey=1, dark grey=4). **b**, Loadings of Atlantic cod stocks on PC1 indicating that most of the stock´s trajectory have a high correlation to the *collapsed* mode. **c**, Loadings of Atlantic cod stocks on PC2 indicating the *recovery* state of cod stocks, i.e. their correlation to the recovery mode indicated by PC2. Stock names and numbers according to Table S3.2.1.
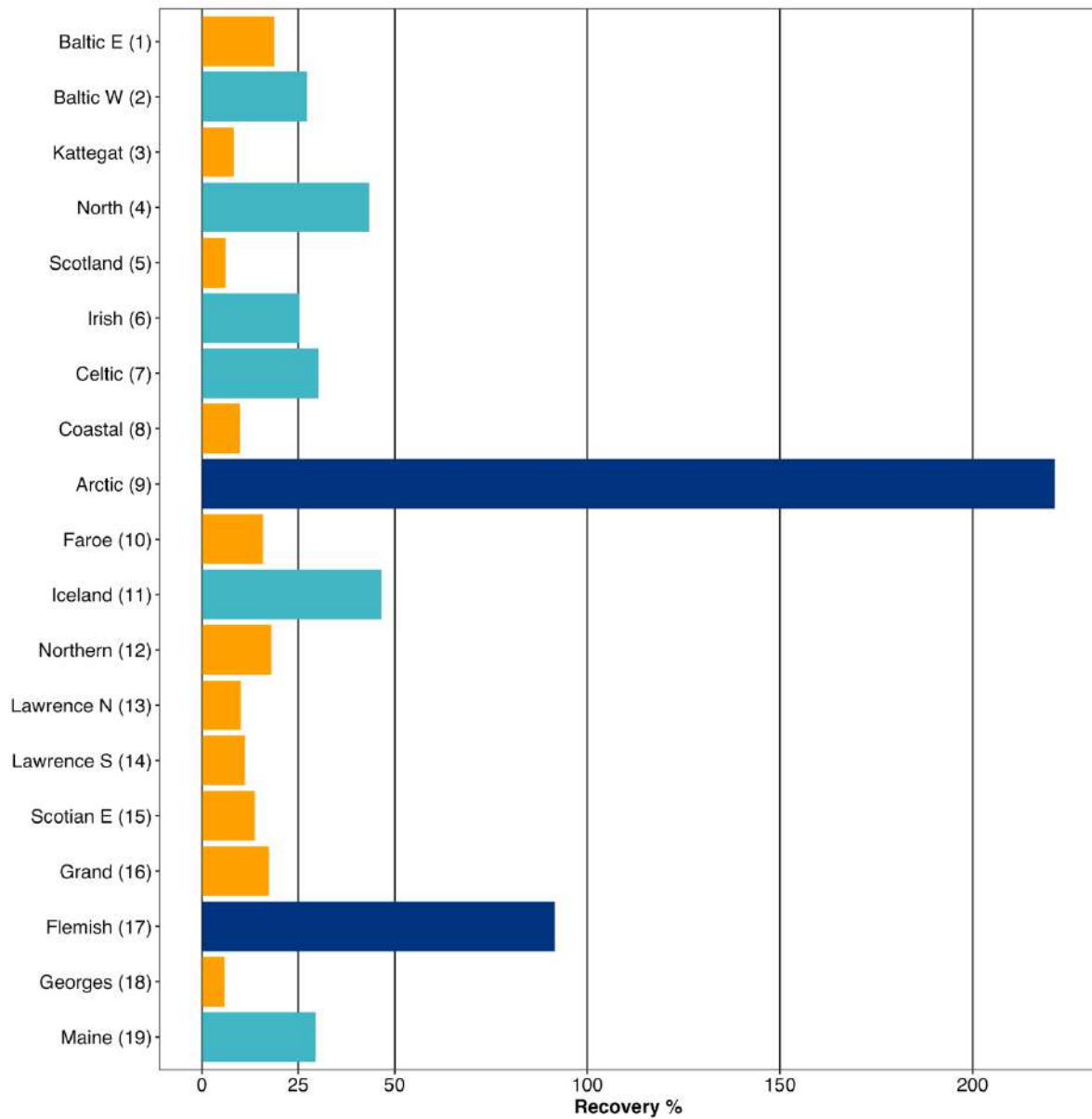
Figure S2.3. Recovery index (RI).
Recovery state of Atlantic cod stocks indicated by a recovery index (SI methods) indicating stocks to be still *collapsed* (orange), *recovering* (light blue) and *recovered* (dark blue). Stock names and numbers according to Table S3.2.1.
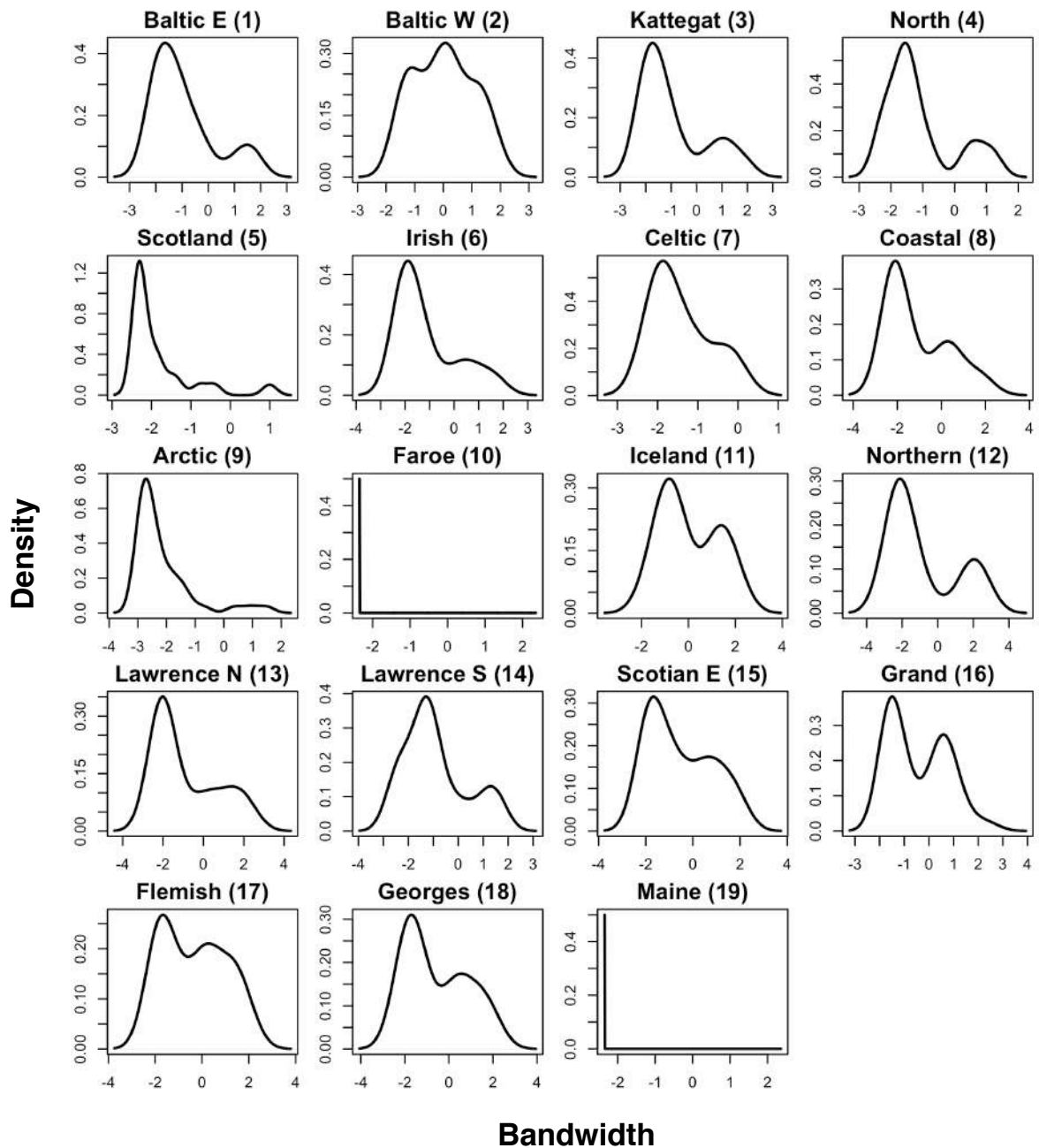
Figure S2.4. Bimodality in the bifurcation set.
Evaluation of bimodality inside the bifurcation set (upper left inlet) as an indicator of validity of stochastic CUSP models for Atlantic cod stocks. Empty plots indicate models with only one point in the bifurcation set. Stock names and numbers according to Table S3.2.1.
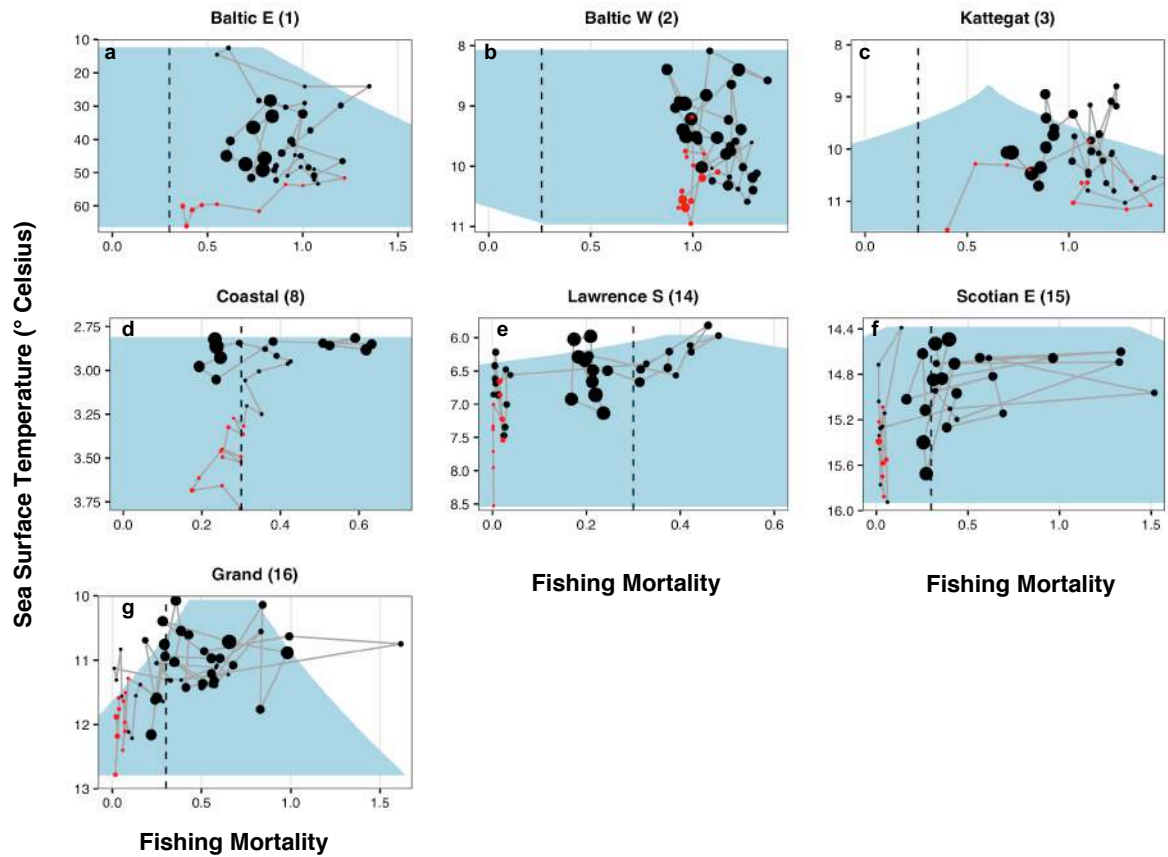
Figure S2.5. 2D representation of CUSP model results.
Stock trajectories of Atlantic cod stocks depending on fishing mortality and sea surface temperature (except for Baltic E which is modelled depending on the extend of anoxic areas; see method). Dot size is scaled according to the annual Spawners biomass of each stock. Red dots represent years ≥2004. The blue area indicates the bifurcation set of the CUSP model. Vertical dotted lines indicate the management target specific for each stock (SI Table 3.2.3) Stock names and numbers according to Table S3.2.1.
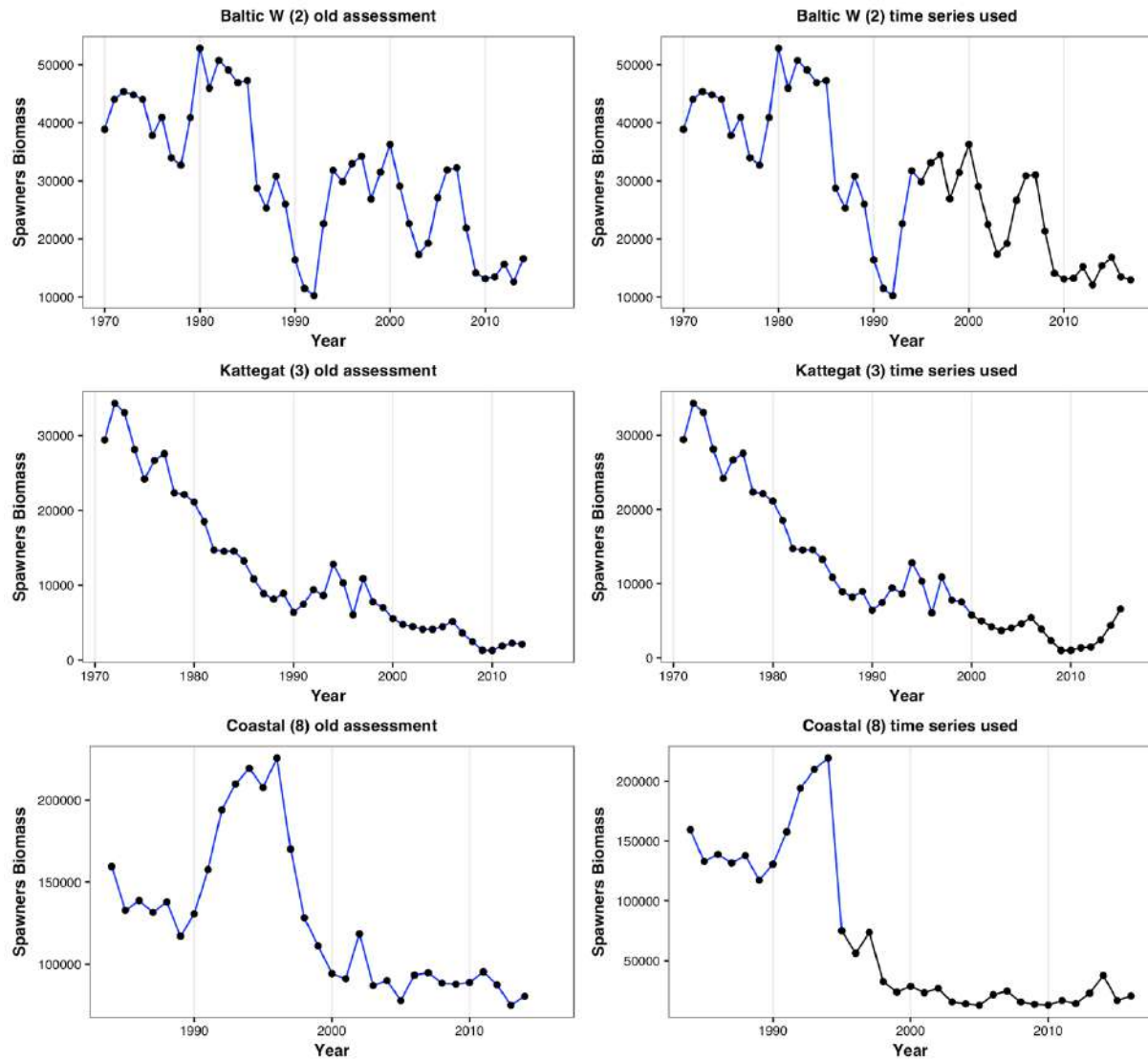
Figure S2.6. Stock assessments series used for three short time series stocks. On the left the time series of SB of the older assessments, 2014, 2015 and 2016 for respectively Western Baltic, Kattegat and Coastal Cod. On the right the combined time series of the old stock assessments (in blue) and of the new 2017 stock assessments (black).

Supplementary Information Tables

Table S2.1. Stock assessment data of Atlantic cod stocks.

No.	Stock name	Abbreviation	Management area	Stock assessment models*	Institution/ group	Contact person or other data source
1	Eastern Baltic[1]	Baltic E	25-32	SAM	ICES/ WGBAFS	Margit Eero
2	Western Baltic[2]	Baltic W	22-24	SAM	ICES/ WGBAFS	Margit Eero
3	Kattegat[1,2]	Kattegat	IIIa/21	SAM	ICES/ WGBAFS	Johan Lövgren
4	North Sea	North	IV – VIId – IIIa	SAM	ICES/ WGNSSK	Alexander Kempf
5	West of Scotland	Scotland	VIa	TSA	ICES/ WGCSE	Rui Catarino
6	Irish Sea	Irish	VIIa	SAM	ICES/ WGCSE	Colm Lordan
7	Celtic Sea	Celtic	VIIe – VIIk	XSA	ICES/ WGCSE	Colm Lordan
8	Coastal Barents Sea[2]	Coastal	I – I	Survey SSB and F from VPA	ICES/ AFWG	Gjert Endre Dingsor
9	Northeast Arctic	Arctic	I – II	XSA	ICES/ AFWG	Gjert Endre Dingsor
10	Faroe Plateau	Faroe	Vb1	XSA	ICES/ NWWG	Petur Steingrund
11	Iceland	Iceland	Va	Forward based statistical catch at age model	ICES/ NWWG	Einar Hjorleifsson
12	Northern cod	Northern	2J3Kl	State space model	DFO	DFO(2016)[3]
13	Northern Gulf of st. Lawrence	Lawrence N	3Pn4Rs	SPA	DFO	Claude Brassard
14	Southern Gulf of st. Lawrence	Lawrence S	4T4Vn	SCA	DFO	Doug Swain
15	Eastern Scotian Shelf	Scotian E	4VsW	VPA	DFO	Swain & Mohn (2012)[4]
16	Grand Banks	Grand	3NO	SPA	NAFO	NAFO (2015)[5]
17	Flemish Cap	Flemish	3M	Bayesian model	NAFO	Diana Gonzalez
18	Georges Bank	Georges	5z	Age structured model	NOAA	Loretta O´Brien
19	Gulf of Maine	Maine	5y	Age structured model	NOAA	Mike Palmer

Stock number (No.), stock name, abbreviation, management area code, stock assessment models used and the institution (or working group within the institution) conducting the stock assessment. Scientists providing data (or other data sources)

* SAM – State-space assessment model, TSA – Analytical age-based assessment (time series analysis), XSA – Extended survivor analysis, SPA – Sequential population analysis, SCA – Statistical catch at age, VPA – Virtual population analysis
[1] Stocks that in the last year failed the assessment
[2] Stocks where, in order to have longer time series, we mixed old assessments and new ones, after checking for same trends and stock dimensions.
[3] DFO (2016) Stock Assessment of Northern Cod (NAFO Divs. 2J3KL) in 2016. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2016/026
[4] Swain DP, Mohn RK (2012) Forage fish and the factors governing recovery of Atlantic cod (Gadus morhua) on the eastern Scotian Shelf. Can. J. Fish. Aquat. Sci. 69: 997–1001.
[5] NAFO (2015) Assessment of the Cod Stock in NAFO Divisions 3NO. NAFO SCR Doc. No. 15/034.

Table S2.2. Summary of data used in the analysis.

No.	SB (t)	FM	SST (°C)	ΔT(°C)	Assessment period
1	62193 – 643064	0.37 – 1.35	6.9 – 9.7	13.5 – 18.9	1966-2013
2	10229 – 52839	0.874 – 1.36	8.0 – 10.9	13. 4 – 19.0	1970-2016
3	977 – 34303	0.4 – 1.52	8.8 – 11.5	11.0 – 16.4	1971-2014
4	43739 – 274855	0.35 – 1.07	9.3 – 11.7	8.9 – 13.2	1963-2016
5	1435 – 40438	0.66 – 1.18	10.0 – 11.4	4.2 – 6.0	1981-2016
6	1389 – 19791	0.76 – 1.38	10.4 – 12.0	6.6 – 9.3	1968-2016
7	3397 – 26324	0.35 – 0.99	12.0 – 13.7	5.6 – 8.5	1971-2016
8	12709 – 219345	0.17 – 0.63	2.8 – 3.8	3.8 – 4.5	1984-2016
9	102610 – 2692927	0.21 – 1.02	2.5 – 3.8	3.7 – 4.8	1946-2016
10	16786 – 123077	0.19 – 0.82	8.9 – 10.3	2.9 – 4.9	1959 -2016
11	121063 – 936957	0.27 – 0.89	5.6 – 7.5	3.3 – 5.7	1955-2016
12	9680 – 940750	0.01 – 0.22	4.6 – 7.2	8.8 – 11.6	1983-2015
13	6774 – 200271	0.03 – 1.96	4.6 – 7.2	14.1 – 17. 6	1974-2015
14	33714 – 348193	0.01 – 0.48	5.8 – 8.5	15.5 – 18.7	1971-2014
15	4412 – 155525	0.01 – 1.52	14.3 – 16.0	11. 4 – 14.0	1970-2010
16	4231 – 125043	0.01 – 1.61	10.0 – 12.7	9.5 – 14.6	1959-2015
17	1697 – 42514	0.003 – 1.52	13.6 – 16.0	6.5 – 9.9	1972-2015
18	4066 – 98527	0.4 – 1.33	13.0 – 15.5	12.8 – 15.6	1978-2014
19	2526 – 21939	0.34 – 1.53	9.0 – 11.7	13.0 – 15.9	1982-2014

Ranges of Spawner Biomass (SB), Fishing Mortality (FM), Sea Surface Temperature (SST) and its annual variability (ΔSST) for the respective assessment period. Stock numbers (No.) according to Table S3.2.1.

Table S2.3. Management reference points for Atlantic cod stocks

No.	FM reference point	FM reference point value
1	-	-
2	F_{MSY}	0.26
3	-	-
4	F_{MSY}	0.33
5	F_{MSY}	0.17
6	F_{MSY}	0.3
7	F_{MSY}	0.35
8	-	-
9	F_{MSY}	0.4
10	F_{MSY}	0.32
11	HR_{MSY}	0.2
12	*	*
13	*	*
14	*	*
15	*	*
16	F_{lim}	0.3
17	F_{lim}	0.13
18	F_{MSY}	0.17
19	F_{MSY}	0.18

Fishing Mortality (FM) management reference points and their values. "-" shows stocks without available stock assessments. "*" indicates stocks for which FM reference points are not given in reports; Stock numbers (No.) according to Table S3.2.1.

Table S2.4| CUSP model evaluation.

No.	Percentage in bifurcation set	Bimodality
1	97.9	(+)
2	100	(+)
3	84	(+)
4	44	(+)
5	61	(+)
6	59.1	(+)
7	10	(-)
8	100	(+)
9	60	(-)
10	1.7	(-)
11	20.9	(+)
12	100	(+)
13	100	(+)
14	88.6	(+)
15	100	(+)
16	82.1	(+)
17	76.7	(+)
18	86.1	(+)
19	3	(-)

Two criteria for a CUSP model to be considered valid; (i) percentage of data points inside the bifurcation area (should be > 10%) and bimodality of the state variable inside the bifurcation area. Models underlined in grey are not valid CUSP models according to these criteria. Stock numbers (No.) according to Table S3.2.1.

Table S2.5. CUSP model results.

No	1	2	3	4	5	6	7
α	0.1193	0.195	0.83	0.6521	1.766	-0.08	-4.183**
$\alpha 1$	-0.8306	-0.169	-1.38*	-1.81*	-3.044	-0.46	3.65*
β	0.7731	4.593	-13.4**	-18.78***	-54.01***	-42.79***	-50.38**
$\beta 1$	3.76E-02*	-0.37	1.53***	1.946***	5.26***	3.94***	3.87**
w0	-2.6***	-2.501**	-2.41***	-3.059***	-2.538***	-2.40***	-2.62***
wi	6.75E-06***	8.41E-05***	1.28E-04***	1.649e-05***	9.272e-05***	1.993e-04***	1.711e-04***
AIC	1164	879	830	1211	684	867	784
R^2	0.77	0.69	0.75	0.38	0.64	0.59	0.006

No	8	9	10	11	12	13
α	-0.68	2.42**	-2.80	4.652***	-1.589*	-0.3361
$\alpha 1$	-0.712	-9.86***	1.904	-14.91***	9.028**	0.07356
β	-10.97***	20.88***	-34.42***	3.96	4.019	-4.384
$\beta 1$	4.49***	-5.51***	3.603***	-0.348*	0.03434	1.432**
w0	-2.568***	-3.17***	-2.311***	-3.166***	-2.479***	-2.532***
wi	2.07E-05***	1.731e-06	2.389e-05***	5.465e-06	5.21E-06***	2.41E-05***
AIC	751	1925	1184	1579	902	952
R^2	0.77	0.78	0.30	0.77	0.94	0.85

No	14	15	16	17	18	19
α	-0.656**	-0.4955**	-0.8824**	-0.5193*	2.017*	-0.117
$\alpha 1$	1.555	0.6841	1.431**	0.5957	-3.463**	-1.186
β	-14.72***	-22.28*	-5.4	-31.38*	-15.12	-27.800**
$\beta 1$	2.526***	1.626*	0.6125	2.198*	1.234*	2.631**
w0	-3.012***	-2.143***	-1.878***	-2.132***	-2.325***	-2.286***
wi	1.35E-05***	2.67E-05***	3.46E-05***	1.12E-04***	4.42E-05***	1.51E-04***
AIC	1036	907	1178	804	762	556
R^2	0.65	0.80	0.62	0.69	0.76	0.25

Estimated parameters (α_0/α_1 for predictor Fishing Mortality; β_0/β_1 for predictor Temperature [except for stock 1 where anoxic areas was used]; w_0/w_1 for the state variable Spawner Biomass. Model validation using AIC (ΔAIC computed as the difference between AIC of the linear and the CUSP model) and R^2 (Cobb´s Pseudo R squared). Stars indicate significance of parameters (* <0.05, ** <0.005, *** <0.0005). Stock by stock plots of the CUSP models can be found in Extended Data. Models highlighted in grey are not valid CUSP models (see Table S4). Stock numbers (No.) according to Table S3.2.1.

Chapter 3: Cod stock-recruitment relationship

Coupling and decoupling of spawner biomass and recruitment explain Atlantic cod collapse and recovery

Camilla Sguotti[1], Romain Frelat[1], Xochitl Cormon[1], Saskia Otto[1], Christian Möllmann[1]

Abstract

Cumulative stressors on marine populations have led to profound changes of population mechanisms and astonishing collapses. The biomass of many Atlantic cod (*Gadus morhua*) stocks collapsed abruptly around the 1980s and 1990s and did not recover since then. Some stocks have experienced a persistent and pronounced recruitment failure. However, the relationship between recruitment and biomass is not fully understood. Here, applying partial wavelet coherence analysis on 17 cod stocks, we show that the stock - recruitment relationship is transient and stock state-dependent. We show that the relationship is particularly strong during collapse and the recovery periods. Moreover, we identify mechanisms of collapse and recovery using phase analysis showing that while collapses were caused by a combination of recruitment failure and overfishing, recovery is mainly driven by recruitment success. Stocks that collapse abruptly are less likely to recover compared to stocks that collapse more gradually, due to a stronger relationship in between recruitment and biomass. Our study sheds light into the complex interplay between stock size and year-class strength and can thus support the application of more efficient management measures, highlighting the need to consider non-linear and state-dependent dynamics in management.

Author´s affiliations
[1]Institute for Marine Ecosystem and Fisheries Science, University of Hamburg, Germany

Introduction

Marine populations have undergone huge changes (Planque *et al.*, 2010; Tu *et al.*, 2018) due to anthropogenic pressures in the last decades, in particular due to fisheries exploitation (Pauly *et al.*, 1998; Myers & Worm, 2003; Hutchings & Reynolds, 2004; Branch *et al.*, 2010) and climate change (Brander, 2010). The interactive effects of these external drivers have often resulted in spectacular collapses of living marine resources (Hsieh *et al.*, 2006; Anderson *et al.*, 2008) and significant ecological reorganizations (Frank *et al.*, 2005; Möllmann *et al.*, 2009; Steneck *et al.*, 2011), with huge economic losses (Allison *et al.*, 2009; Srinivasan *et al.*, 2012). To promote the recovery of collapsed stocks, fisheries management has partly adopted drastic measures to exploitation pressure (Hilborn, 2007; Melnychuk *et al.*, 2016). However, in many cases recovery of fish populations was delayed or did not happen at all even after decades of good management (Hutchings, 2000; Lotze *et al.*, 2011). Non-linear, discontinuous and non-stationary dynamics may be underlying these failed comebacks of many marine resource populations (Frank et al. 2011).

Non-linearity and chaos are the prevalent dynamics in nature (May & Oster, 1976; Sugihara, 1994; Beninkà *et al.*, 2008) and emerge due to the inherent complexity of natural dynamical systems governed by multiple pressures (Hsieh *et al.*, 2006; Anderson *et al.*, 2008; Glaser *et al.*, 2014). In the marine environment, non-linear discontinuous dynamics resulting in ecological surprises have been recorded at different organizational levels (Beaugrand *et al.*, 2015; Möllmann *et al.*, 2015; Perretti *et al.*, 2017). Forecasting the trajectory of fish populations which exhibit these non-linear dynamics is fundamental in order to anticipate their response to human and natural stressors (Glaser *et al.*, 2014; Schindler & Hilborn, 2015; Ye *et al.*, 2015; Dakos *et al.*, 2016), but is often overlooked due to the difficulty of incorporating non-stationarity and discontinuity in statistical models (May, 1976b; May & Oster, 1976; Ye *et al.*, 2015). However, during the last decades a number of methods have been developed and applied to account for non-stationarity allowing a better understanding of fluctuations of natural populations. These methods range from statistical non-parametric methods to spectral analysis methods, such as the wavelet analysis (Sugihara 1994; Cazelles et al. 2008; Ye et al. 2015; Deyle et al. 2018).

Decomposing times series into harmonic components in order to identify regular frequencies of fluctuations has been a common practice in ecology since more than 50 years, using especially Fourier decomposition. However, time series were often assumed to be stationary, with invariant statistical properties over time (Platt & Denman, 1975; Chatfield, 1989). With the increasing evidence of non-stationarity of natural systems, new methods have been developed also in spectra analysis. Wavelet analysis, for instance, decomposes time series in time and frequency allowing to consider non-stationary dynamics (Torrence & Compo, 1998; Grinsted *et al.*, 2004; Cazelles *et al.*, 2008). The main principle of the method is to compare the studied time series to multiple functions, the so-called wavelets, similar in shape but more or less dilated. Decomposing the signals over multiple functions, wavelet analysis detects variations in time series at multiple frequencies, thus its results are superior to other alternative techniques like the windowed Fourier decomposition where the frequency is invariant over time

(Cazelles *et al.*, 2008). Even though suffering from apparent lack of quantitative results, wavelet has been applied to many research questions in ecology, oceanography, anthropology and physics, such as the analysis of association between animal populations and environment change (Downey *et al.*; Rohani *et al.*, 2003; Klvana *et al.*, 2004; Cazelles *et al.*, 2005).

Recruitment is the most important mechanism controlling the dynamics of marine fish populations (Houde, 1987; Britten *et al.*, 2016), and in fisheries science is defined as the number of juveniles entering the adult, fishable stock. Recruitment is directly coupled to adult biomass, and this coupling provides fisheries management with estimates of incoming year-class strength as a basis for setting fishing opportunities (Houde, 1987; Kraus *et al.*, 2000; Perretti *et al.*, 2015). However, the stock recruitment relationship is also one of the unsolved mysteries of fishery science and its existence is often questioned since parametric models generally fail to account for the often high recruitment variability (Myers *et al.*, 1996; Cardinale & Arrhenius, 2000; Olsen *et al.*, 2011; Perlala *et al.*, 2017). Alternative hypotheses suggest that the relationship between recruitment and adult biomass might be non-linear and discontinuous (Ye *et al.*, 2015; Harford *et al.*, 2017; Deyle *et al.*, 2018), or non-stationary depending on stock conditions, i.e. recruitment is strongly correlated with adult biomass only when the stock size is low (Myers & Barrowman, 1996; Brander, 2005). The high uncertainty regarding the coupling between recruitment and spawning stock biomass has been further complicated by the fact that recruitment is influenced by many exogenous variables such as temperature (Sparholt, 1996; Planque *et al.*, 1999; Walters & Kitchell, 2001; Stige *et al.*, 2006; Stiasny *et al.*, 2016). Finally, like the egg and the chicken causality dilemma, it is still debated whether the adult population is conditioned on recruitment or vice-versa (Szuwalski *et al.*, 2015).

Here we used wavelet analysis to understand the variability in the coupling between adult biomass and recruitment of 17 cod stocks distributed all over the North Atlantic. This species is particularly suitable for our analyses because it underwent abrupt collapses around the 1980s and the 1990s due to unsustainable fishing pressure and temperatures changes (Myers *et al.*, 1997; Rose, 2004; Frank *et al.*, 2016). Moreover, cod stocks present hysteresis to recovery (i.e. delayed or absent recovery), discontinuous dynamics in stock biomass and, in many cases, show failure in recruitment success (Myers et al. 1994; Hutchings 2000; Brander 2005). Furthermore Atlantic cod is not only an iconic and economically valuable species for fisheries, but also an important species in the food webs of many ecosystems (Frank *et al.*, 2011). Therefore, understanding the dynamics of the coupling between recruitment and adult biomass in Atlantic cod stocks can help to understand mechanisms of collapse and recovery and potential consequences for management. We here used partial wavelet coherence analysis that evaluates coupled fluctuations between two time series. Our aim was to investigate whether (i) cod adult biomass and recruitment show temporally coupled or decoupled fluctuations, (ii) whether coupling/decoupling of these fluctuations can be related to observed stages of collapse and recovery (iii) and identify the sequence of a coupling (i.e. whether the adult population is conditioned on recruitment or vice-versa) as a mechanism explaining temporal patterns of collapse and recovery.

Materials and Methods

Data

We analysed the relationship between Recruitment (R, i.e. number of fish that recruit to the adult stock in thousands) and Spawning Stock Biomass (SSB, i.e. biomass of mature fish in tonnes) based on assessment data of 17 Atlantic cod stocks. Data were provided by the International Council for the Exploration of the Sea (ICES), the National Oceanic and Atmospheric Administration of the USA (NOAA), the Northwest Atlantic Fisheries Organization (NAFO), the Department of Fisheries and Ocean in Canada (DFO) and by personal communication (Supplementary Information, Table S3.1). Recent assessments for cod stocks in the Kattegat, the Western Baltic as well as the Norwegian coast have been conducted only for reduced periods. Therefore, we combined the recent and older stock assessments after consistency checks of SSB and R time-series. We used sea surface temperature (SST) to represent changes in environmental conditions experienced by each stock. Although SST does not fully reflect the thermal habitat of cod, a predominately demersal (bottom-dwelling) species, it has previously been shown to be a strong predictor influencing cod recruitment and in general stock dynamics, such as reproduction and growth (Brander, 1995; Drinkwater, 2005; Ottersen *et al.*, 2013). SST data were collated from the NOAA Extended Reconstructed Sea Surface Temperature dataset (ERSST, www.ncdc.noaa.gov) version 4. The dataset represents a reconstruction of SST from 1854 to the present and comprises monthly anomalies computed with respect to the period 1971-2000, resolved in a 2°x 2° grid of spatial resolution. Data on life history traits were also collected for every stock (Wang *et al.*, 2014).

Wavelet analysis

Fluctuations and changes in the time series were analysed using a wavelet transform decomposition (Torrence & Compo, 1998; Rouyer *et al.*, 2008a) (Supplementary Information, Figure S3.1-S3.2). In practice, this analysis can be thought of as a cross-correlation of a time series with multiple wavelets (Cazelles *et al.*, 2008). Results are traditionally summarized into a wavelet coefficient map, displaying the correlations between the studied time series and the wavelet functions as a function of time (x-axis) and dilation (y-axis). The wavelet transform decomposes the time series over a translated function called "mother wavelet" with 0 mean and localized both in time (τ) and scale (*a*). Here, we used the Morlet wavelet as "mother wavelet" since it allows for precision in both dimensions. Therefore, time series *x(t)* of SSB and R were decomposed as a wavelet transform:

$$W_x(a, \tau) = \frac{1}{\sqrt{a}} \int_{-\infty}^{+\infty} x(t)\varphi(\frac{t-\tau}{a})\, dt \qquad (1)$$

where φ is the Morlet wavelet of the form:

$$\varphi(t) = \pi^{\frac{-1}{4}} \exp(-i2\pi f_0 t) \exp(-t^2/2) \qquad (2)$$

where *t* is a non-dimensional time parameter and *f* a non-dimensional frequency parameter. In order to fit the wavelet and to avoid false periodic events, the edges of the time series needed

to be artificially increased adding zero-values (zero padding). Thus, the results of the spectra at the edge of the time series are usually lacking accuracy and should be interpret with caution (Torrence & Compo, 1998; Cazelles *et al.*, 2008; Rouyer *et al.*, 2008a). To highlight these areas in our plots, we computed the cone of influence for all the spectra, in which the results are inaccurate. Finally, 300 Monte Carlo randomizations were performed and a subsequent X^2 test to assess whether the patterns and fluctuations identified by wavelet transform were significant (significance level 0.05) (Cazelles *et al.*, 2008; Rouyer *et al.*, 2008b; Gouhier *et al.*, 2016).

Once this first analysis was performed, we explored the wavelet coherence between R and SSB of Atlantic cod stocks. Wavelet coherence is a method developed to analyse the coupling between two time series. To enhance our analysis interpretation, we used the partial wavelet coherence (PWTC). This technique allows to remove the effect of a third variable, to understand better and more precisely the relationship between the remaining variables (Ng *et al.*, 2012) (Supplementary Information, FigureS3.3). In our case, we select as third variable SST, since it has an effect on Atlantic cod R and it is also correlated with climate change (Brander, 2005; Stige *et al.*, 2006). The coherence between two time series y and x (i.e. R and SSB) can be considered as the strength of their association and can be written as:

$$R^2(x, y) = \frac{|s[W(x,y)]|^2}{s[W(x)] * s[W(y)]}$$ (3)

where *s* is the smoothing operator.

The partial wavelet coherence was computed like:

$$RP^2(y, x1, x2) = \frac{|R(y,x1) - R(y,x2) * R(y,x1)|^2}{[1 - R(y,x2)]^2 [1 - R(x2,x1)]^2}$$ (4)

The result of the partial coherence analysis is a spectrum defining in time and scale where changes in correlations between the two variables, R and SSB can be detected. Significantly paired fluctuations of R and SSB have been detected using 300 Monte Carlo randomizations and a subsequent X^2 test (Ng *et al.*, 2012). To check for the presence of coupling between R and SST we computed the PWTC, removing SSB.

Finally, our last objective was to detect the sequence of coupling i.e. whether changes in the synchronization between R and SSB could be detected. To understand if the two signals oscillate at the same time, we analyse the phases of our decomposed time series. Phase analysis is a non-linear technique which allows to study also weak interactions (Cazelles *et al.*, 2008). The phase is one of the components originating from the decomposition of a time series by the PWTC. It represents the angle between a point in the spectrum (x,y) and the x-axis representing time (Cazelles & Stone, 2003). Two signals are phase synchronized if the phases are locked together in a stable relationship. However, phases will often be locked only in certain times, and signals can be defined as in-phase, if they fluctuate both in the same direction (i.e. for a maximum of y corresponds a maximum of x), antiphase, if they fluctuate in opposite directions

(i.e. for a maximum of y corresponds a minimum of x), and delayed in time if one of the time series cycle starts before the other one. Therefore, using this analysis we were able to identify how R and SSB fluctuated relative to each other.

We summarized the results and detected common trends among Atlantic cod stocks by averaging the wavelet spectra derived from the PWTC, the results of the phase analysis, and the standardized time series of SSB and R. To average the phase analysis results, we firstly averaged the sine and cosine of the phase angle. Afterwards we back-transformed these Cartesian coordinates into angles using the inverse tangent, and obtained a mean phase for all the stocks. We then compared the results of the single stocks with the average to detect anomalous dynamics. In order to better explain the different dynamics, we categorized stocks depending on their status (recovered, collapsed) and the type of collapse they experienced (abrupt and gradual, see Supplementary Information, Table S3.2) and also averaged the PWTC within each category. To explain differences between stocks in the recovery patterns, due to different R-SSB coupling, we performed multiple Generalized Linear Models (GLM with a binomial distribution) using the presence of recovery as dependent and F, life history traits and the type of collapse as explanatory variables. Similarly, we use the same explanatory variables to explain the results in the phase analysis, however without testing for significance, since the sample sizes were too small (Supplementary Information, Table S3.3).

Statistical change point analysis
We conducted statistical change point analysis to identify abrupt changes in SSB and highlight periods of collapse and recovery. To detect the change points we applied two alternative approaches, (i) Bayesian Change Point (BCP) Analysis (Barry & Hartigan, 1993; Erdman & Emerson, 2007), and (ii) a binary segmentation algorithm (Rohrbeck; Killick & Eckley, 2013). BCP uses Bayesian statistics to calculate the probability that a change occurred at every point of the time series. Probabilities > 70% are considered to indicate significant changes. Binary segmentation uses a general likelihood ratio test to detect significant changes in the mean over the entire time series. After the first change has been detected, the time series is divided in two, and significant changes in these two parts are identified. We combined the results of both techniques to unequivocally define periods of significant changes in SSB. We defined periods instead of single years since the collapse or recovery of long-living demersal fish might be spread over multiple years. We subsequently evaluated whether changes in the coupling of R and SSB indicated by PWTC and phase analysis occurred during the periods of change highlighted by the change point analysis. This would indicate that SSB-R relationship is non-stationary and dependent on stock size. Finally, we categorized Atlantic cod stocks into those showing abrupt or gradual dynamics, depending on the reduction in biomass and the duration of the collapse. Collapses were considered abrupt if the biomass declined of more than 50% in a time between 6-8 years, commonly referred as one generation in Atlantic cod.

All the analyses were performed in R (R Core Team, 2017, version 3.3.1) using the packages: *bcp* (Erdman & Emerson, 2007), *changepoint* (Killick & Eckley, 2013) and *biwavelet* (Gouhier *et al.*, 2016).

Results

Trends and changes in Atlantic cod stocks

Change point analysis revealed that all Atlantic stocks collapsed around the late 1980s and early 1990s apart for the northern ones (Greenland (10), Iceland (9) and North-East Arctic cod (8)) that collapsed earlier, i.e. around the 1960s (Figure3.1). Since we were focusing on the stocks' collapse dynamics, we restricted the further analyses to the years between 1985 and 2010 for each stock in the Eastern and Western parts of the North Atlantic, also to be able to compare all the stocks. However, since the three northern stocks collapsed earlier and have longer time series available (Figure3.1(10,9,8)), we considered for them the period between 1960 and 2010. All Western stocks collapsed quickly around the 1990, while the Eastern stocks (Figure3.1) were more variable. Out of 17 stocks 10 displayed abrupt dynamics, in particular all Western stocks, Greenland cod in the North (10), and the two Eastern stocks, the Eastern Baltic (1) and West of Scotland (5) (Figure3.1, Supplementary Information, TableS3.2). The remaining stocks showed more or less gradual declines (Figure1, Supplementary Information, TableS3.2).
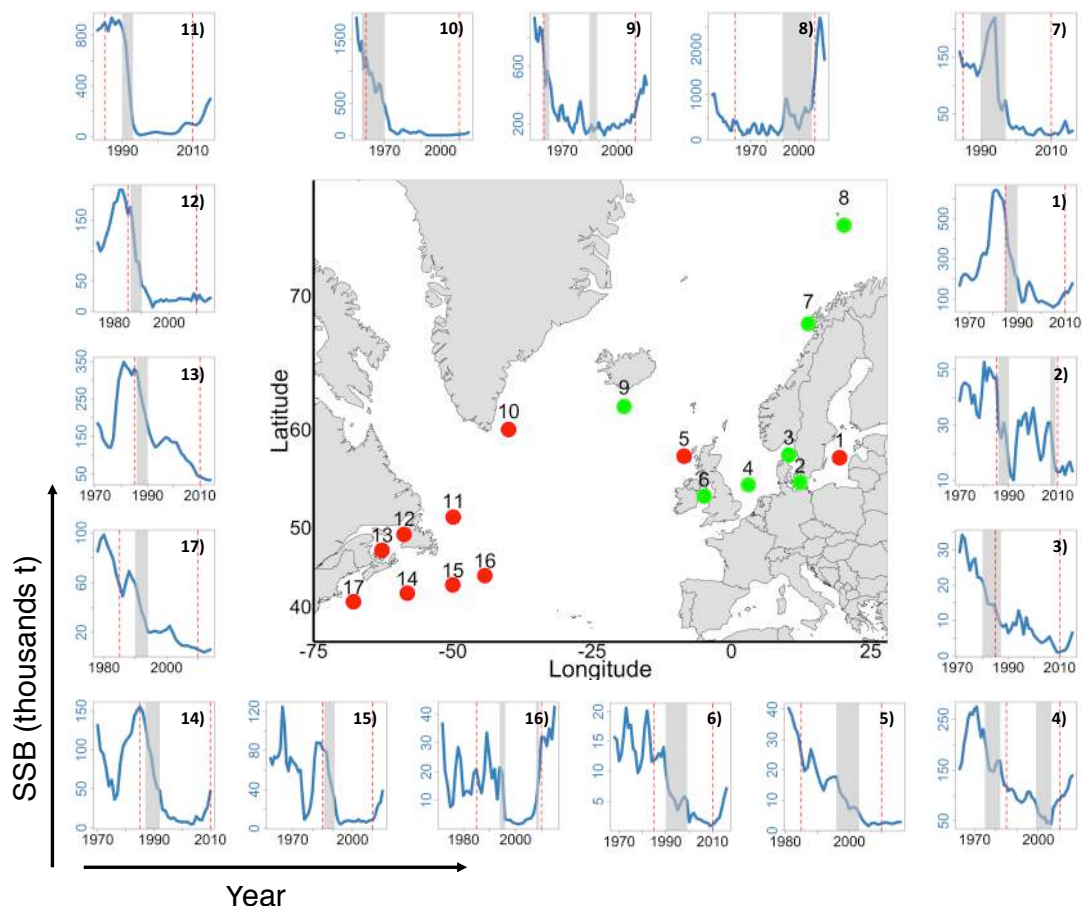
Figure 3.1: **Trends in spawning stock biomass (SSB) of 17 North Atlantic cod stocks.** In the middle, a map with the location of the 17 cod stocks. Numbers are according to Table S3.1 in the Supplementary Information (1=Eastern Baltic, 2=Western Baltic, 3=Kattegat, 4=North Sea, 5=Irish Sea, 6=West of Scotland, 7=Coastal Norwegian, 8=North-East Arctic, 9= Iceland, 10=Greenland, 11=Northern cod, 12=North Lawrence, 13=South Lawrence, 14=Eastern Scotian Shelf, 15=Grand Banks, 16=Flemish Cap, 17=Georges Bank). Red dots are stocks that collapse abruptly, while the green dots indicate more gradual dynamics. Note that the x and y axes are adjusted to fit the stock biomass range and the period of the time series and hence vary among plots. Grey shades indicate periods with changes in stock status. Vertical red dotted lines show the time series used for the wavelet and the change point analyses between 1985 and 2010, or, for the northern stocks between 1960 and 2010.

Partial wavelet coherence (PWTC) analysis between recruitment (R) and Spawning Stock Biomass (SSB) of Atlantic cod stocks, allowed us to understand the coupling of these two variables accounting for the effect of sea surface temperature (SST). Single stock plots, showed that the R-SSB relationship was not stable and its strength changed over time (Supplementary Information Figure S3.4-3.5; low strength in blue and high strength in red). In particular, PWTC revealed a change in the coupling between R and SSB at the same time as the change point analysis identified changes in biomass dynamics. Our analyses allowed us to identify 4 major stages in the dynamics of Atlantic cod, i.e. "healthy", "collapsing", "hysteresis" and "recovery kick-off". The identification of these 4 stages confirmed that the R-SSB coupling was highly state-dependent (Figure3.2). The 4 stages were also found in the single stock time series, but depending on the stock dynamics, not all four stages were present for all the stocks (Figure3, Supplementary Information, FigureS3.4-S3.5).
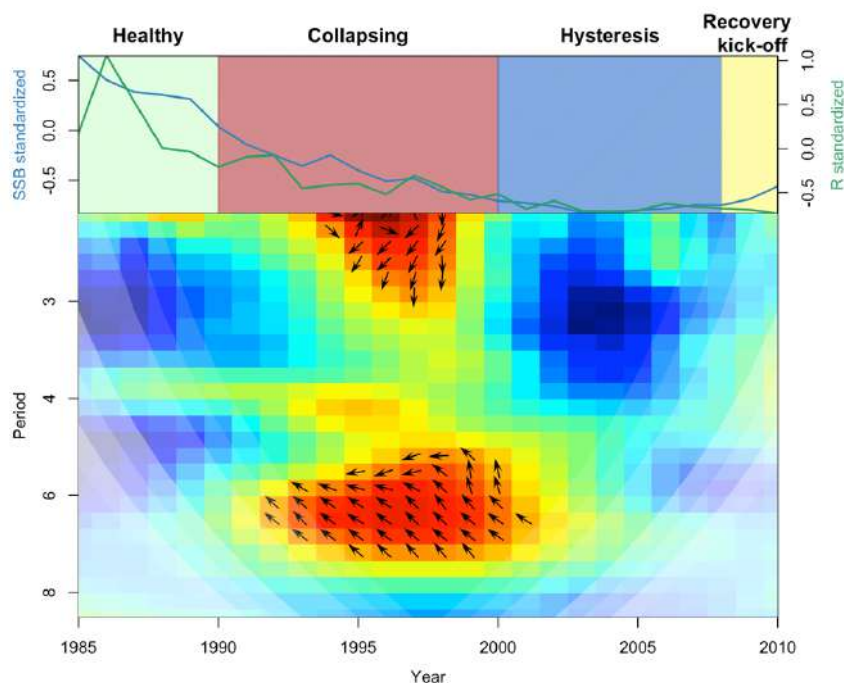

***Figure 3.2*: The 4 stages of Atlantic cod stock dynamics.** The upper plot shows the average of the standardized R and SSB time series among cod stocks (SSB in blue and R in green). Colours indicate the 4 stages of Atlantic cod stocks based on the PWTC results and the stock dynamics. Corresponding results of the average PWTC between R and SSB for all Atlantic cod stocks is given below. Time is shown on the x axis, while period in the y axis. The colours correspond to the strength of the R-SSB coupling (red=strong, blue=weak). The arrows correspond to the average result of the phase analysis. Arrows pointing up indicate that SSB drives R, pointing down that R drives SSB, pointing left that the signal are antiphase and pointing right in phase. The white shadow represents the cone of influence of every stock; the stronger the white shadow the more uncertain the results.

The 4 stages of Atlantic cod stock dynamics
The healthy stage – Using PWTC we detected on average a strong decoupling of R and SSB in Atlantic cod stocks before c. 1990, i.e. before the overall collapse period (Figure 3.2, in blue). During this period both biomass and recruitment were relatively high, but fluctuating independent from each other. We observed this first stage in the dynamics of Atlantic cod in all the stocks with slight differences in timing related to when the collapse occurred (Figure3.3). For instance, in North Sea and in Flemish cod, the decoupling between R and SSB weakened before the 1990 (Figure3.3). Since the two variables were decoupled during the healthy stage, the phase analysis gave non-significant results. After 1990s, almost all the stocks collapsed and moved from the healthy to the collapsing stage.
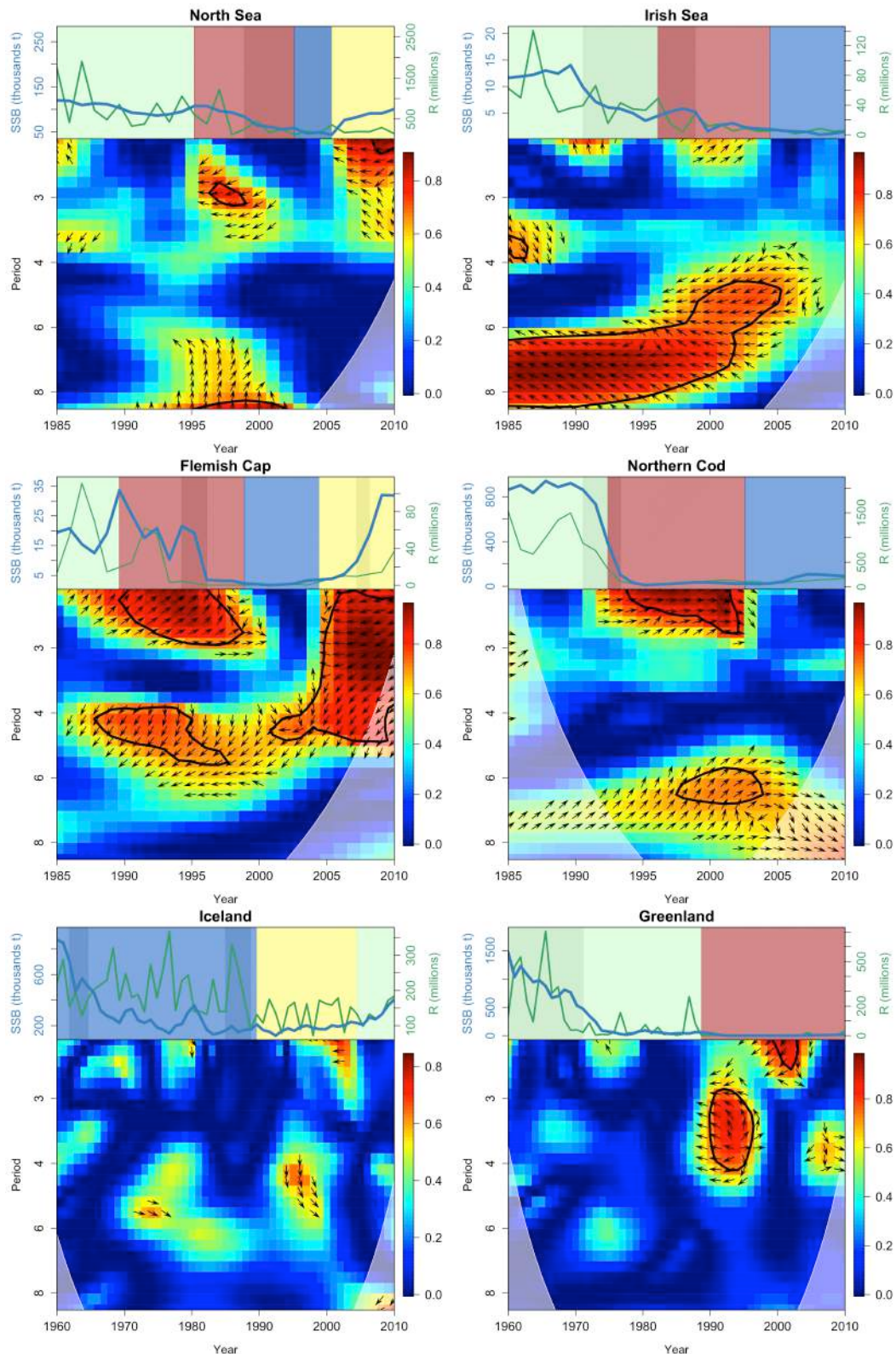
Figure 3.3: **Results of the Partial Wavelet Coherence Analysis (PWTC) for selected Atlantic cod stocks.** The upper plot in each panel shows the R (green) and SSB (blue) time series. The colours of the different periods correspond to the stages highlighted in Figure3.2. The shaded areas represent the period of the change point, defined by the change point analysis. Below the corresponding results of the PWTC between R and SSB are given for each stock. Time is shown on the x axis, while period on the y axis. Colours correspond to the strength of the R-SSB coupling (red=strong, blue=weak). The black line identifies significant changes from the mean. The arrows correspond to the average result of the phase analysis. Arrows pointing up indicate that SSB drives R, pointing down that R drives SSB, pointing left that the signal is in antiphase and pointing to the right it is in phase. The white shadow represents the cone of influence where the results are uncertain.

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Table 3.1: **Stages characteristic of the 17 Atlantic cod stocks.** Stocks, stocks numbers and the presence of recovery stage are indicated in the first 3 columns. The last columns show the drivers of collapse of Atlantic cod stocks at short and long period, and the drivers of recovery at short period, identified by the phase analysis.

Stock	N°	Existence of Recovery Kick-off stage	Driver short cycle collapse	Driver long cycle collapse	Driver recovery
Eastern Baltic	1	no	SSB	SSB	-
Western Baltic	2	yes	R	SSB	SSB
Kattegat	3	no	-	-	-
North Sea	4	yes	R	SSB	SSB
West of Scotland	5	no	R	-	-
Irish Sea	6	no	SSB	R	-
Coastal Norwegian	7	yes	-	SSB	R
North-East Arctic	8	yes	-	-	R
Iceland	9	yes	-	-	R
Greenland	10	no	R	-	-
Northern	11	no	in phase	SSB	-
North Lawrence	12	no	R	SSB	-
South Lawrence	13	no	R	-	-
Eastern Scotian	14	no	SSB	SSB	-
Grand Banks	15	no	-	R	-
Flemish Cap	16	yes	SSB	R	R
Georges Bank	17	no	R	SSB	-

The collapse stage – Between 1990 and 2000 all Eastern and Western Atlantic cod stocks collapsed (Figure 3.2, 3.3, Supplementary Information, Figure S3.4-S3.5). During this stage of cod dynamics, we found a strong coupling between R and SSB at both short (around 3-4 years) and long time periods (around 6-8 years). This strong coupling was related to the synchronous decline of R and SSB detected by the change point analysis. Phase analysis revealed which variable initiated this strong coupling (Figure 3.2, arrows). At longer periods, in 70% of the stocks the main driver was SSB (arrows pointing up), while at short periods the main driver was R (arrows pointing down, in 58% of the stocks) (Table 3.1). For instance, the North Sea and the Northern cod followed exactly the described pattern, while Irish Sea and Flemish Cap cod displayed a reverse pattern, with the short R-SSB coupling being dominated by SSB and the long one by R (Figure 3.3, Table 3.1). In order to understand why stocks experienced a different sequence of coupling, we visually related their drivers at short and long period with the mean fishing pressure, the mean temperature and the age at 50% maturity during the collapsing stage (Supplementary Information, Table 3.3). We found that R was the driver during the short period coupling when fishing pressure was high, but temperatures and age at maturity low (Figure 3.4a). Instead, during the long period, SSB was the driver in particular when fishing pressure was high (Figure 3.4b).
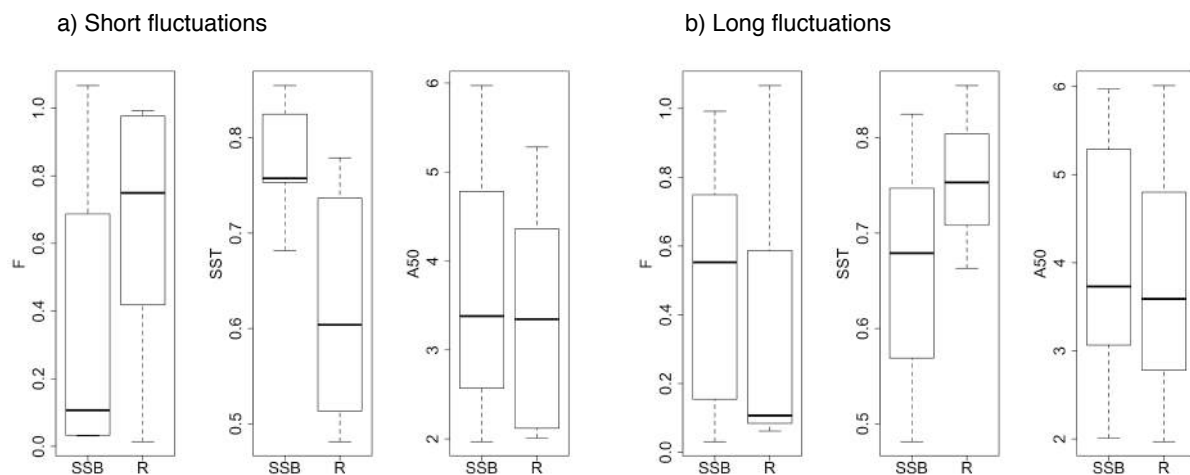
a) Short fluctuations   b) Long fluctuations

Figure 3.4: **Relation between drivers and state variables. a) the short and b) the long period coupling between R and SSB.** On the x axis the main driver of the R-SSB relationship plotted against mean F during the collapse, mean standardize SST during the collapse and Age at 50% maturity (A50) from Wang et al., 2014.

The hysteresis stage – We identified a period of hysteresis to exist after the collapse of Atlantic cod, where the stocks showed no signs of recovery even if the fishing activities were strongly reduced. Hysteresis to recovery appeared in all cod stocks, apart from South Lawrence which started the collapse later (Figure 3.3, Supplementary Information, Figure S3.4-S3.5). The hysteresis stage is hence characterized by SSB and R being low, and importantly both variables were decoupled especially at shorter periods (Figure 3.2). Again, the results of the phase analysis were not significant. The length of the period varied, e.g., in Northern and Irish Sea cod lasted until 2010 while in North Sea and Flemish Cap until around 2005, and these stocks started to recover afterwards (Figure 3.3).

The recovery kick-off stage – This last stage of Atlantic cod dynamics was identified just in 6 stocks (Figure 3.3). The average partial wavelet coherence did not really show any more coupling of R and SSB after the hysteresis phase except a small sign in the last two years of the time series (yellow area, Figure 3.2). Therefore, to investigate whether a recovery sign could be detected, we computed the mean PWTC separated for recovering and still collapsed stocks (Figure 3.5, Supplementary Information, Table S3.2). The 6 recovering stocks showed a new coupling between R and SSB in the last years of the time series at short periods (Figure 5a). R was the driver of this coupling in all stocks apart from North Sea and Western Baltic, as revealed by the phase analysis (Table 3.1, Figure 3.5a). Iceland and North-East Arctic cod showed this stage as well but not at the end of the time series. Indeed, once these stocks were fully recovered and the biomasses were high again, the coupling between R and SSB ceased again (Figure 3.3). Hence these stocks reached again a healthy stage, highlighting the cyclic nature of these stages. To understand why some stocks showed the recovering phase while others not, we related the presence of the recovering stage to a range of variables like mean fishing pressure, mean temperature, age at 50% maturity and the type of collapse during the last 5 years using generalized linear models (Supplementary Information, Table S3.3 and Figure S3.6). We only

found collapse type to be significant (p value< 0.05), indicating that stocks that underwent abrupt collapses were less likely to show the recovery kick off stage compared to gradual collapsing stocks (Supplementary Information, FigureS3.7-S3.8).
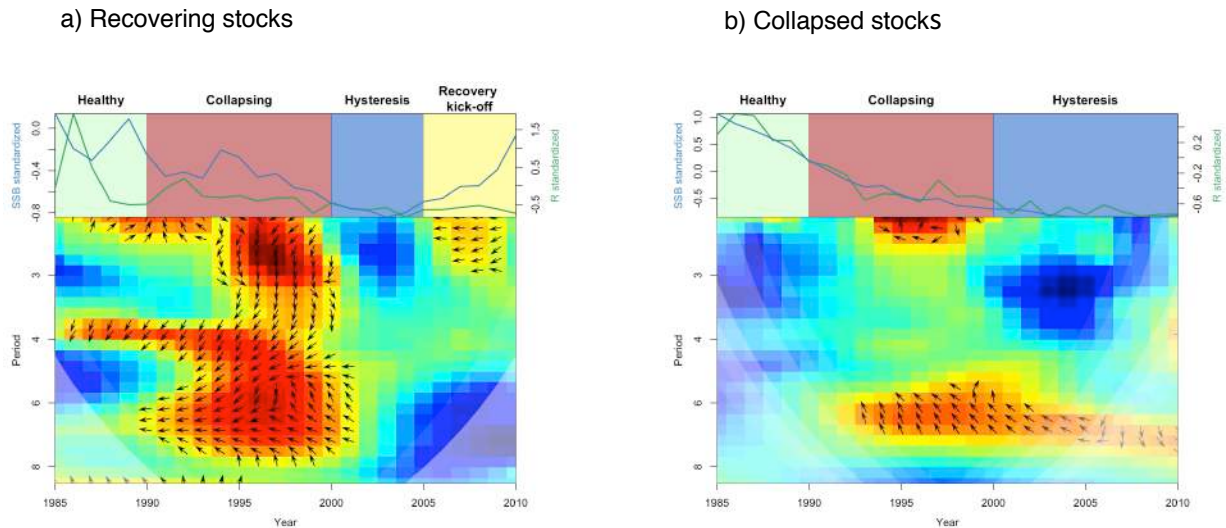

Figure 3.5: PWTC of recovering (a) and still collapsed (b) stocks. The upper plot show the average of the standardize R and SSB time series of recovering and still collapsed cod stocks defined in Table S3.2 (in blue SSB, in green R). The colours in which the time series is divided represent the stages of Atlantic cod stocks. Below the corresponding results of the average PWTC between R and SSB for all Atlantic cod stocks. Time is shown on the x axis, while period in the y axis. The colours correspond to the strength of the R-SSB coupling (red=strong, blue=weak). The arrows correspond to the average result of the phase analysis. Arrows pointing up indicate that SSB drives R, pointing down that R drives SSB, pointing left that the signal are antiphase and pointing right in phase. The white shadow represents the cone of influence of every stock; the stronger the white shadow the more uncertain the results.

Discussion

The nature of the coupling between parent stock size (spawning stock biomass – SSB) and subsequent reproductive success manifested by the number of young individuals recruiting to the fisheries (recruitment – R) is considered one of the unsolved mysteries in fisheries science. The existence of the SSB – R relationship hence has been frequently questioned due to the lack of correlation between both variables (Myers & Barrowman, 1996; Marshall *et al.*, 1998; Rothschild, 2000). Moreover, it is discussed whether the reverse R – SSB relationship is not more important for the dynamics of exploited marine fish populations (Szuwalski *et al.*, 2015). Unlike traditional approaches to investigating SSB – R relationships which usually apply parametric statistical models, here we applied a frequency domain analysis, the partial wavelet coherence analysis (PWTC), that allowed for the investigation of relative changes in periodic fluctuations between SSB and R. Our study demonstrates that the association between SSB and R of Atlantic cod, species of ecologically, but also socially and economically importance, is strongly variable over time but follows clearly definable common patterns.

First of all, our analysis confirmed earlier studies indicating the coupling between SSB and R to be weak when the stock is in a healthy state, i.e. at a high SSB, and recruitment variability is more dependent on physical oceanographic changes related to climate as well as the interactions with other species (Ottersen *et al.*, 1994; Berg & Pedersen, 2001; Begg & Marteinsdottir, 2002;

Dalpadado *et al.*, 2014). Furthermore we found the coupling between SSB and R to become tighter and more significant when stocks have collapsed, confirming previous studies indicating a strong SSB – R coupling at low stock sizes (Myers & Barrowman, 1996; Brander, 2005; Ottersen *et al.*, 2013).

The strong coupling of SSB and R at low stock size was visible in the PWTC at short and long periods. We interpreted the latter as the manifestation of the long-term stock dynamics which is generally dependent on stock size. This was particularly obvious in heavily overexploited cod stocks such as Northern cod, and Northern Lawrence, confirming findings from other species (Szuwalski *et al.*, 2015). However, Flemish Cap and Irish Sea cod showed contradicting dynamics, demonstrating a reverse R – SSB coupling on longer time scales, determined by fluctuations in R. Obviously in these stocks environmental and other external drivers, such as predation and competition, are stronger drivers than SSB even if stock size is low (Kudlo & Boystov, 1979; Planque & Fox, 1998; Borovkov *et al.*, 2005; Morgan & Lilly, 2005; Beggs *et al.*, 2014). Moreover, this long term relationship was in some cases quite extended in time, especially for stocks that collapsed quite abruptly (e.g. in Northern Lawrence), indicating that these abrupt collapses may have altered the recruitment mechanisms more dramatically and permanently, influencing future recovery potential (Hutchings, 2000; Hsieh *et al.*, 2006).

The short-term periodical fluctuations between SSB and R during the collapsed stage indicate the existence of transient mechanisms that may have reinforced the collapse of the stocks. Reinforcing mechanisms are typical for unstable stocks with eroded resilience (Hsieh *et al.*, 2006; Anderson *et al.*, 2008; Kuparinen *et al.*, 2014; Tu *et al.*, 2018). Short-term periodical fluctuations dominated by R indicate that recruitment failure exacerbated the effect of overfishing during cod stock collapses. For instance, in the North Sea and in Northern cod low year-class strength was caused by changes in prey composition and extremely cold temperatures (Myers *et al.*, 1996; Beaugrand *et al.*, 2003). Other stocks such as Irish Sea and Flemish Cap cod demonstrated a transient SSB – R coupling dominated by SSB, possibly indicating recruitment overfishing. Recruitment overfishing occurs when overexploitation pressure caused SSB levels too low to sustain healthy stock levels (Myers *et al.*, 1994). In our analyses recruitment overfished stocks typically have a longer life cycle, indicating higher vulnerability, and a very high F, and thus suggesting that different exploitation patterns combined with different life history traits, might be the cause for different collapse mechanisms.

We found the SSB – R coupling to vanish after the collapses of Atlantic cod stocks, a period we termed the hysteresis stage. This period is characterized in most of the stocks by no recovery despite lowered fishing pressure which may be results of mechanisms such as depensation/cultivations (Walters & Kitchell, 2001). Hysteresis, the delayed or absent recovery due to the presence of new feedback mechanisms in the system is typical of shifting systems (Beisner *et al.*, 2003). Only six cod stocks have left the hysteresis stage and showed signs of a recovery. We found collapse type (abrupt vs gradual) to be a significant predictor of recovery. Indeed, abruptly collapsed stocks, such as Northern cod, Northern Lawrence , that have longer life cycles and very high exploitation rates are less likely to recover, due to their higher fragility

and the stronger existence of mechanisms impairing recruitment after the collapse (Hutchings, 2000; Lotze *et al.*, 2011).

In almost all cases improved R is the main driver for recovery showing the importance of single good year recruitment (Drinkwater 2005, Sguotti et al. Chapter 2). However, we stress the importance of continued low fishing pressure for the recovery to be successful indicated by the fates of Coastal Norwegian and Western Baltic cod. These stocks show a recovery kick-off in c. 2010, but unsustainable fishing pressure in subsequent years prevented the stocks to recover. On the contrary, North Sea cod shows signs of recovery driven by reduced SSB (and not improved R) indicating that management measures are crucial to recover Atlantic cod stocks. Other stocks such as Irish Sea cod recently increased in SSB while no new association between SSB and R was visible. This indicates that the stock is not back to a healthy state because its internal mechanisms are not completely restored, as shown in previous studies (Planque *et al.*, 1999; Lotze *et al.*, 2011).

Using the frequency domain analysis PWTC our study demonstrated time-variant patterns in the coupling and decoupling of SSB and R in Atlantic cod stocks. Based on this non-traditional statistical analysis we were able to define common stages in the dynamics of cod stocks in the North Atlantic with an emphasis on mechanism of collapse and recovery. Our results suggest that SSB and R have a state-dependent relationship, largely depending on stock size. Our study hence contributes to the accumulating evidence that population dynamics of heavily exploited species are regularly non-linear and state-dependent (Ye *et al.*, 2015; Perlala *et al.*, 2017). We hence conclude that ignoring such dynamics in fisheries management unintentionally increases the likelihood of stock collapses, especially under increasing anthropogenic pressure and the expected consequences of climate change, but as well negatively influences stock recovery potential and hence social and economic benefits for fisheries communities.

Supplementary Information Chapter 3

Supplementary Information Tables

Table S3.1: Stock assessment data of Atlantic cod stocks.

Stock name	Stock N°	Management area	Geographical Area	Stock assessment models*	Institution/ group	Contact person or other data source
Eastern Baltic[1]	1	25-32	East	SAM	ICES/ WGBAFS	Margit Eero
Western Baltic[2]	2	22-24	East	SAM	ICES/ WGBAFS	Margit Eero
Kattegat[1,2]	3	IIIa/21	East	SAM	ICES/ WGBAFS	Johan Lövgren
North Sea	4	IV – VIId – IIIa	East	SAM	ICES/ WGNSSK	Alexander Kempf
West of Scotland	5	VIa	East	TSA	ICES/ WGCSE	Rui Catarino
Irish Sea	6	VIIa	East	SAM	ICES/ WGCSE	Colm Lordan
Coastal Barents Sea[2]	7	I – I	East	Survey SSB and F from VPA	ICES/ AFWG	Gjert Endre Dingsor
Northeast Arctic	8	I – II	North	XSA	ICES/ AFWG	Gjert Endre Dingsor
Iceland	9	Va	North	Forward based statistical catch at age model	ICES/ NWWG	Einar Hjorleifsson
Greenland	10	1	North	XSA		Karl Werner
Northern cod	11	2J3Kl	West	State space model	DFO	DFO(2016)[3]
Northern Gulf of st. Lawrence	12	3Pn4Rs	West	SPA	DFO	Claude Brassard
Southern Gulf of st. Lawrence	13	4T4Vn	West	SCA	DFO	Doug Swain
Eastern Scotian Shelf	14	4VsW	West	VPA	DFO	Swain & Mohn (2012)[4]
Grand Banks	15	3NO	West	SPA	NAFO	NAFO (2015)[5]
Flemish Cap	16	3M	West	Bayesian model	NAFO	Diana Gonzalez
Georges Bank	17	5z	West	Age structured model	NOAA	Loretta O´Brien

Stock name, stock number (as in Figure1), abbreviation, management area code, stock assessment models used and the institution (or working group within the institution) conducting the stock assessment. Scientists providing data (or other data sources)

* SAM – State-space assessment model, TSA – Analytical age-based assessment (time series analysis), XSA – Extended survivor analysis, SPA – Sequential population analysis, SCA – Statistical catch at age, VPA – Virtual population analysis
[1] Stocks that in the last year failed the assessment
[2] Stocks where, in order to have longer time series, we mixed old assessments and new ones, after checking for same trends and stock dimensions.
[3] DFO (2016) Stock Assessment of Northern Cod (NAFO Divs. 2J3KL) in 2016. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2016/026
[4] Swain DP, Mohn RK (2012) Forage fish and the factors governing recovery of Atlantic cod (Gadus morhua) on the eastern Scotian Shelf. Can. J. Fish. Aquat. Sci. 69: 997–1001.
[5] NAFO (2015) Assessment of the Cod Stock in NAFO Divisions 3NO. NAFO SCR Doc. No. 15/034.

Table S3.2*: Change point analysis.*

Stock name	Period of the main shift	%SB after the shift compare SB before	Speed of collapse	Abrupt	Recovery status
Eastern Baltic	1985-1990	39	5	Yes	collapsed
Western Baltic	1986-1990	57	4	No	recovering
Kattegat	1980-1987	42	7	No	collapsed
North Sea	1999-2006	52	7	No	recovering
West of Scotland	1996-2003	32	7	Yes*	collapsed
Irish Sea	1990-1999	52	9	No	recovering
Coastal Barents Sea[2]	1990-1997	56	7	No	collapsed
Northeast Arctic	1990-2008	210	18	*increase	recovered
Greenland	1958-1970	32	12	Yes	collapsed
Iceland	1985-1989	104	4	*increase	recovering
Northern cod	1990-1993	11	3	Yes	collapsed
Northern Gulf of st. Lawrence	1986-1990	24	4	Yes	collapsed
Southern Gulf of st. Lawrence	1986-1993	37	7	Yes*	collapsed
Eastern Scotian Shelf	1987-1992	36	5	Yes	collapsed
Grand Banks	1986-1991	37	5	Yes	collapsed
Flemish Cap	1994-1996	16	2	Yes	recovered
Georges Bank	1990-1994	34	4	Yes	collapsed

Description of the SB decline type of each stock, derived from the trend analysis. The combination of the Bayesian Change Point analysis and trend analysis helped to identify the "most probable year" in which shift happened over the time series (visualized in the previous Figure). % of SB after the shift compared to SB before is also shown. A stock was considered to change abruptly if the SB declined to around 50% of the initial biomass in 5-7 years. Stocks that collapse or change abruptly are shown. In the last column the recovery status based on Sguotti et al., is listed.

Table S3.3: Atlantic cod stocks traits table

Stock	Mean F 1985-90	Mean F 2005-10	FMSY	Mean st T 1985-90	Mean st T 2005-10	L_inf	K	Age 50%	Collapse
Eastern Baltic	0.98	0.69	-	0.45	0.82	-	-	3.17	abrupt
Western Baltic	1.17	0.99	0.26	0.39	0.74	103	0.15	2.96	gradual
Kattegat	1.2	1.20	-	0.35	0.70	105	0.13	2.28	gradual
North Sea	0.98	0.70	0.33	0.32	0.68	126	0.127	3.73	gradual
West of Scotland	0.89	0.98	0.17	0.29	0.78	105	0.16	2.12	abrupt
Irish Sea	0.92	1.07	0.3	0.38	0.85	99	0.309	1.97	gradual
Coastal Norwegian	0.48	0.28	-	0.06	0.61	123	0.11	5.29	gradual
North-East Arctic	0.78	0.44	0.4	0.28	0.70	134	0.109	8.01	gradual
Iceland	0.77	0.46	0.2	0.31	0.71	149	0.121	6.76	gradual
Greenland	0.6	0.30	0.15	0.3	0.71	-	-	-	abrupt
Northern	0.2	0.03	*	0.22	0.68	81	0.243	5.97	abrupt
North Lawrence	0.55	0.42	*	0.18	0.53	110	0.16	5.28	abrupt
South Lawrence	0.25	0.01	*	0.19	0.51	-	-	4.36	abrupt
Eastern Scotian	0.43	0.03	*	0.31	0.76	-	-	-	abrupt
Grand Banks	0.45	0.06	0.3	0.33	0.66	130	0.12	6.01	abrupt
Flemish Cap	0.68	0.11	0.13	0.39	0.75	98	0.243	3.59	abrupt
Georges Bank	0.65	0.80	0.17	0.34	0.48	132	0.166	2.01	abrupt

Supplementary Information Figures

Figure S3.1: Wavelet decomposition for SSB of all Atlantic cod stocks. On the y axis is shown the period (length) of the wavelet, while on the x axis the Year. The colours of the plots increase intensity (from blue to red) as the correlation between the time series and the wavelets increase, thus the red areas are changes in the mean of the time series. Significant changes are surrounded by black line (p value 0.05).
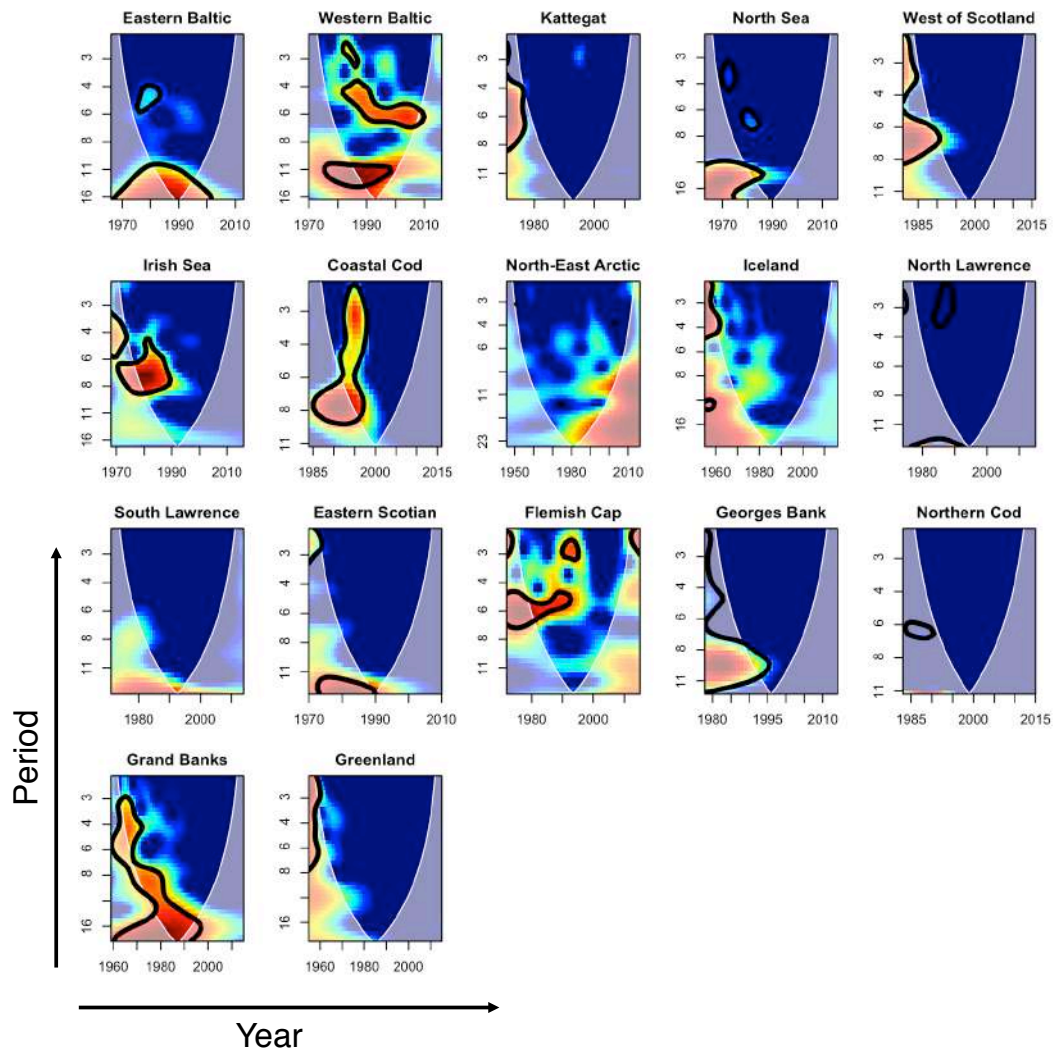
Figure S3.2: Wavelet decomposition for R of all Atlantic cod stocks. On the y axis is shown the period (length) of the wavelet, while on the x axis the Year. The colours of the plots increase intensity (from blue to red) as the correlation between the time series and the wavelet increase, thus the red areas are changes in the mean of the time series. Significant changes are surrounded by black line (p value 0.05).
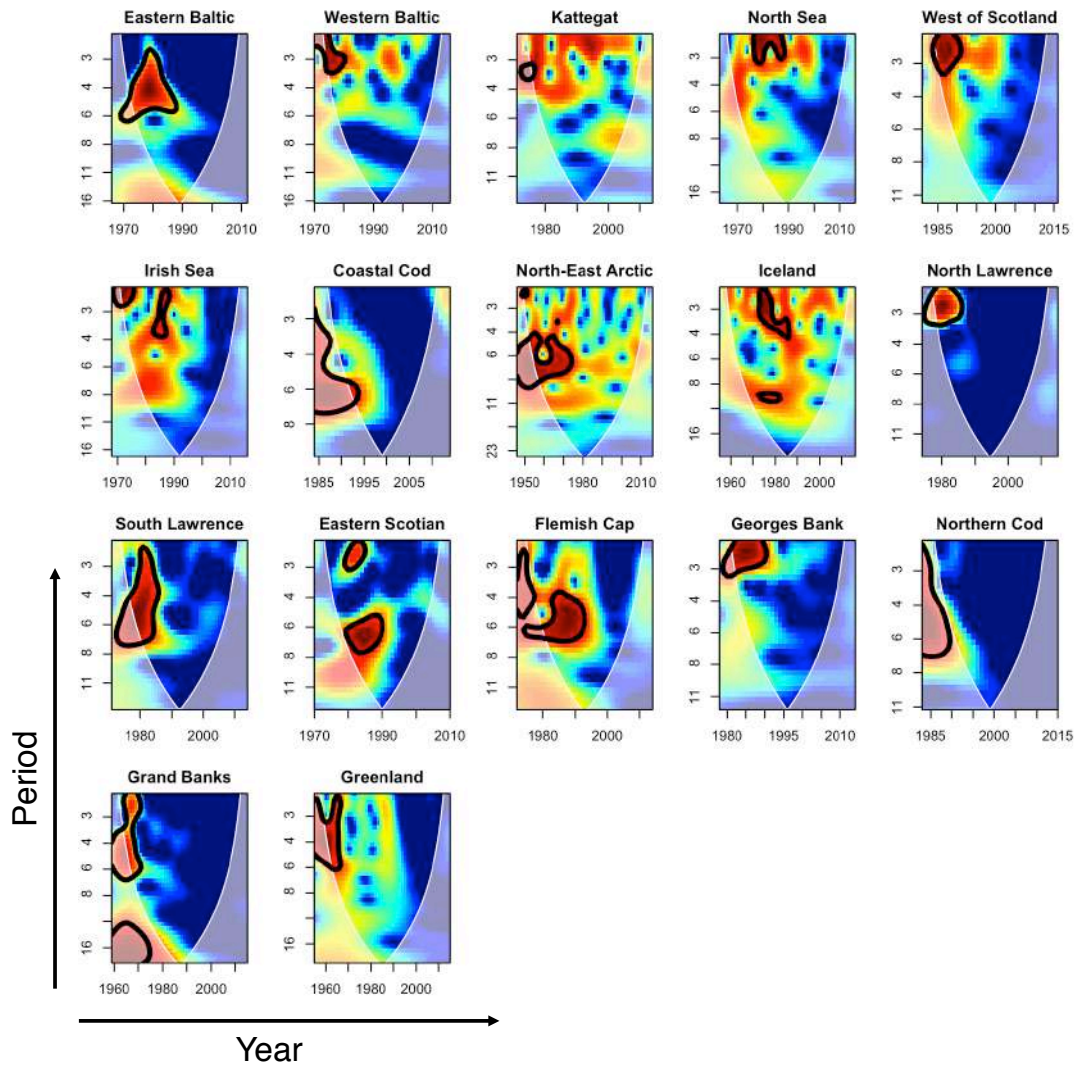
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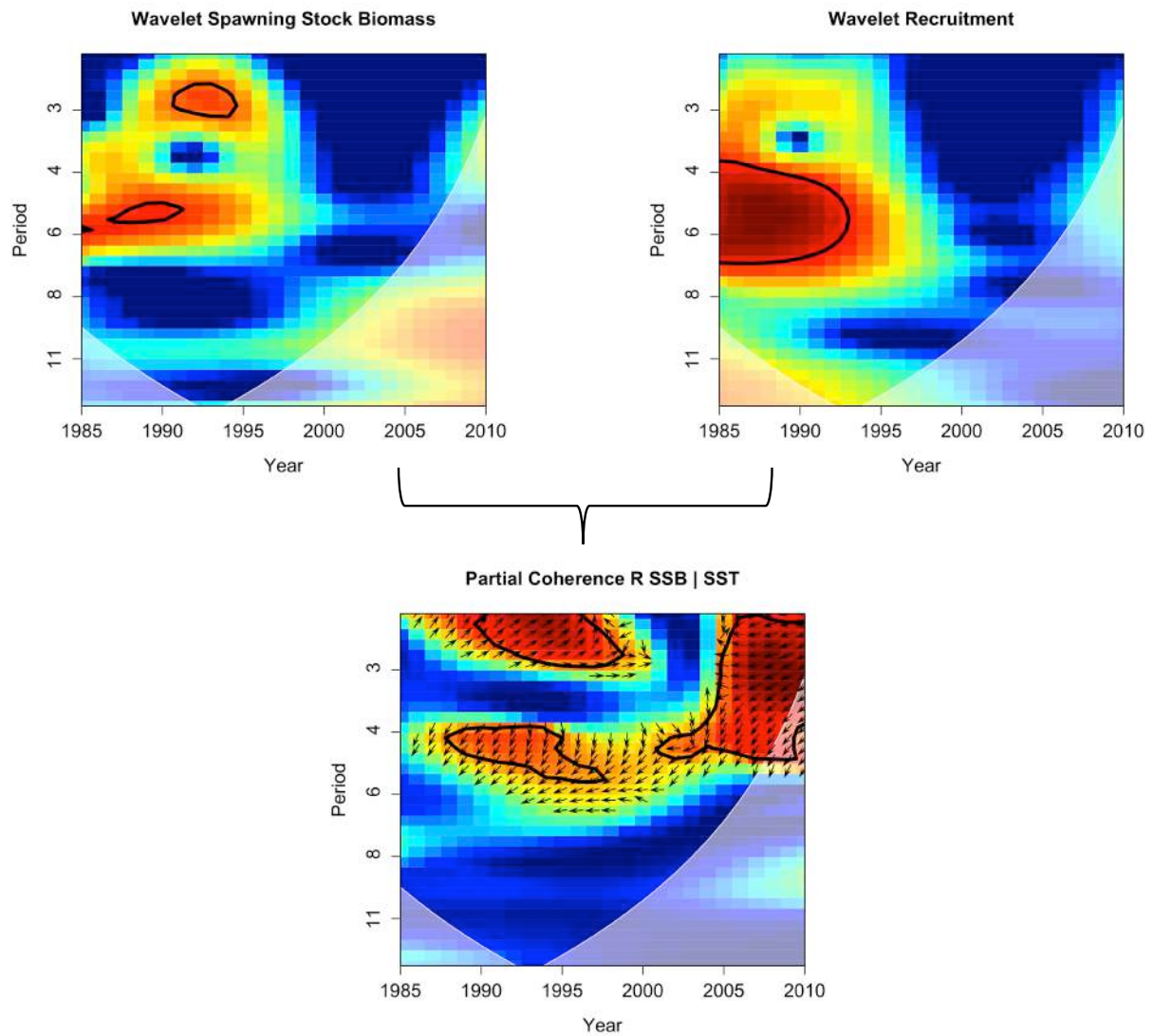
Figure S3.3: Visual explanation of the partial wavelet coherence. a) the wavelet decomposition of the SSB. b) The wavelet decomposition of recruitment. c) The partial wavelet coherence. In this case, the areas in red are areas where strong correlation can be identified between SSB and R (once subtracted the effect of temperature), thus where R and SSB show similar wavelet decomposition. The arrows are the phase of this relationship: if they point up it means that x is driving y so in our case SSB is driving R. If they point down y is driving x, R drives SSB. If they arrow point right the two signals are in phase, otherwise they are put of phase.

Figure S3.4: Time series of PWTC for single stocks. The upper plot show R and SSB time series (in blue SSB, in green R). The colours of the different periods correspond to the stages highlighted in Figure3.2. The darker areas represent the period of the change point, defined by the change point analysis. Below the corresponding results of the PWTC between R and SSB for each stock. Time is shown on the x axis, while period in the y axis. The colours correspond to the strength of the R-SSB coupling (red=strong, blue=weak). The black line identifies significant changes from the mean. The arrows correspond to the average result of the phase analysis. Arrows pointing up indicate that SSB drives R, pointing down that R drives SSB, pointing left that the signal are antiphase and pointing right in phase. The white shadow represents the cone of influence where the results are uncertain.
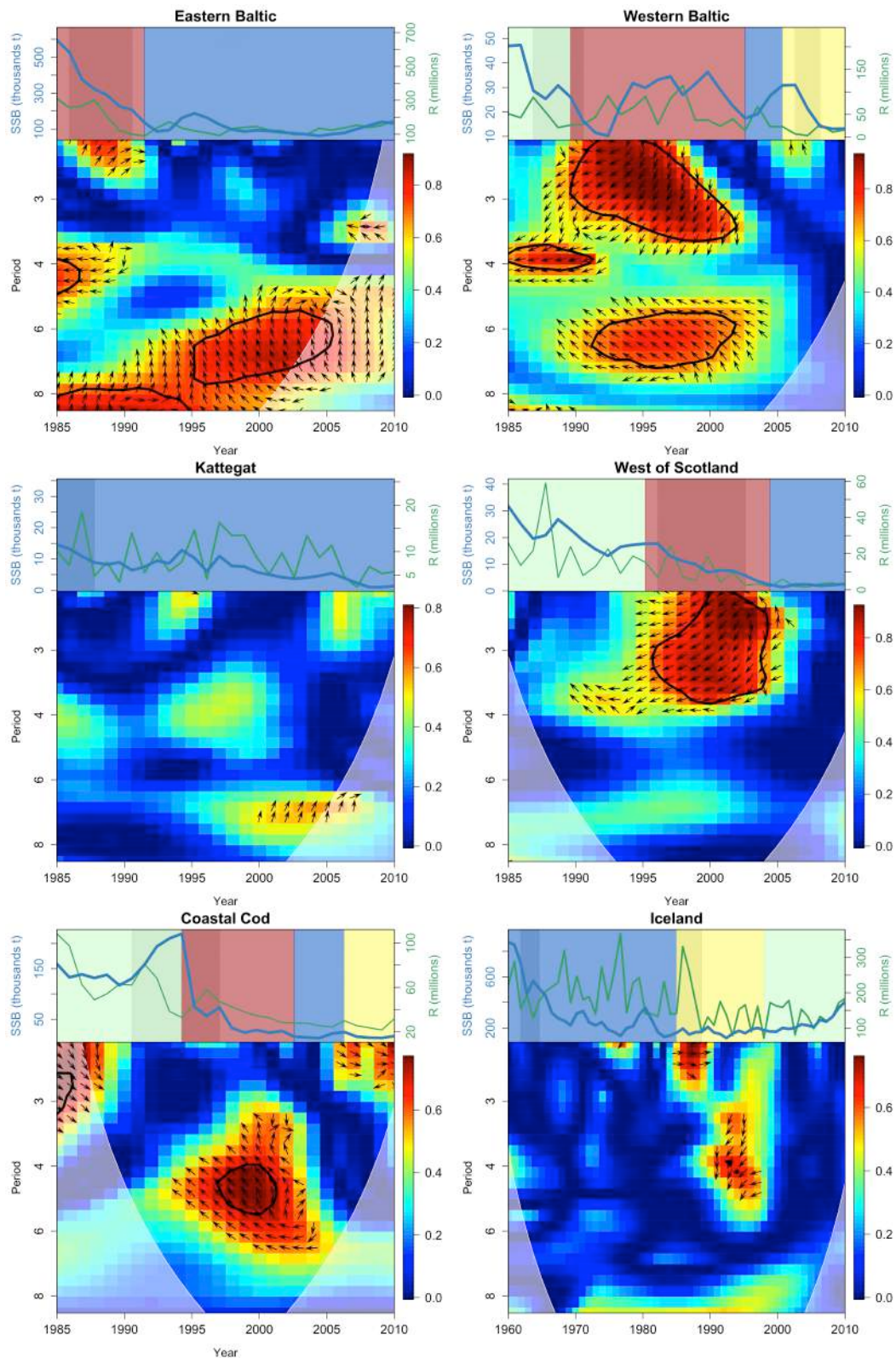
Figure S3.5: Time series of PWTC for single stocks. The upper plot show R and SSB time series (in blue SSB, in green R). The colours of the different periods correspond to the stages highlighted in Figure3.2. The darker areas represent the period of the change point, defined by the change point analysis. Below the corresponding results of the PWTC between R and SSB for each stock. Time is shown on the x axis, while period in the y axis. The colours correspond to the strength of the R-SSB coupling (red=strong, blue=weak). The black line identifies significant changes from the mean. The arrows correspond to the average result of the phase analysis. Arrows pointing up indicate that SSB drives R, pointing down that R drives SSB, pointing left that the signal are antiphase and pointing right in phase. The white shadow represents the cone of influence where the results are uncertain.

Figure S3.6: average PWTC of R and T. The upper plot show the average of the standardize R and T time series among recovering cod stocks (in blue SSB, in green R). Below the corresponding results of the average PWTC between R and T for all Atlantic cod stocks. Time is shown on the x axis, while period in the y axis. The colours correspond to the strength of the R-T coupling (red=strong, blue=weak).
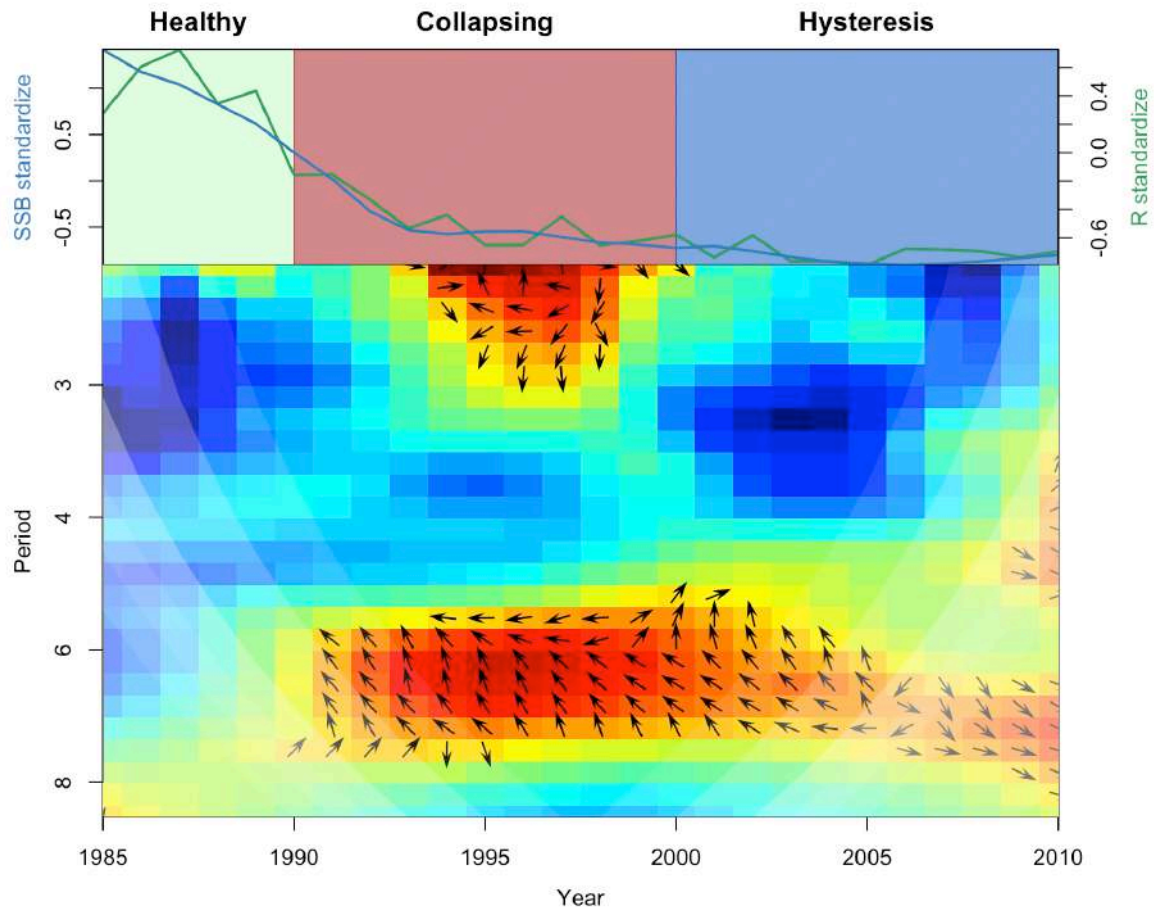
Figure S3.7: PWTC of abrupt collapsed stocks (excluding Flemish Cap cod). The upper plot show the average of the standardize R and SSB time series among abrupt collapsed cod stocks (in blue SSB, in green R). The colours in which the time series is divided represent the stages of Atlantic cod stocks based on Figure3.2. Below the corresponding results of the average PWTC between R and SSB for all Atlantic cod stocks. Time is shown on the x axis, while period in the y axis. The colours correspond to the strength of the R-SSB coupling (red=strong, blue=weak). The arrows correspond to the average result of the phase analysis. Arrows pointing up indicate that SSB drives R, pointing down that R drives SSB, pointing left that the signal are antiphase and pointing right in phase. The white shadow represents the cone of influence of every stock; the stronger the white shadow the more uncertain the results.
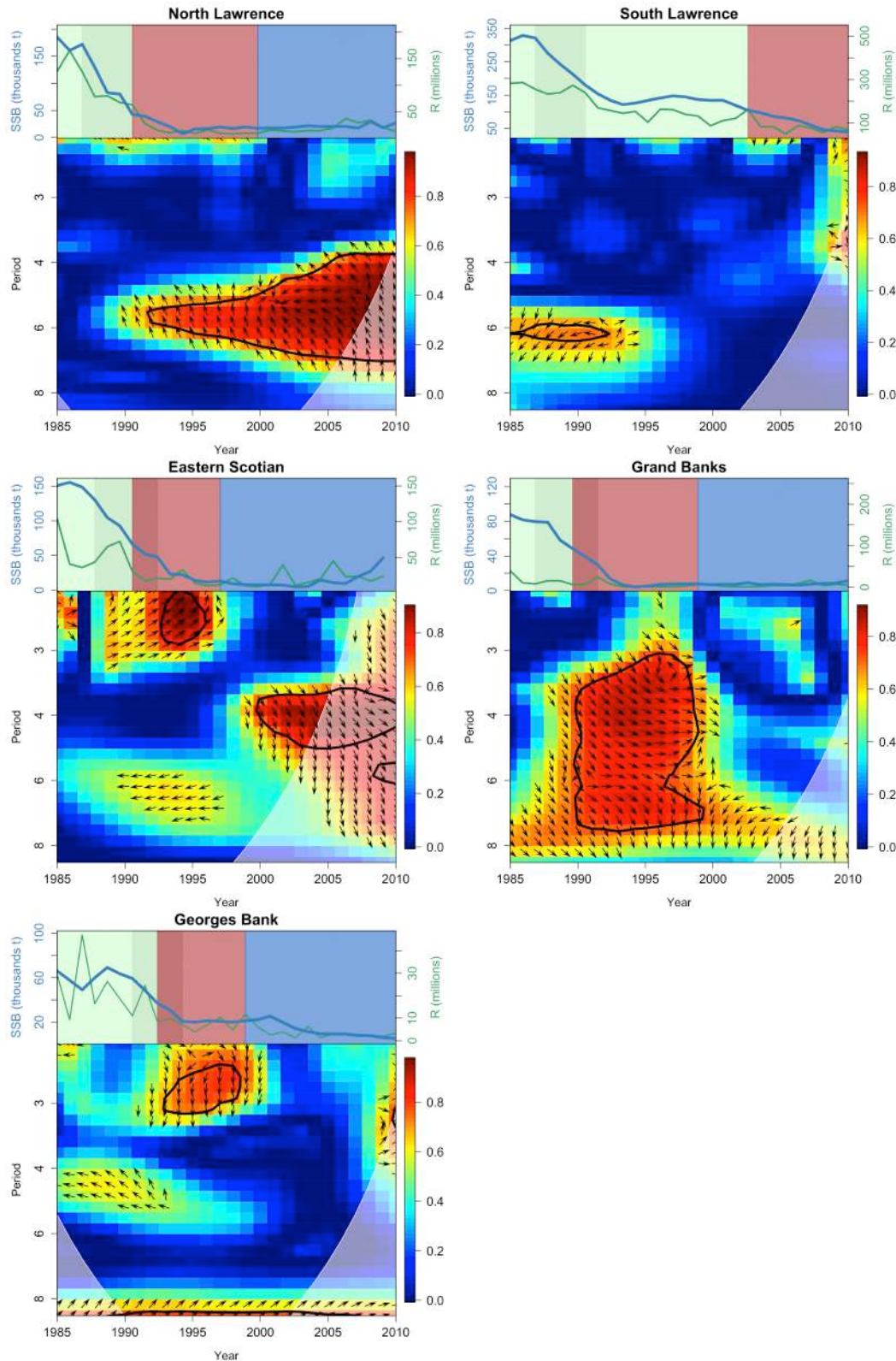
Figure S3.8: PWTC of gradual collapsed stocks. The upper plot show the average of the standardize R and SSB time series among gradual collapsed cod stocks (in blue SSB, in green R). The colours in which the time series is divided represent the stages of Atlantic cod stocks based on Figure3.2. Below the corresponding results of the average PWTC between R and SSB for all Atlantic cod stocks. Time is shown on the x axis, while period in the y axis. The colours correspond to the strength of the R-SSB coupling (red=strong, blue=weak). The arrows correspond to the average result of the phase analysis. Arrows pointing up indicate that SSB drives R, pointing down that R drives SSB, pointing left that the signal are antiphase and pointing right in phase. The white shadow represents the cone of influence of every stock; the stronger the white shadow the more uncertain the results.
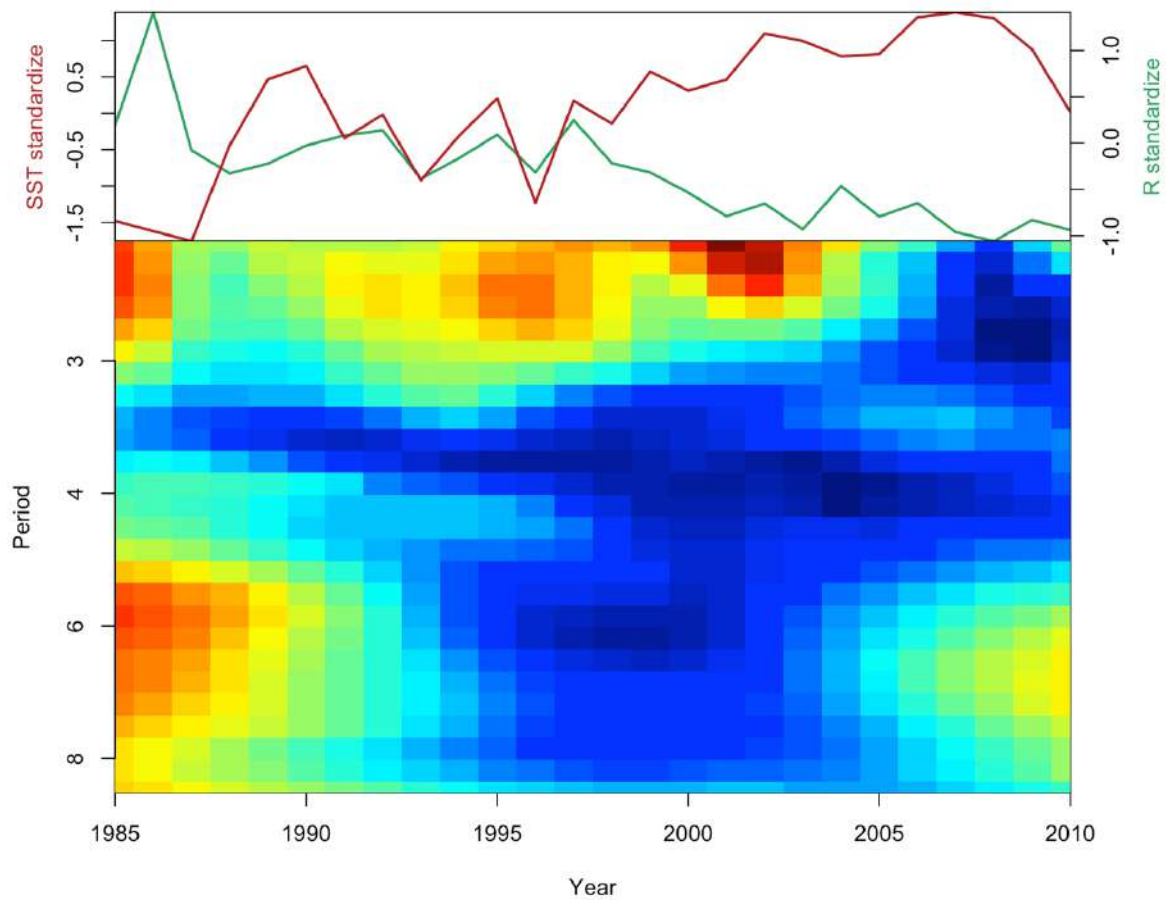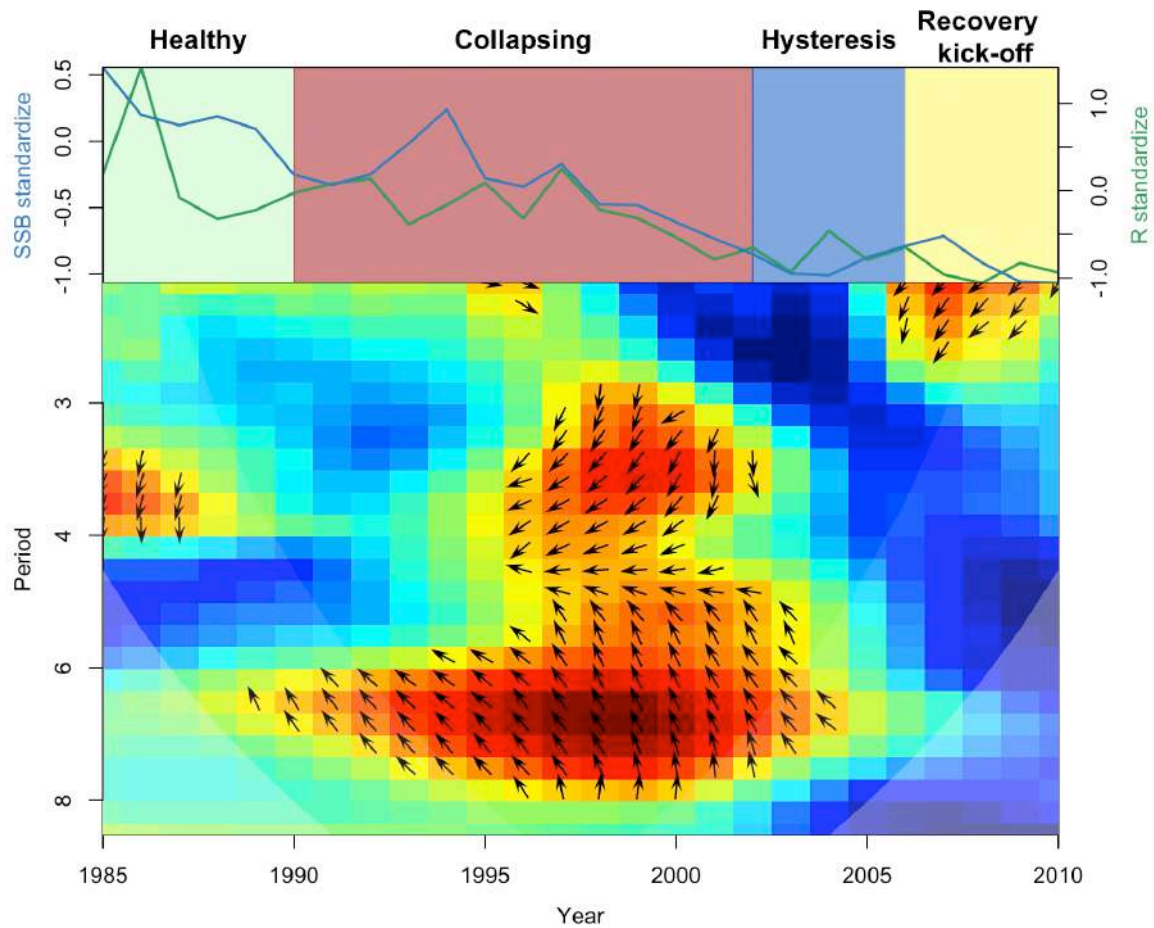
Chapter 4: Multi-model approach on stock-recruitment

Non-linearity in stock-recruitment relationships of Atlantic cod: insights from a multi-model approach

Camilla Sguotti[1]**,** Saskia Otto[1], Xochitl Cormon[1], Karl M. Werner[2], Ethan Deyle[3], George Sugihara[3], Christian Möllmann[1]

Abstract

The stock-recruitment relationship is the basis of any stock prediction and thus fundamental for fisheries management. Traditional parametric stock-recruitment models often poorly fit empirical data, nevertheless they are still the rule in fish stock assessment procedures. We here apply a multi-model approach to predict recruitment of 20 Atlantic cod (*Gadus morhua*) stocks as a function of adult biomass and environmental variables. We compare the traditional *Ricker model* with two non-parametric approaches; (i) the *stochastic CUSP model* from catastrophe theory and (ii) *Multivariate Simplex Projections* from the *Empirical Dynamic Modelling*, based on attractor state-space reconstruction. We show that the performance of each model is contingent on the historical dynamics of individual stocks, and that stocks which experienced abrupt and state-dependent dynamics are best modelled using non-parametric approaches. These dynamics are pervasive in western stocks highlighting a geographical distinction between cod stocks which has implications on their recovery potential Furthermore, the addition of environmental variables always improved the models´ predictive power indicating that they should be considered in stock assessment and management routines. Using our multi-model approach, we demonstrate that we should be more flexible when modelling recruitment and tailor our approaches to the dynamical properties of each individual stock.

Author´s affiliations
[1]Institute for Marine Ecosystem and Fisheries Science, University of Hamburg, Germany
[2]Thuenen Institute for Sea Fisheries, Bremerhaven, Germany
[3]Scripps Institution of Oceanography, UC San Diego, La Jolla, California, USA

Introduction

Forecasting complex trajectories of marine resources is essential for fishery management and one of the major challenges of our time (Schindler & Hilborn, 2015; Ye *et al.*, 2015). An important factor to be considered in fisheries management is the stock-recruitment relationship (SRR), which serves as a basis for any stock assessment (Houde, 1987; Perretti *et al.*, 2015). SRRs are based on the assumption that recruitment (the number of fishes that enter the adult population) is directly related to adult stock size (Houde, 1987; Kraus *et al.*, 2000). Parametric approaches, such as the Ricker model, were developed around the 1950s (Ricker, 1954; Beverton & Holt, 1993) and still represent the method of choice in stock assessments. These models are very specific in the type of functional response curve to describe the SRR, and are linear, in the sense that, depending on the parameters´ value, the relationship between recruitment and biomass can be linearized (Ye *et al.*, 2015). However, they often fail to capture the high variability in recruitment data and this has led to questioning the existence of the relationship itself (Szuwalski *et al.*, 2015; Britten *et al.*, 2016; Perlala *et al.*, 2017). The fit of the SRR is sometimes so poor, that short-term predictions are conducted using an average of recruitment over a particular number of years prior to the starting point of the prediction, instead of a model (Deyle *et al.*, 2018). Both approaches, using average recruitment or a parametric model, assume that natural systems behave in a linear way, which may lead to biased fisheries management decisions when stocks show complex dynamics such as aperiodic chaos, non-linearity or non-stationarity (Ye & Sugihara, 2016; Perlala *et al.*, 2017; Deyle *et al.*, 2018).

Chaos and non-stationary dynamics are pervasive in natural systems and characterize many marine ecosystems and populations (May & Oster, 1976; Scheffer *et al.*, 2001; Möllmann *et al.*, 2015). These dynamics emerge from the inherent complexity of nature, governed by a multitude of factors (Ye *et al.*, 2015; Deyle *et al.*, 2016; Tu *et al.*, 2018). Assuming linearity and stability in recruitment models can, thus, result in wrong stock predictions (Glaser *et al.*, 2014; Ye *et al.*, 2015). As a consequence, new non-parametric modelling frameworks were developed to predict stock trajectories accounting for state-dependent and chaotic behaviour, such as the Empirical Dynamic Modelling (EDM) framework (Sugihara *et al.*, 2012; Ye *et al.*, 2015; Deyle *et al.*, 2018). EDM is a minimal assumptive approach based on time series observations, which reconstructs the temporal dynamics of a system by constructing a so-called attractor manifold (Sugihara *et al.*, 2012; Ye *et al.*, 2015). EDM is able to predict the future system trajectory based on its past dynamics (Ye *et al.*, 2015; Deyle *et al.*, 2018), thus accounting for state-dependent dynamics (Sugihara, 1994). This approach, and in particular Multivariate Simplex Projection (MSP) has been applied to predict non-linear fish recruitment dynamics in a range of studies, and has also been applied directly to management, e.g. for the menhaden stocks along the East Coast of the USA (Sparholt, 1996; Perretti *et al.*, 2015; Ye *et al.*, 2015; Deyle *et al.*, 2018).

Another non-parametric approach suitable for modelling state-dependent and discontinuous recruitment dynamics is the stochastic CUSP model (SCM), which is based on catastrophe theory (Zeeman, 1976; Thom, 1977; Grasman *et al.*, 2009; Petraitis & Dudgeon, 2016). Here, a state variable Z (for instance recruitment), depends on two control variables *alpha* and *beta*. The model allows Z to move from a state A (e.g. high recruitment) to a state B (e.g. low

recruitment) following either a continuous or discontinuous path (Diks and Wang, 2016). SCM has been widely applied to economic and behavioural studies (van der Maas *et al.*, 2003; Diks & Wang, 2016), but to a lesser degree to marine ecological studies (Jones and Walters, 1976; Jones, 1977; Petraitis and Dudgeon, 2015).

Another point often neglected in recruitment prediction is the effect of multiple external drivers and potential interactions such as predation, competition and environmental variables (Myers *et al.*, 1995; Brander, 2005; Ottersen *et al.*, 2006; Stiasny *et al.*, 2016). However, in multiple cases the relationship between recruitment and environment can be spurious, non-linear or non-stationary, and therefore is often not considered in stock assessments (Myers, 1998; Perlala *et al.*, 2017). Parametric models, assuming fixed parameters, often fail to correctly incorporate the environmental information, since they just consider additive effect of SSB and climate variables. Instead, models like MSP and SCM, can model interactions between the different drivers (i.e. biomass and climate variables) and thus may be able to integrate the climate information correctly (Ye *et al.*, 2015; Deyle *et al.*, 2018). This is important since for effectively predicting the status of living marine resources the integration of environmental variables is becoming crucial given the widespread impacts of climate change on ecosystems and marine resources such as commercially important fish (Britten *et al.*, 2016; Gaines *et al.*, 2018).

Atlantic cod (*Gadus morhua*) is an iconic species from ecological, cultural and economic points of view (Myers *et al.*, 1996). In recent decades, most North Atlantic cod stocks have collapsed, followed by prolonged periods of no recovery even after the application of strict management measures (e.g. fishing moratoria) (Myers *et al.*, 1996; Hutchings, 2000; Hutchings & Rangeley, 2011; Frank *et al.*, 2016). This failed recovery of Atlantic cod stocks suggests the presence of discontinuous dynamics and hysteresis (Frank *et al.*, 2011; Steneck *et al.*, 2011). Eastern and western Atlantic stocks differ in life history traits, exploitation trajectories and recovery potential (Pörtner *et al.*, 2008; Wang *et al.*, 2014; Frank *et al.*, 2016). Indeed, stocks in the West collapsed more abruptly compared to stocks in the East which on average show more gradual declines (Frank *et al.*, 2016). Cod recruitment is highly state-dependent, depending on the dimension of the stock and environment conditions. Recruitment is fundamental to Atlantic cod recovery (Myers and Barrowman, 1996; Brander, 2005; Ye *et al.*, 2015) and influenced by climate change (Myers & Drinkwater, 1989; Planque *et al.*, 1999; Stige *et al.*, 2006; Pörtner *et al.*, 2008; Pershing *et al.*, 2015b). We here used stock assessment data from 20 Atlantic cod stocks to i) investigate whether cod recruitment can be best described by the parametric Ricker model, by the non-parametric, "discontinuous" SCM, or by the non-parametric, state-dependent MSP approach, and ii) test whether the model's predictive power can be optimised when including environmental variables. We show that the adoption of a multi-model approach should be considered when modelling stocks presenting different dynamics.

Materials and Methods

Data

We used recruitment (i.e. number of fish for a particular age and stock that recruit to the adult biomass in thousands, R) and spawning stock biomass (i.e. biomass of mature fish in tonnes,

 SSB) data derived from stock assessments of 20 Atlantic cod stocks (Figure 4.1, Supplementary Information Figure S4.1). Data were provided by the International Council for the Exploration of the Sea (ICES), the National Oceanic and Atmospheric Administration of the USA (NOAA), the Northwest Atlantic Fisheries Organization (NAFO), the Department of Fisheries and Ocean in Canada (DFO) and by personal communication (Supplementary Information, Table S4.1). Recent assessments for cod stocks in the Kattegat, the Western Baltic as well as the Norwegian coast have been conducted only for reduced periods. Therefore, we combined recent and older stock assessments after consistency checks of SSB and R time-series (see Supplementary Information, Figure S4.2).
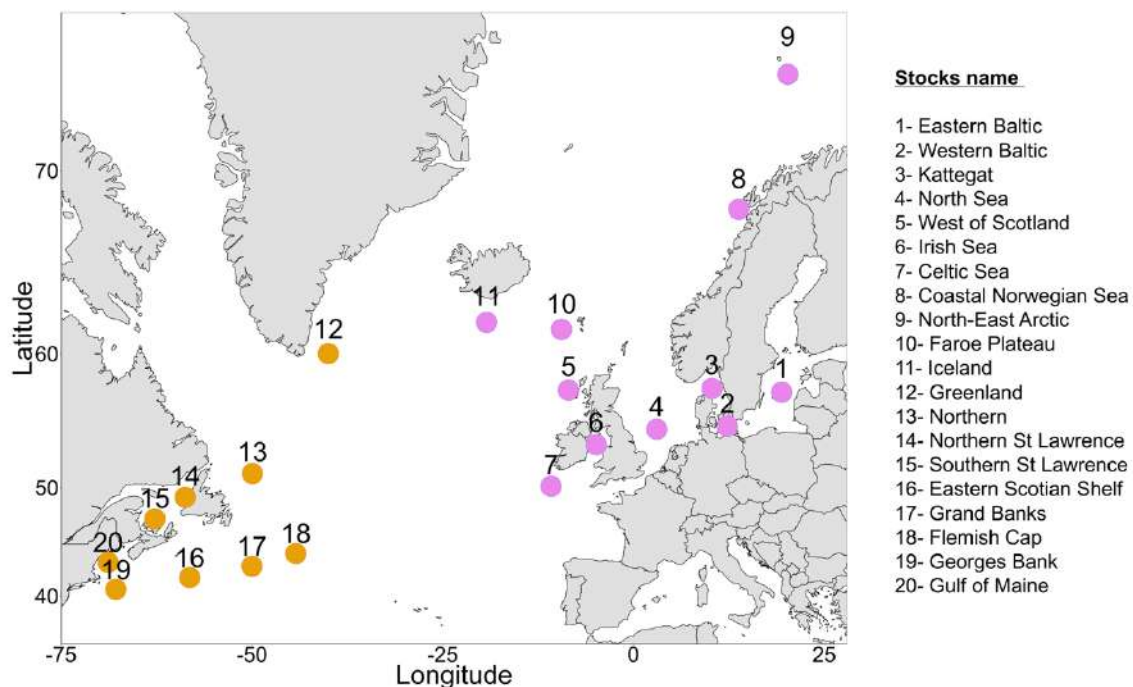
Figure 4.12: Map of Atlantic cod stocks over the North Atlantic. Each circle corresponds to the centre of distribution of an Atlantic cod stock. The colour code corresponds to the division between western stocks (orange) and eastern ones (pink).

We selected sea surface temperature (SST) and the indices of the North-Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO) as climate predictors in our models. SST data were collected from the NOAA Extended Reconstructed Sea Surface Temperature dataset (ERSST, www.ncdc.noaa.gov) version 4. The dataset represents a reconstruction of SST from 1854 to the present and comprises monthly anomalies computed with respect to the period 1971-2000, resolved in a 2°x 2° grid of spatial resolution. The data were averaged per year and per management unit. SST was chosen because of its importance for recruitment of Atlantic cod and is also a proxy for climate change at a local scale (Planque *et al.*, 1999). NAO and AMO were used as indices of climate variability at the supraregional scale. In particular NAO has been shown to highly correlate with Atlantic cod recruitment (Stige *et al.*, 2006), while AMO is a good proxy for climate change at longer time scales in this area. The NAO is a large scale, high frequency (7-25 years) climatic index depending on the different atmospheric pressure at sea level between Iceland and Azores. The AMO is instead a large-scale, low frequency (60 years) multi-decadal index representing climate-related SST changes in the Atlantic Ocean. The data for both indices were collected from the Earth System Research

Laboratory of NOAA (www.esrl.noaa.gov), and the AMO was averaged to annual values, while the NAO was averaged annually but just between December and March.

Modelling strategy

We compared multiple stock-recruitment models, the traditional *Ricker* model, the *Stochastic CUSP model* (SCM) and *Multivariate Simplex Projections* (MSP, from the Empirical Dynamic Modelling (EDM) framework). Recruitment models include either SSB alone or SSB in combination with one of the climate variables (i.e. SST, NAO and AMO) as predictors. Since recruitment can be influenced by climatic factors at different life-stages (i.e. eggs, larvae and juveniles), we applied multiple lags on the climate variables depending on recruitment age (Supplementary Information, Table S4.1). We assessed the predictive power of the different models (three modelling approaches and explanatory variables and corresponding lag selection) on the test data using 5-fold cross validation, which randomly splits the time series in 5 parts using 4 (training data) to predict the last one (test data). In each of the five iterations, we compared the predicted with the observed test values using Pearson correlation coefficients (ρ) (Ye *et al.*, 2015; Deyle *et al.*, 2018). We repeated this procedure 100 times to increase the robustness and eventually used the median of the 500 values of ρ for model comparison.

The recruitment models

The *Ricker* Model fits a curve between recruitment and SSB depending on parameters α and β (Ricker, 1954). These parameters allow the curve to bend in the middle, so that at very high SSB values recruitment will be low due to density dependent effects. However, this model can be considered linear, in the sense that, depending on the parameters´ value, the relationship between recruitment and biomass can be linearized through transformation, thus, we will refer to it as a linear model throughout the text. Climate effects can be added through a new parameter (γ):

$$R_t = SSB_t \exp\left(\alpha - \beta SSB_{t-ageR}\right) \tag{1a}$$
$$R_t = SSB_t \exp\left(\alpha - \beta SSB_{t-ageR} + \gamma climate_{t-lags}\right) \tag{1b}$$

where *ageR* is the age at recruitment, and *lags* the offset between the effect of a *climate* variable and *R* depending on the age of recruitment.

Stochastic CUSP modelling (SCM) is based on the cusp, one of the seven canonical forms of catastrophe theory that describe sudden changes in a system (Thom, 1977; van der Maas *et al.*, 2003; Petraitis & Dudgeon, 2016). The cusp model is based on a cubic differential equation and describes discontinuous transitions in a state variable Z_t controlled by two control variables α and β.

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

In SCM, a stochastic differential equation was developed allowing the estimation of Z_t, α and β in Eq. 2 as a linear function of exogenous variables using a likelihood approach:

$$Z_t = w_0 + w_1 y_1 + w_2 y_2 + \cdots w_y y_y \qquad (3a)$$
$$\alpha_t = \alpha_0 + \alpha_1 x_1 + \alpha_2 x_2 + \cdots \alpha_y x_y \qquad (3b)$$
$$\beta_t = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \cdots \beta_y x_y \qquad (3c)$$

with w, α and β being the coefficients (Diks & Wang, 2016). α is also called asymmetry parameter and controls the dimension of Z_t. β is called the bifurcation parameter since it controls whether the state variable follows a continuous or discontinuous path (Petraitis and Dudgeon, 2015; Diks and Wang, 2016). The system will present multiple equilibria if it follows a discontinuous path (i.e. two stable and one unstable) and just one if it follows a continuous path. The number of equilibria of the system depends on the solution of equation (2) from which the Cardan´s discriminant (δ) is derived:

$$\delta = 27\alpha^2 - 4\beta^3 \qquad (4)$$

If $\delta > 0$ the system has one equilibrium, indicating a continuous path. Whereas if $\delta < 0$ the system has three equilibria, indicating a discontinuous path (Diks & Wang, 2016). Therefore, SCM allows the detection of interactive effects of the two control variables on the state variable. Any changes in the bifurcation parameter β, will lead to changes in the relationship between α and Z_t and consequently dramatic changes of the state variable (Supplementary Information, Figure S4.3). In order to test the predictive power of the model, we first produced the linear predictors of the parameters and the state variable. These were then fit into the equation to predict the new points on the surface. The model was built as:

$$Z_t = w_0 + w_1 R_t \qquad (5a)$$
$$\alpha_t = \alpha_0 + \alpha_1 SSB_{t-ageR} \qquad (5b)$$
$$\beta_t = \beta_0 + \beta_1 SSB_{t-ageR} \text{ or } \beta_t = \beta_0 + \beta_1 climate_{t-lags} \qquad (5c)$$

Multivariate Simplex Projection is based on the EDM framework. The cornerstone of this framework is the Simplex projection method. The principle of EDM is to reconstruct the dynamics of one or multiple time series in a multidimensional space, i.e. an attractor manifold, and predict the future trajectory of the system based on these past dynamics (Sugihara *et al.*, 2012; Ye *et al.*, 2015; Chang *et al.*, 2017). Reconstructing the past dynamics of a system (in our case recruitment) is possible either using multiple variables (i.e. SSB or climate indices) or just time lags of the system itself (i.e. recruitment) (Sugihara *et al.*, 2012). We here used differentiated recruitment time series to build the attractor for each cod stock, and Simplex Projection (Eq.6-8) to approximate the attractor dynamics of the system (Sugihara *et al.*, 2012; Ye *et al.*, 2015; Deyle *et al.*, 2018). The time series is transformed in a set of time-delayed coordinate vectors:

$$x_t = \{x_t, x_{t-\tau}, x_{t-2\tau}, x_{t-3\tau}, \dots x_{t-(E-1)\tau}\}, \qquad (6)$$

where x is recruitment, t is time, τ is the time lag and E the Embedding dimension. E represents the dimensionality of the attractor (Ye *et al.*, 2015). E is selected by predicting the attractor

manifold one step ahead into the future (using leave-one-out cross validation) then comparing the predictive power of models with a varying E. In order to predict the system into the future, $\hat{x}_{t+1}$, Euclidean Distance is used and the system is predicted using nearest neighbourhood estimations

$$\hat{x}_{t+1} = \left(\sum_{i=1}^{E+1} w_{i,t}\, x_{i,t+1}\right) \Big/ \sum_{i=1}^{E+1} w_{i,t} \tag{7}$$

where w_i represents the weights, which are the Euclidean distance to the neighbour vector i relative to the nearest neighbour $\bar{d}$.

$$w_i = \exp\left(-\frac{d(X_t, X_i)}{\bar{d}}\right). \tag{8}$$

Multivariate Simplex Projection (MSP) uses again Eq. 7, but with the attractor reconstruction of recruitment (R) based on SSB (instead of recruitment itself) alone or together with climate variables:

$$R_t = \left\{SSB_{t-ageR}\right\} \tag{9a}$$
$$R_t = \left\{SSB_{t-ageR}, climate_{t-lags}\right\} \tag{9b}$$

In order to perform the MSP, it was necessary to perform two preliminary tests, the S-Map and the Convergent Cross Mapping (CCM) to unravel recruitment dynamics and relationship between recruitment and explanatory variables, respectively.

EDM-specific preliminary tests S-Map & CCM

The S-Map, was performed after the attractor reconstruction with Simplex Projection. This test includes a tuning parameter θ that controls the weights w_i from Eq. 7, and, if bigger than 0 indicates non-linearity (Sugihara, 1994; Klein *et al.*, 2016; Dakos *et al.*, 2017). Significance of non-linearity was assessed using a null distribution generated from 500 surrogate time series for each S-Map model. The surrogate time series were created following Deyle *et al.* (2018) and were phase-randomized which preserves the basic statistical properties of the original time series (Ebisuzaki, 1997). We averaged the S-Map results for all Atlantic cod recruitment time series to understand the overall dynamics.

We performed Convergent Cross Mapping (CCM) between recruitment and SSB and the climate variables (SST, NAO and AMO), a technique to understand causality between time series without assuming any distribution (Sugihara *et al.*, 2012; Deyle *et al.*, 2016; Pierre *et al.*, 2018). CCM is based on the principle that, if SSB or climate variables have an influence, then the recruitment time series will contain information about the past state of these variables. CCM is performed using Eq. 7 (see Deyle *et al.*, 2018).

Software

All analyses were performed in the programming environment R (R Core Team, 2017, version 3.3.1) using the packages *FSA* (Ogle, 2016), *cusp* (Grasman *et al.*, 2009), *rEDM* (Ye *et al.*, 2016)

Results

In our multi-model approach, we compared the parametric, linear Ricker model with two non-parametric, state-dependent approaches, i.e. the catastrophic stochastic CUSP model (SCM) and the state-dependent Multivariate Simplex Projection (MSP), with or without environmental variables as predictors (Figure 4.2). The two preliminary tests of the Empirical Dynamic Modelling (EDM), necessary to perform the MSP, revealed on average significantly non-linear dynamics in recruitment of Atlantic cod stocks, and an appropriate choice of explanatory variables (Supplementary Information, Figure S4.4-S4.5), thus allowing us to proceed with the analyses. For most of the Atlantic cod stocks, the best performing models produced high correlations between observed and predicted values ($0.7 < \rho < 0.8$). An exception were North-East Arctic, Iceland and Gulf of Maine cod stocks where the predictive power was reduced (about $\rho = 0.4$). Differences between the three model types were in general low (Figure 4.2). The Ricker model performed best for six stocks, the SCM for nine stocks and the MSP four stocks (Figure 4.2, Supplementary Information, Table S4.2). For stocks where SCM was the best, the MSP generally showed also a high predictive power, indicating that both models can well describe abrupt dynamics (e.g. Figure 4.2h,i,j,m). The addition of climate variables as explanatory variables to the baseline SSB models generally increased the predictive power, independently of the model type, even though SSB was often the most correlated explanatory variable (Figure 4.2, Supplementary Information Table S2 and as shown in CCM, Figure S5). SST and AMO were selected, based on the predictive power of the model, in eight stocks and NAO in the remaining four stocks, generally agreeing with CCM results (Figure 4.3, Supplementary Information, Figure S4.5). However, adding a climate variable had only a weak or even no additional effect when the baseline SSB model performed already poorly (e.g. Figure 4.2s, Ricker model).
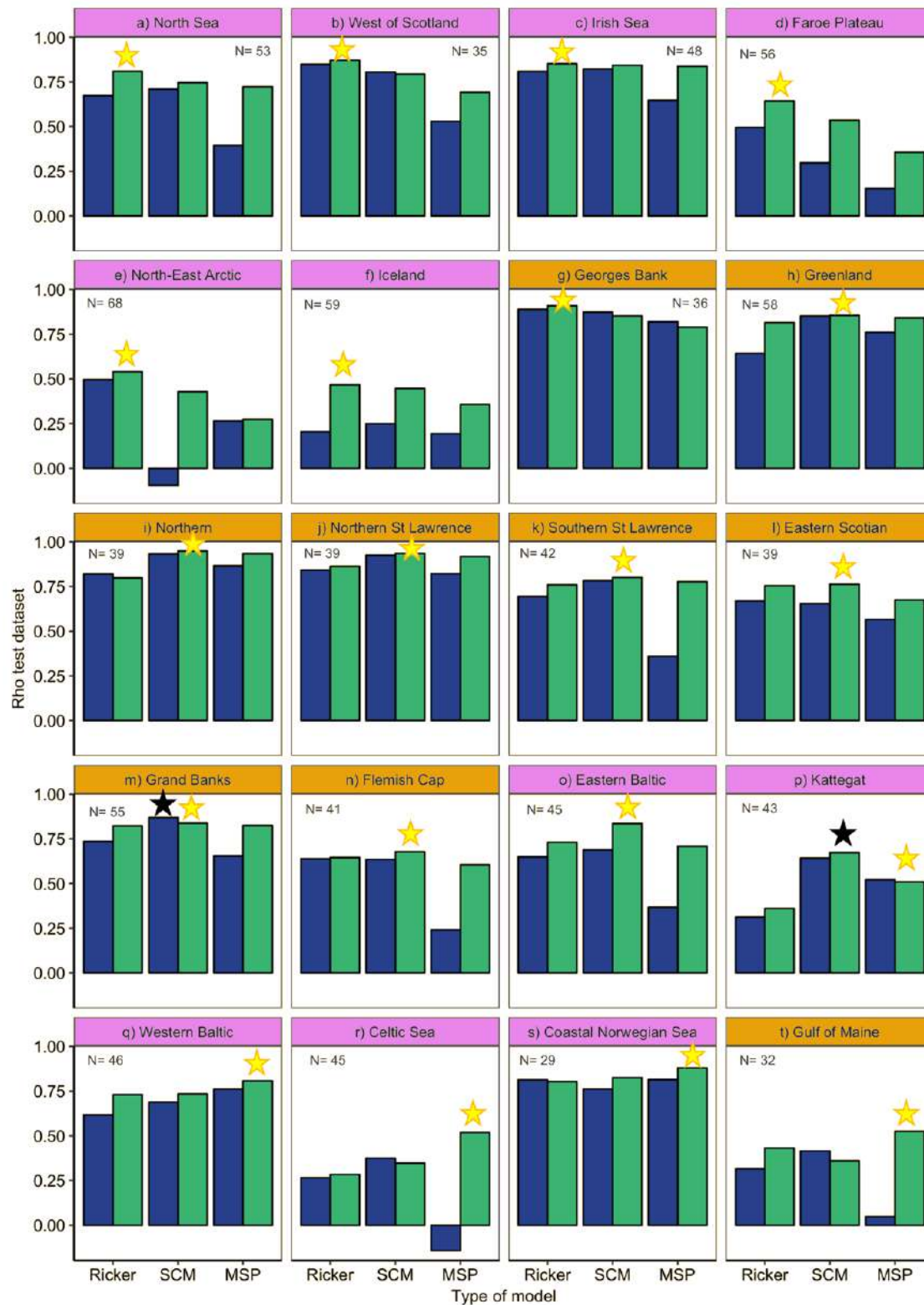
Figure 4.13: Stock-recruitment model comparison. The comparison between the predictive power of the best models resulting from the model selection of the Ricker, Stochastic CUSP model (SCM) and Multivariate Simplex Projection (MSP). The median of the predictive power, derivate from the cross-validation is shown for the three models without (blue) and with (green) the inclusion of the climate variables. The best model between the three, i.e. the model presenting the highest Pearson ρ, is for each stock indicated by a star. The black star indicates the best models which however had a poor fit to recruitment and thus were substituted by the second-best model. The environmental variable that resulted in the best predictions can be found in Figure4. 3 and Supplementary Information, Table S4.2. The number of years in the time series are indicated for each stock. The titles' colours correspond to the geographical location of the stock, pink in the East Atlantic, and orange in the West.

The Ricker model best represented more gradual declines in recruitment, typical for cod stocks around the British Isles (i.e. North Sea, West of Scotland and Irish Sea), those closer to the Arctic (i.e. Faroe Plateau, North-East Arctic and Iceland cod) and Georges Bank cod (Figure 4.3a-g, Supplementary Information, Table S4.3), as illustrated by their individual time series (Supplementary Information, Figure S4.1). All of these stocks, except Georges Bank, displayed strong density-dependence in recruitment at high SSB levels, which is characteristic for the Ricker model. Furthermore, Ricker models clearly revealed that recruitment in warmer years is usually lower for the same level of SSB when compared to colder conditions (as indicated by low SST, NAO or AMO in Figure 4.3a,d,g). The only exception with the reverse pattern of higher recruitment values at warmer conditions were North-East Arctic and Iceland cod, hence the only cod stocks that really profited from climate warming (Figure 4.3e,f).

SCM instead is an approach from catastrophe theory which models best discontinuous dynamics characterized by abrupt sudden shifts and hysteresis (i.e. in this case delayed recovery). The recruitment and SSB time series of Canadian stocks on the Western Atlantic side, but also Greenland and Eastern Baltic cod (Supplementary Information, Figure S4.1) show this type of dynamics, and hence SCM was the best approach for these stocks. SCM identified discontinuous stock-recruitment dynamics caused by the interaction of SSB and the climate variable. Moreover, SCM can identify catastrophic collapse which occurs when SSB is found in the "folded" area, or area of instability (see blue shaded areas in Figure 4.3h-o, Supplementary Information, Figure S4.3). Recruitment collapsed in these stocks, when in the instability area, in response to only small reductions in stock size (Figure 4.3 h-o). Consequently, SSB was a significant predictor in all SCMs, controlling the stocks dimension, while the climate variables modified the relationship between recruitment and SSB rendering it discontinuous, and thus inducing hysteresis (Supplementary Information, Table S4.4). These two factors lead to the presence of stable low recruitment levels towards the end of the time-series. Low SSB coupled with warming (as indicated by climate variables SST, NAO and AMO, Supplementary Information, Table S4.4) had the potential to stabilize low recruitment. This is indicated by values outside the bifurcation area as best demonstrated by Northern and Grand Banks cod (Figure 4.3i,m). Other cod stocks such as those from the Gulf of St. Lawrence, on the Eastern Scotian Shelf and off Greenland were at the boarder of stable low recruitment levels (Figure 4.3h,j,k,l).

Eventually, we found MSP to be the best model for recruitment of stocks that did not show collapses, but mostly fluctuating dynamics such as cod in the Western Baltic, the Kattegat (since, even if the SCM was the best the model, the fit was invalid), the Celtic Sea, the Norwegian coast and in the Gulf of Maine (Figure 4.3p-t, Supplementary Information, Figure S4.1). The MSP however, seemed also appropriate to model catastrophic dynamics, but less effectively than the SCM. In contrast to the stocks best modelled with SCM and Ricker, stocks best modelled with MSP showed a mixed response to recent warming with a clear negative effect on recruitment in the Western Baltic only (Figure 4.3q).
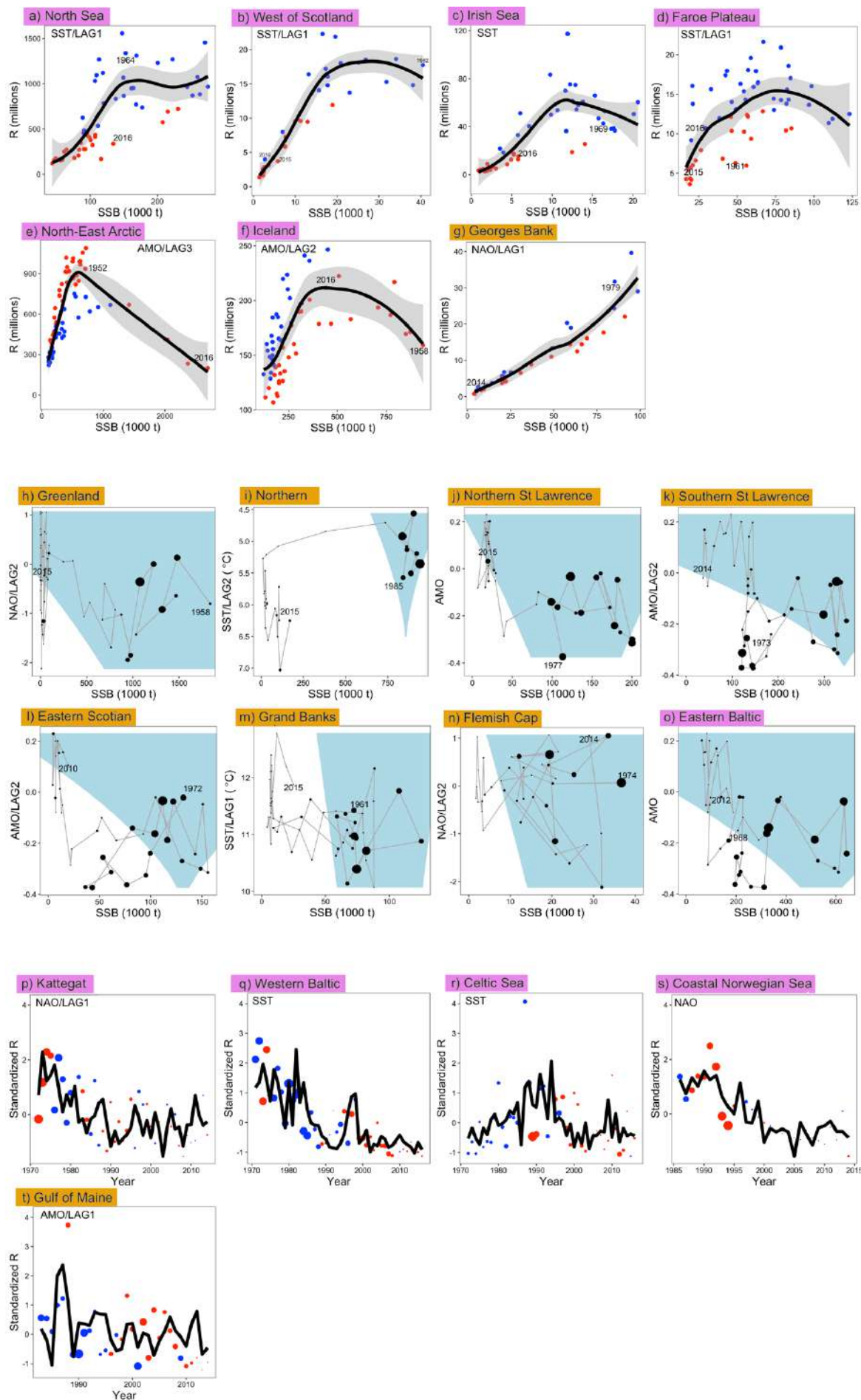
Figure 4.14: *Best model visualization.* Every stock is plotted using the resulted best model from the model comparison. The titles' colours correspond to the geographical location of the stock, pink in the East Atlantic, and orange in the West. a-g) The results of the Ricker model, showing density-dependent effects on the stock-recruitment relationship. On the x-axis SSB in thousand t and on the y-axis recruitment in millions. The colour of the dots corresponds to the state of the climate variable indicated, red above the mean, blue below the mean. The line represents the smoothed predicted trend of the SRR. h-o) The results of the stock-recruitment stochastic CUSP models (SCM) on stocks showing catastrophic dynamics. On the x-axis Spawning Stock Biomass (SSB) in thousand tonnes, on the y-axis the best climate predictor, either Sea Surface Temperature (SST), North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO). The dimension of the dots corresponds to the recruitment dimension. The blue area corresponds to the instability area, thus the fold in the 3D visualization (Supplementary Information FigureS3) where 3 equilibria are possible. p-t) The results of the Multivariate Simplex Projection (MSP) for stocks showing more fluctuating but still state-dependent dynamics. On the x-axis the time in Year and on the y-axis recruitment. The dimension of the dots is proportioned to the dimension of SSB. Also in this case, the colour corresponds to the state of the climate variable indicated, red above the mean, blue below the mean. The line showed the predicted trend of recruitment over time.

Discussion

Short-term predictions of the size of an incoming year-class is essential to modern assessments of commercial fish species, but often suffers from the accuracy of available models predicting recruitment based on continuous, linear relationship with spawning stock biomass (SSB). In our study, we investigated whether (i) recruitment dynamics in Atlantic cod stocks are better predicted by non-parametric, state-dependent or catastrophic statistical methodology compared to traditional parametric, linear approaches such as the Ricker stock-recruitment model, and (ii) if using climate variables as predictors in addition SSB improves the predictive performance of such models.

The main result of our study is that predicting fish stock recruitment can be improved by tailoring the modelling approach to the dynamical properties of each individual stock. We found cod stocks with more gradual and mostly linear dynamics to be best predicted by the traditional linear Ricker model, while stocks that experienced sudden abrupt changes in recruitment and stock size are best described by the stochastic CUSP model (SCM). SCM, based on catastrophe theory, is well suited to represent such discontinuous regime shift dynamics (Thom, 1972; Grasman *et al.*, 2009; Diks & Wang, 2016). SCM allows for the identification of drivers and how their interaction results in unstable recruitment dynamics and hence provides a form of vulnerability assessment that can be instrumental in management (Petraitis & Dudgeon, 2015; Diks & Wang, 2016). Eventually, Multivariate Simplex Projection (MSP) was most appropriate for stocks that displayed more chaotic and fluctuating behaviours (Sugihara *et al.*, 2012; Ye *et al.*, 2015). Indeed, being a minimally assumptive model the most complex dynamics are better captured by it. MSP as part of the EDM (Empirical Dynamic Modelling) suite of methods is based on attractor reconstruction and accounts for state-dependent dynamics (Ye *et al.*, 2015). which makes it a suitable approach to model also discontinuous dynamics (Ye *et al.*, 2015; Deyle *et al.*, 2018). Mostly, both SCM and MSP models performed similarly in our analysis and their relatively high predictive power indicated the importance of using state-dependent and/or discontinuous approaches to model recruitment (Ye *et al.*, 2015; Deyle *et al.*, 2018; Munch *et al.*, 2018).

Our study highlights that important differences exist between cod stocks in the Eastern and Western areas of the North Atlantic (Frank *et al.*, 2016). Stocks from the Western Atlantic and in particular off Canada and Greenland often experienced pronounced catastrophic dynamics,

i.e. abrupt and sudden changes in stock size and recruitment. Eastern Atlantic stocks instead showed more continuous dynamics and thus a higher degree of stability. In general Western Atlantic cod stocks seemed to be less resilient to abrupt collapses due to more fragile life history traits, an overall more extreme and difficult environment, and different exploitation histories (Rätz & Lloret, 2003; Pörtner et al., 2008; Wang et al., 2014; Frank et al., 2016). Moreover, sea surface temperature (SST) was selected in Eastern Atlantic cod stocks models, while for Western stocks the climate indices explained better the recruitment variability. This difference might indicate that the Eastern cod stocks are more influenced by local processes, while in the Western Atlantic large scale climatic fluctuations are more important. Nevertheless, the addition of the climate factors in the best stock-recruitment models almost always increased its predictive power and thus highlights the importance of using environmental information also in stock assessment and management considerations to consider broader ecosystem dynamics (Punt et al., 2013; Skern-Mauritzen et al., 2015).

These results highlight the presence of multiple dynamics in cod stocks which are also supported by the results of the preliminary S-Maps tests revealing a significant level of non-linearity in recruitment time-series of Atlantic cod stock. However, the non-linearity signal is lower than expected, which we assume is due to the nature of the stock assessment data we used, and thus could be an underestimation (Brooks et al., 2015). Such model output tends to be smoother and more linear than survey data (Storch et al., 2017), which are unfortunately not available for all cod stocks and longer time-periods needed for our study.

Finally, the different models allow us to draw conclusions about the recovery potential of collapsed Atlantic cod stocks. Most of the stocks are negatively influenced by warming and climate change, since the lowest recruitment and SSB coincide with the highest temperature (Brander, 2005; Drinkwater, 2005; Pörtner et al., 2008). The only two exceptions are North-East Arctic cod and Iceland where a warming environment positively influences recruitment, since these two stocks reside at the northern distribution limit of the species (Pörtner et al., 2008). The stocks for which the traditional Ricker model performed best, such as the ones from the North Sea and around the British Isles, show continuously low recruitment and SSB in recent years and a continuous relationship between these parameters. These imply that, with low exploitation pressure these stocks have a higher recovery potential, but with climate change the productivity will likely remain low (Drinkwater, 2005). The situation is even worse for stocks that are best described by the SCM such as the Western Atlantic stocks where the relationship between recruitment and SSB is discontinuous and thus the stocks display a strong hysteresis effect. Most of them are at present in a stable low state, suggesting that recovery might be even further delayed and productivity will remain low.

Conclusions

We demonstrated that discontinuous, state-dependent dynamics are pervasive in at least half of Atlantic cod stocks and need to be considered when predicting year-class strength. Furthermore, we show the importance of accounting for environmental factors in recruitment predictions. Our findings indicate the need for more flexibility in the stock assessment process and highlight the importance for an adaptive multi-model approach that accounts for the inherent dynamics

of living marine resource populations (Punt *et al.*, 2016). Flexible models and adaptive management are fundamental to move towards an ecosystem-based management approach, especially in the face of climate change. To achieve this, we need to move away from fixed and established model procedures and explore other options, to be ready to adapt to the new challenges that climate change will pose (King *et al.*, 2015).

Supplementary Information Chapter 4

Supplementary Information Tables

Table S4.1: The stocks assessment models of the Atlantic cod stocks. Stock number and corresponding name have been listed together with management area code, stock assessment models used, age at recruitment (in years), and the institution (or working group within the institution) conducting the stock assessment. Last column provides the person or organisation responsible for the data

Stock name	Stock N°	Management area	Stock assessment models*	Age at R	Institution/ group	Contact person or other data source
Eastern Baltic[1]	1	25-32	SAM	2	ICES/ WGBAFS	Margit Eero
Western Baltic[2]	2	22-24	SAM	1	ICES/ WGBAFS	Margit Eero
Kattegat[1,2]	3	IIIa/21	SAM	1	ICES/ WGBAFS	Johan Lövgren
North Sea	4	IV – VIId – IIIa	SAM	1	ICES/ WGNSSK	Alexander Kempf
West of Scotland	5	VIa	TSA	1	ICES/ WGCSE	Rui Catarino
Irish Sea	6	VIIa	SAM	1	ICES/ WGCSE	Colm Lordan
Celtic Sea	7	VIIe – VIIk	XSA	1	ICES/ WGCSE	Colm Lordan
Coastal Barents Sea[2]	8	I – I	Survey SSB and F from VPA	2	ICES/ AFWG	Gjert Endre Dingsor
Northeast Arctic	9	I – II	XSA	3	ICES/ AFWG	Gjert Endre Dingsor
Faroe Plateau	10	Vb1	XSA	2	ICES/ NWWG	Petur Steingrund
Iceland	11	Va	Forward based statistical catch at age model	3	ICES/ NWWG	Einar Hjorleifsson
Greenland	12	1	XSA	2	Thünen Institute of Sea Fishery	Karl Micheal Werner
Northern cod	13	2J3Kl	State space model	2	DFO	DFO(2016)[3]
Northern Gulf of st. Lawrence	14	3Pn4Rs	SPA	3	DFO	Claude Brassard
Southern Gulf of st. Lawrence	15	4T4Vn	SCA	2	DFO	Doug Swain
Eastern Scotian Shelf	16	4VsW	VPA	2	DFO	Swain & Mohn (2012)[4]
Grand Banks	17	3NO	SPA	2	NAFO	NAFO (2015)[5]
Flemish Cap	18	3M	Bayesian model	2	NAFO	Diana Gonzalez
Georges Bank	19	5z	Age structured model	1	NOAA	Loretta O´Brien
Gulf of Maine	20	5y	Age structured model	1	NOAA	Mike Palmer

* SAM – State-space assessment model, TSA – Analytical age-based assessment (time series analysis), XSA – Extended survivor analysis, SPA – Sequential population analysis, SCA – Statistical catch at age, VPA – Virtual population analysis

[1] Stocks that in the last year failed the assessment

[2] Stocks where, in order to have longer time series, we mixed old assessments and new ones, after checking for same trends and stock dimensions.

[3] DFO (2016) Stock Assessment of Northern Cod (NAFO Divs. 2J3KL) in 2016. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2016/026

[4] Swain DP, Mohn RK (2012) Forage fish and the factors governing recovery of Atlantic cod (Gadus morhua) on the eastern Scotian Shelf. Can. J. Fish. Aquat. Sci. 69: 997–1001.

[5] NAFO (2015) Assessment of the Cod Stock in NAFO Divisions 3NO. NAFO SCR Doc. No. 15/034.

Table S4.2: Results of the model selection for each stock

Stock name	Model	Selected variables	Predictive power	Stock name	Model	Selected variables	Predictive power
Eastern Baltic	Ricker	SSB	0.65	**Western Baltic**	Ricker	SSB	0.62
		SSB + NAO_lag2	0.73			SSB + AMO_lag1	0.73
	CUSP	SSB	0.69		CUSP	SSB	0.69
		SSB + AMO	0.83			SSB + AMO_lag1	0.73
	EDM	SSB	0.37		EDM	SSB	0.76
		SSB + SST	0.7			SSB + SST	0.81
Kattegat	Ricker	SSB	0.31	**North Sea**	Ricker	SSB	0.67
		SSB + AMO	0.36			SSB + SST_lag1	0.81
	CUSP	SSB	0.64		CUSP	SSB	0.7
		SSB + NAO_lag1	0.67			SSB + SST_lag1	0.74
	EDM	SSB	0.52		EDM	SSB	0.39
		SSB + NAO_lag1	0.5			SSB + AMO_lag1	0.72
West of Scotland	Ricker	SSB	0.85	**Irish Sea**	Ricker	SSB	0.8
		SSB + SST_lag1	0.87			SSB + SST	0.85
	CUSP	SSB	0.8		CUSP	SSB	0.82
		SSB + SST_lag1	0.79			SSB + SST	0.84
	EDM	SSB	0.52		EDM	SSB	0.64
		SSB + SST_lag1	0.69			SSB + AMO_lag1	0.83
Celtic Sea	Ricker	SSB	0.26	**Coastal Norwegian**	Ricker	SSB	0.81
		SSB + SST_lag1	0.28			SSB + SST	0.8
	CUSP	SSB	0.37		CUSP	SSB	0.76
		SSB + SST_lag1	0.34			SSB + SST_lag1	0.82
	EDM	SSB	-0.14		EDM	SSB	0.81
		SSB + SST_lag1	0.51			SSB + NAO	0.88
North-East Arctic	Ricker	SSB	0.49	**Faroe Plateau**	Ricker	SSB	0.49
		SSB + AMO_lag3	0.54			SSB + SST_lag1	0.64
	CUSP	SSB	-0.09		CUSP	SSB	0.29
		SSB + NAO_lag3	0.42			SSB + SST_lag1	0.53
	EDM	SSB	0.26		EDM	SSB	0.15
		SSB + AMO_lag2	0.27			SSB +SST_lag1	0.36
Iceland	Ricker	SSB	0.2	**Greenland**	Ricker	SSB	0.64
		SSB + AMO_lag2	0.47			SSB + SST_lag2	0.81
	CUSP	SSB	0.25		CUSP	SSB	0.85
		SSB + AMO_lag2	0.44			SSB + NAO_lag2	0.85
	EDM	SSB	0.19		EDM	SSB	0.76
		SSB + NAO_lag3	0.36			SSB + NAO_lag2	0.84

Stock	Model	Variable	Value	Stock	Model	Variable	Value
Northern	Ricker	SSB	0.82	**Northern Lawrence**	Ricker	SSB	0.84
		SSB + AMO	0.8			SSB + SST	0.86
	CUSP	SSB	0.93		CUSP	SSB	0.92
		SSB + SST_lag2	0.95			SSB + AMO	0.94
	EDM	SSB	0.87		EDM	SSB	0.82
		SSB + SST	0.93			SSB + SST_lag3	0.91
Southern Lawrence	Ricker	SSB	0.69	**Easter Scotian Shelf**	Ricker	SSB	0.76
		SSB + AMO_lag2	0.76			SSB + NAO_lag2	0.75
	CUSP	SSB	0.78		CUSP	SSB	0.65
		SSB + AMO_lag2	0.8			SSB + AMO_lag2	0.76
	EDM	SSB	0.36		EDM	SSB	0.56
		SSB + AMO	0.78			SSB + NAO_lag2	0.67
Grand Banks	Ricker	SSB	0.73	**Flemish Cap**	Ricker	SSB	0.64
		SSB + NAO	0.82			SSB + SST	0.64
	CUSP	SSB	0.87		CUSP	SSB	0.63
		SSB + SST_lag1	0.83			SSB + NAO_lag2	0.68
	EDM	SSB	0.65		EDM	SSB	0.24
		SSB + AMO_lag2	0.82			SSB + SST_lag1	0.6
Georges Bank	Ricker	SSB	0.89	**Gulf of Maine**	Ricker	SSB	0.31
		SSB + NAO_lag1	0.9			SSB + NAO	0.43
	CUSP	SSB	0.87		CUSP	SSB	0.41
		SSB + AMO_lag1	0.85			SSB + NAO_lag1	0.36
	EDM	SSB	0.81		EDM	SSB	0.06
		SSB + SST	0.79			SSB + AMO_lag1	0.52

For every stock the results of the best Ricker model, SCM, and EDM with and without environmental variable is shown. The Predictive power corresponds to the median of the 500 Pearson rho, obtained from the cross-validation.

Table S4.3: Results of the best Ricker stock-recruitment model

	North Sea	West of Scotland	Irish Sea	Faroe Plateau
a	4.781e+04	1.270e+04	7.600e+07	9.044e+03
b	2.316e-06	3.988e-05	5.243e-05	1.644e-05
c	-8.630e-01	-8.486e-01	-1.462e+00	-1.014e+00
residual	13.7	8.5	45.7	16.9
Better than BH	***	*	**	***
	North-East Arctic	**Iceland**	**Georges Bank**	
a	3.297e+00	1.017e+00	2.403e-01	
b	1.474e-06	1.716e-06	-1.220e-06	
c	1.229e+00	-9.752e-01	-2.692e-01	
residual	24.4	5.9	10	
Better then BH	*	***	*	

a,b,c are the parameter fitted in the model for the climate effect (c) and the density dependent effects (a and b)
residual sum of square indicates the model fit
The last line show whether the Ricker model constitutes a significant improvement from a Beverton and Holt model

Table S4.4: Results of the best Stochastic CUSP model

	Greenland	Northern cod	Northern St Lawrence	Southern St Lawrence
alpha	-2.409**	-7.6**	-1.75**	-2.234**
alhpa1	1.824e-06**	8.872e-06**	1.347e-05**	6.511e-06*
beta	3.614***	9.375**	2.403***	3.082***
beta1	0.7237**	-1.432*	2.21E+00	8.301***
Z	-2.268e+00***	-2.451***	-2.21***	-3.013***
Z1	7.06e-06***	3.08E-06	2.246e-05***	8.978e-06***
delta AIC	1416	834	884	1009
R squared	0.78	0.81	0.79	0.64
	Eastern Scotian Shelf	**Grand Banks**	**Flemish Cap**	**Eastern Baltic**
alpha	-1.546**	-3.306***	-2.333**	-1.554**
alhpa1	1.175e-05*	3.575e-05**	7.044e-05*	2.873e-06**
beta	1.999**	-0.2526	2.784***	2.701***
beta1	4.51**	0.2357	0.2302	5.27***
Z	-2.27***	-2.142***	-2.187***	-2.826***
Z1	2.873e-05***	1.734e-05***	3.697e-05***	6.834e-06***
delta AIC	836	1260	877	1107
R squared	0.5	0.66	0.69	0.73

alpha, beta and Z represents the intercept of respectively the asymmetry variable, the bifurcation variable and the State variable, while alpha1, beta1 and Z1 shows the coefficients. The stars indicate the significance (*=0.05, **=0.005, ***<0.0005). Delta AIC show the improvement of the Stochastic CUSP model (SCM) compared to the same linear model. Finally, the R squared show how well the SCM fits to the data.

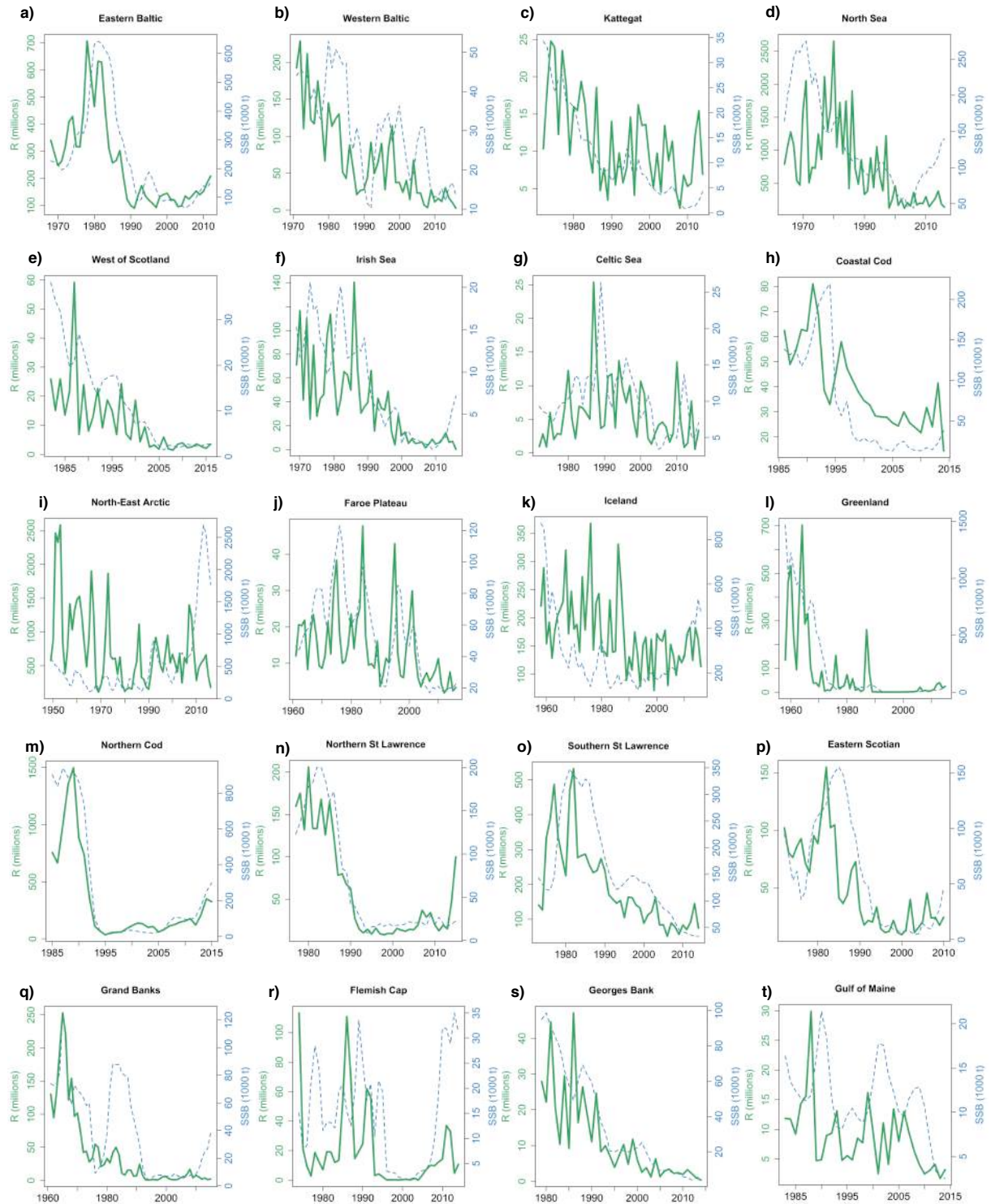## Supplementary Information Plots

Figure S4.1: Recruitment and Spawning Stock Biomass (SSB) trend over time for Atlantic cod stocks. On the x axis year, on the y axis recruitment in millions and SSB in thousands tons. Recruitment is shown in green, while SSB in blue dotted line. The data come from the stock assessment indicated in Supplementary Information, Table4.1.
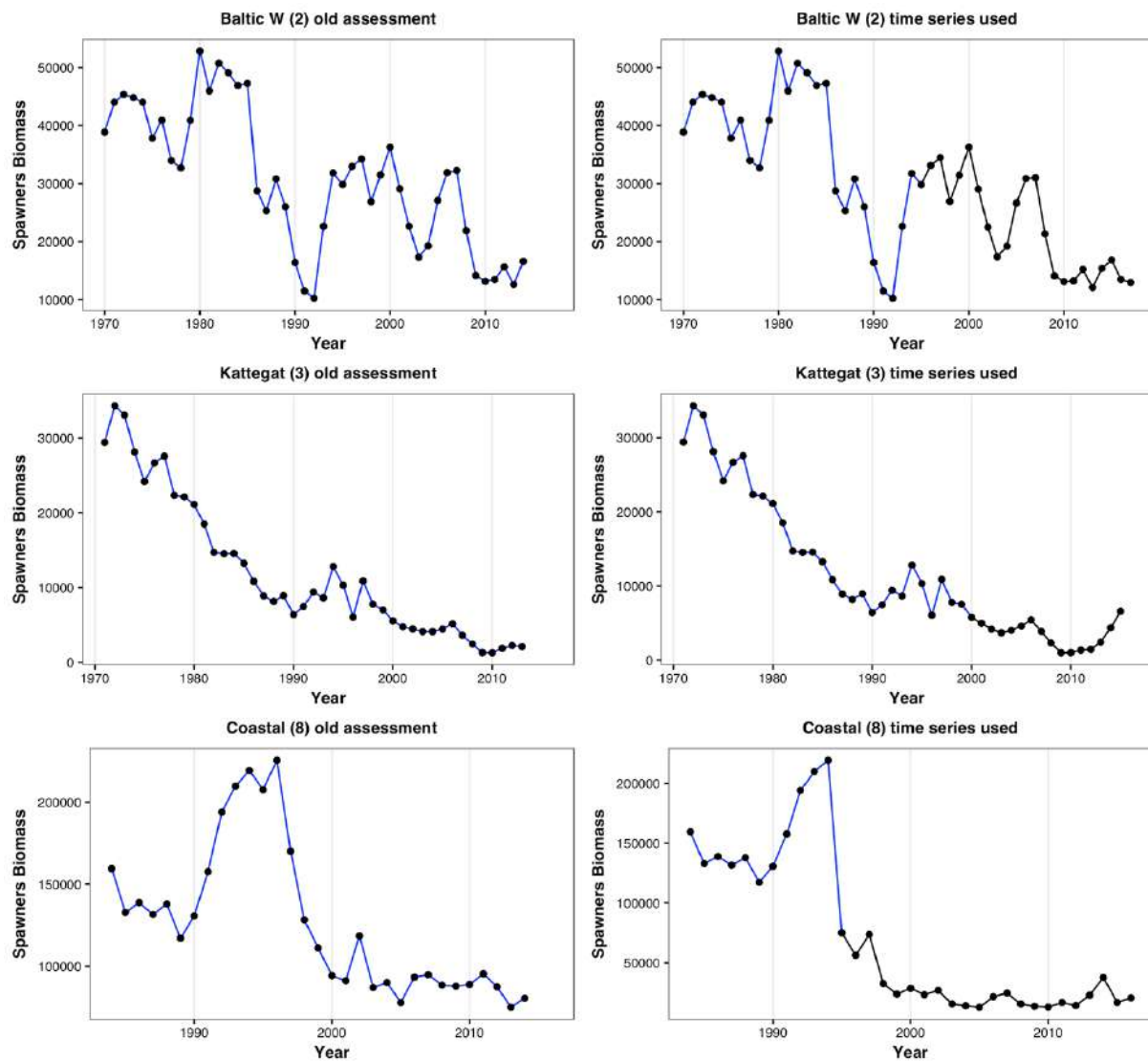
Figure S4.2: Stock assessment used for short time series stocks. The plots represent SSB in tonnes over time. On the left panel, the older stock assessments. On the right panel the new stock assessment (black lines), merged with the old stock assessment (blue lines). We merged them together because we needed a long time series, but also we wanted to have the more recent stock assessments, from 2017.
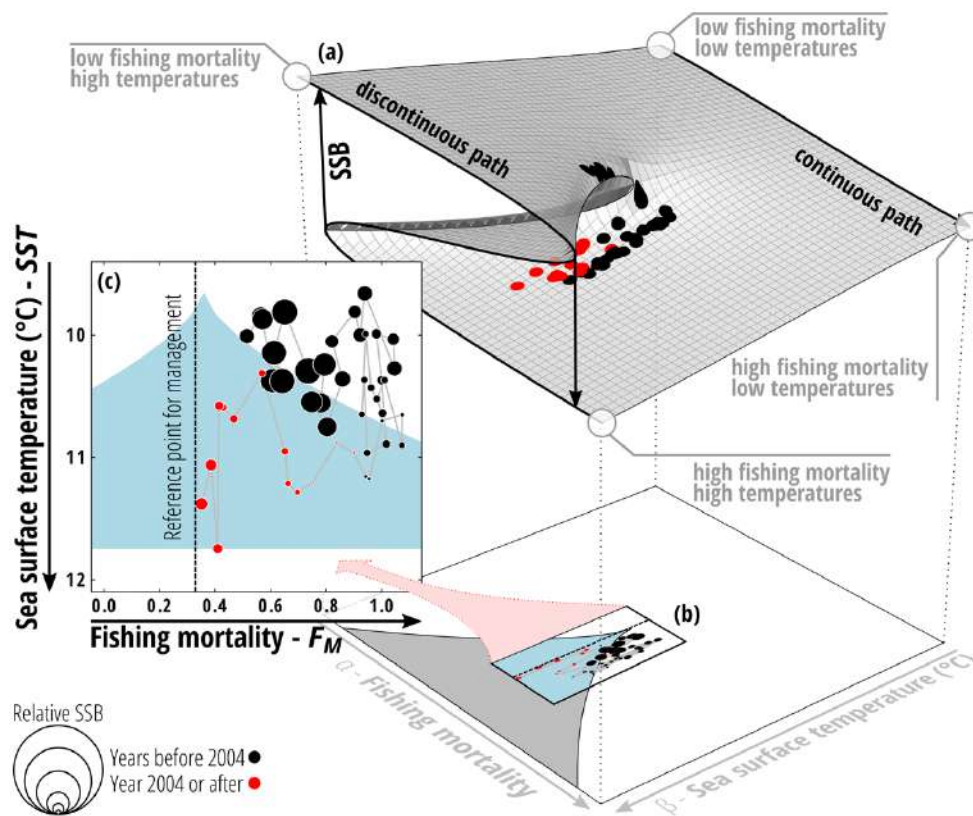
Figure S4.3: Example of the Stochastic CUSP model. In this example, the state variable is spawning stock biomass (SSB) and the predictors are seat surface temperature (SST) and fishing Mortality (F). The CUSP model can be visualized as a 3D landscape (a) in which SSB is controlled by two control variables, here Fishing Mortality (F, α) and SST (β). F is the so called "asymmetry variable" and controls the dimension of SSB; indeed, SSB will be in the higher fold (i.e. high SSB) when F would be low and in the lower fold (i.e. low SSB) when F would be high. Instead, SST, the "bifurcation variable" controls whether the moving on SSB happens in a continuous or discontinuous way. In this example, at low SST the SSB will have a continuous dynamic and will respond in a continuous way to increase in F, while at high SST, the SSB will cross the fold, indicating a discontinuous path. The fold is the so called "instability areas", where 3 equilibria (2 stable, 1 unstable) are possible. The same representation can be seen in 2D (b-c). The instability area is the blue area in the plot. The SSB follows a discontinuous path, since it is always closed or crossing the instability area. (c) At the beginning of the time series F was low and SSB high. At the increasing of F, SSB started to oscillate close to the instability area to finally collapse in the lower fold and into the unstable state (small dots). Even with reduction of F, SSB is now in a low state and it is pushed from the higher SST even more into the instability area, thus the stock resilience is low. Therefore, higher SST modifies the relationship between F and SSB, causing hysteresis and discontinuous, non-linear dynamics.
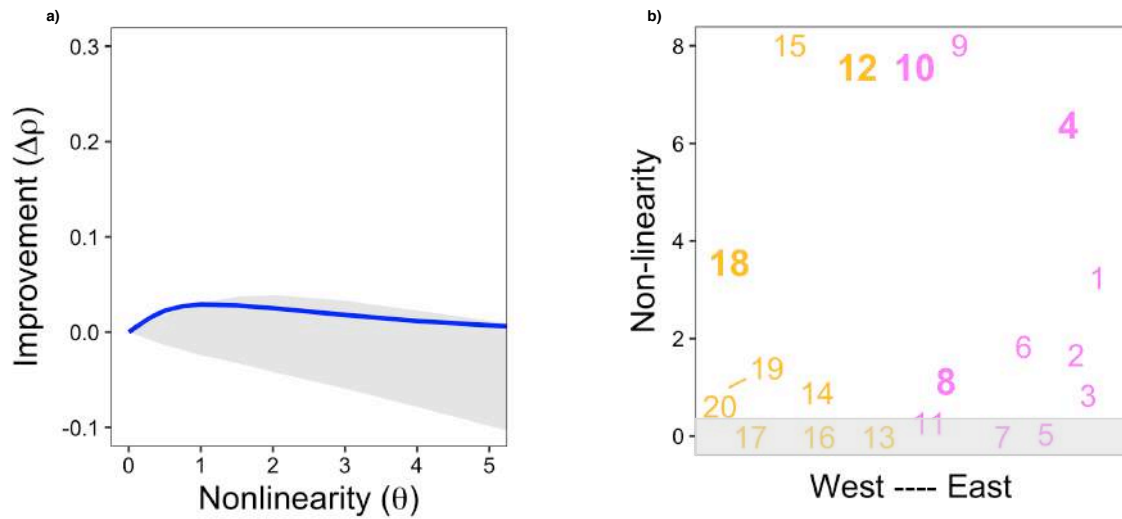
100

Figure S4.4: Non-linearity test on Recruitment data. a) Average of the S-map results among Atlantic cod stocks. The y axis shows the improvement in the predictability (ρ), while the x axis show the parameter θ, which represent the non-linearity. The grey area represents the null distribution of the non-linearity test. The best prediction was obtained at a θ of 1 and outside of the null distribution, indicating a significant non-linear trend in recruitment time series. b) The results of the non-linear test for each stock (represented by the numbers showed in Figure4.1). Y axis represent the value of θ which corresponded to the best prediction. The stocks above the grey area show non-linear trend, and the stocks in bold are significantly non-linear. The colour of the numbers refers to the East (pink) West (orange) division.
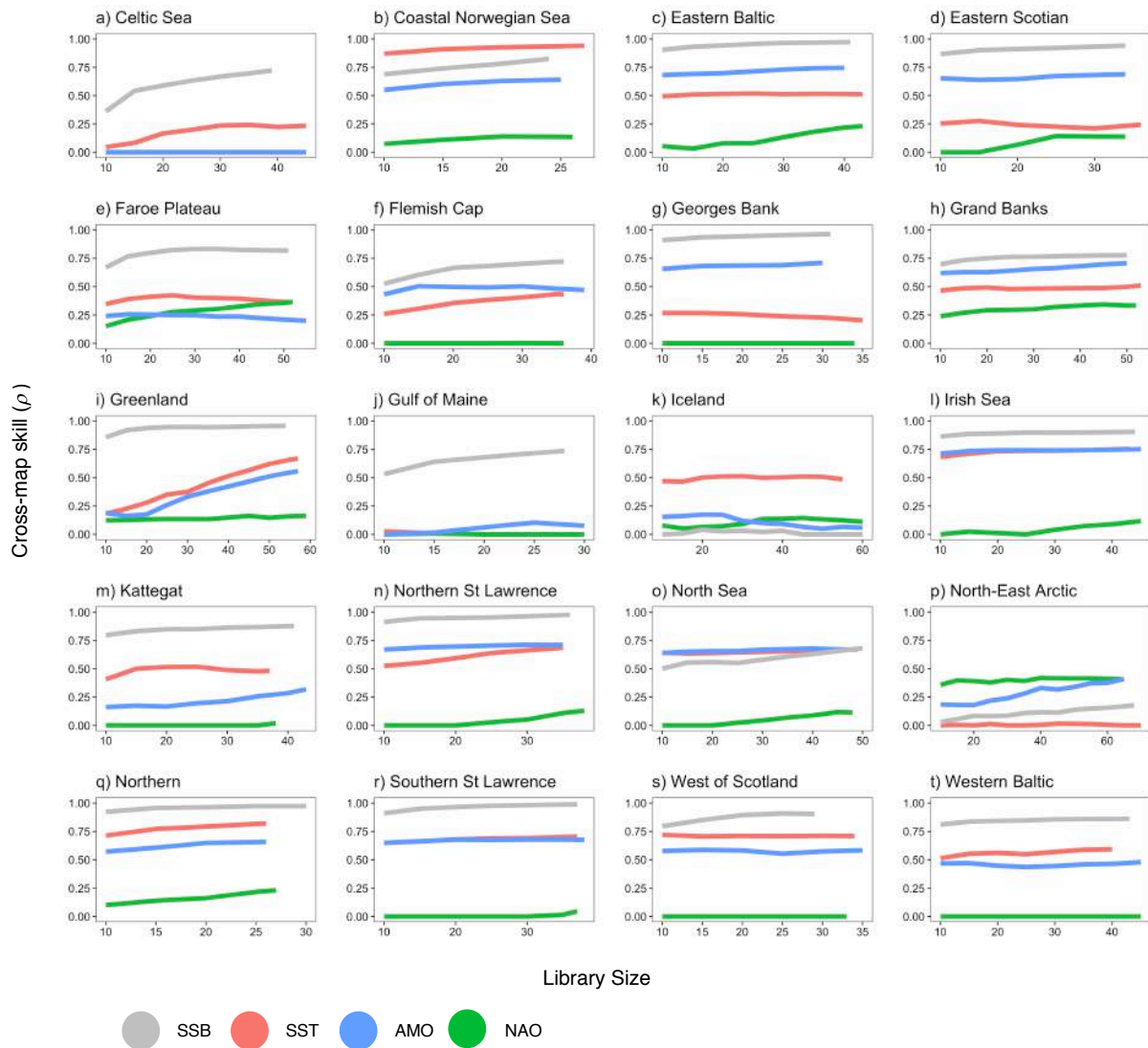
Figure S4.5: Convergent Cross Mapping (CCM) correlation of recruitment (R) with biomass (SSB) and environment. Cross-mapping skills are calculated as Pearson ρ between observed and predicted values using equation (2). Library size represents the time series length. CCM aims to detect correlation between variables, in our case R, SSB and environment. In a full deterministic system with zero noise, we expect the cross-map skill to increase with increasing time series length, i.e. with the reconstruction becoming denser. The colour of the frame refers to the East (dark blue) West (light blue) division.

Chapter 5: Non-linear dynamics in North Atlantic herring

Detection of discontinuous behaviour causing shifts in North Atlantic herring stocks

Leonie Färber[1], **Camilla Sguotti**[2], Joël M. Durant[1], Øystein Langangen[1], Saskia A. Otto[2] and Christian Möllmann[2]

Abstract

Sudden structural changes, often termed regime shifts, have been increasingly documented for marine ecosystems with climate change as major driver, interacting with anthropogenic pressures such as overfishing. Whether observed changes can be classified as true catastrophic transitions, characterized by abrupt shifts, discontinuity in the response to drivers, and entering of a new state of prolonged duration, is still largely unclear and widely debated. Here, we tested whether 14 stocks of the commercially important Atlantic herring (*Clupea harengus,* Clupeidae) showed true catastrophic dynamics. First, we developed a new approach for detecting abrupt and significant regime changes in adult spawner biomass by using an ensemble of change point analyses. Then, we applied the stochastic CUSP model, built on the catastrophe theory, to test if stocks showed discontinuous behaviour and potentially hysteresis. We modelled potential catastrophic changes depending on fishing mortality as well as temperature or predation by cod (*Gadus morhua,* Gadidae). We found that North Sea autumn-spawning, Norwegian spring-spawning, and Georges Bank/Gulf of Maine herring stocks showed abrupt and true catastrophic changes over the last 4-6 decades. These catastrophic changes were mostly due to overfishing but modulated by temperature or predation by cod. By using a combination of novel approaches to detect discontinuous dynamics based on time-series, we show that Atlantic herring stocks were resilient to environmental changes when sustainably harvested. Management can make use of thresholds indicated by the cusp model to define limits for fishing pressure, in consideration of e.g. climatic change and predator-prey interactions and ensure a sustainable harvest.

Author´s affiliations

[2]Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, Norway
[1]Institute for Marine Ecosystem and Fisheries Science, University of Hamburg, Germany

Introduction

Sudden structural and synchronous changes have been increasingly documented in the marine realm (deYoung *et al.*, 2004; Möllmann & Diekmann, 2012), e.g. in the North Sea (Beaugrand, 2004), the Baltic Sea (Möllmann *et al.*, 2009), or the western North Atlantic (Choi *et al.*, 2004). Those changes are often driven by alterations in the ocean climate for example through natural variability in large scale climatic indices (Stenseth *et al.*, 2003). The North Atlantic Oscillation (NAO) is one example, where its transition from a negative phase to a positive phase in the late 1980s leading to an increase in sea temperature, caused drastic changes in several trophic levels, among others, in the ecosystems of the North, the Baltic, and Mediterranean Seas (Alheit & Bakun, 2010). In addition, direct anthropogenic influences, such as fishing, can alter an ecosystem in an intense manner and can lead to changes in species interactions (Jackson *et al.*, 2001). In the North Atlantic, the severe abundance decrease of large predatory demersal fishes, such as Atlantic cod (*Gadus morhua,* Gadidae) as a major example, were partly at least due to overfishing (Cook *et al.*, 1997; Choi *et al.*, 2004). Also small pelagic fish such as Atlantic herring (*Clupea harengus,* Clupeidae) were drastically overfished and this in combination with unfavourable environmental factors contributed to changes in their abundance (Overholtz & Friedland, 2002; Toresen & Østvedt, 2008; Dickey-Collas *et al.*, 2010).

Those drastic changes in single species to entire food webs are often termed "regime shift". However, the definition of a regime shift is not always clear (Lees *et al.*, 2006), the term being used for smooth, abrupt, and discontinuous changes alike (Collie *et al.*, 2004). In this work, we study regime shifts, which we term "catastrophic shifts" or "catastrophic transitions" (Scheffer *et al.*, 2001, 2009), where species populations underwent abrupt changes of several orders of magnitude and with discontinuous behaviour in their functional response to drivers. In addition, we define such catastrophic shifts to be persistent in time (deYoung *et al.*, 2004), meaning the system is locked into a possibly new state by internal feedbacks which could potentially lead to the occurrence of hysteresis (Scheffer *et al.*, 2001). Hysteresis is a highly unwanted property in ecosystem management, since restoring the system is shown to be a lengthy and costly process, if at all possible (Mäler, 2000). It is usually not enough to return the forcing variable to its previous conditions, but often much more and drastic changes need to happen to push the response variable back to its previous state (Mäler, 2000; Scheffer *et al.*, 2001). A system displaying discontinuous behaviour passes through an unstable state, which is highly unpredictable. In this state, since it is unstable, the system can switch between desired and undesired states. The bistability exists until the systems settles into a new stable state (Scheffer *et al.*, 2001; Collie *et al.*, 2004; Carpenter, 2005).

Being able to detect such shifts and instability is particularly relevant in the management of commercially important fish stocks such as Atlantic herring. In this paper, we investigate if we can detect catastrophic shifts in past time-series of 14 Atlantic herring stocks in the North Atlantic (Figure 5.1). Understanding these dynamics might help direct a sustainable management. Atlantic herring is an important harvested resource and amounts to 2 % of the global marine capture production (FAO, 2018b). Furthermore, it is an important key-species in many food webs (Trenkel *et al.*, 2014), thus keeping the stocks in a predictable state should be a goal from many perspectives.

We explore the dynamics of the 14 herring stocks using a two-step approach: First, we test for statistically significant abrupt changes in the spawning stock biomass time-series of the herring stocks by combining three different statistical tools for change point analysis with the duration and magnitude of the shift (Fig 5.2.1). Second, we test for discontinuous behaviour in the system dynamics in response to external drivers (Figure 5.2.2) using the stochastic CUSP model (Grasman *et al.*, 2009) that builds on catastrophe theory (Thom, 1975b).

We specifically investigate the interplay of fishing and environmental drivers i.e. temperature and cod abundance. Atlantic cod is a major predator of herring (Link *et al.*, 2009) and we test for potential predation pressure relief for the herring after the cod stock collapses (Bakun & Weeks, 2006; Overholtz & Link, 2006). With this method, we are able to determine the threshold values, at which the stock jumps from one stable state, into a potentially persistent new alternative state, thus the system is showing bistability and potentially hysteresis, when it comes to recovery. Our study shows that for resource species that are vulnerable to catastrophic transitions, a sustainable fisheries management explicitly needs to consider the stabilizing or destabilizing effects of environmental factors such as climate change or species interactions.

Material and Methods

Table 5.1 Overview of analysed herring stocks, including regions, short names and IDs used in the figures and tables. Further information on the data sources for each stock are found in Appendix Table S1.

Region	Population	Short name	ID_no
Eastern Baltic Sea	Central Baltic herring	cb_her	1
Western Baltic Sea	Western Baltic spring-spawning herring	wbc_her	2
North Sea	North Sea autumn-spawning herring	ns_her	3
Barents Sea/Norwegian Sea	Norwegian spring-spawning herring	nss_her	4
Irish Sea	South Irish Sea herring	irish_her	5
	North Irish Sea herring	nirish_her	6
Celtic Sea and West of Scotland	Celtic Sea and West of Scotland herring	westscot_her	7
Icelandic Sea	Iceland summer-spawning herring	ice_her	8
Scotian Shelf	Scotian Shelf herring	scot_her	9
Georges Bank	Georges Bank/Gulf of Maine herring	geob_her	10
Southern Gulf of St. Lawrence	Southern Gulf of St. Lawrence autumn-spawning herring	slaw_her_aut	11
	Southern Gulf of St. Lawrence spring-spawning herring	slaw_her_spr	12
Northern Gulf of St. Lawrence	Northern Gulf of St. Lawrence spring-spawning	nlaw_her_spr	13
	Northern Gulf of St. Lawrence autumn-spawning	nlaw_her_aut	14

We analysed the spawning stock biomass (SSB) of six Northwest and eight Northeast Atlantic herring stocks (Table 5.1, Figure 5.1, Supplementary Information) for abrupt and persistent changes, and discontinuous behaviours in two steps. Atlantic herring is widely distributed in the North Atlantic and consists of several smaller to larger populations (Trenkel *et al.*, 2014).

Many herring stocks undertake extensive feeding and/ or spawning migrations, thus their influence can extent to more than one ecosystem (Trenkel *et al.*, 2014). Herring in the northern areas, such as the Norwegian spring-spawning herring, mature at around 3-6 years with a maximum life span of 20 years, whereas more southern distributed stocks, for example the Georges Bank/ Gulf of Maine herring stock, have a younger age of maturity and a lifespan of around 14 years (Trenkel *et al.*, 2014).

Step 1: Analyses of abrupt and significant change

All studied herring stocks display considerable historical biomass changes (Figure 5.1). We investigated whether these changes represent statistically significant abrupt changes using three criteria (Figure 5.2.1):
   a) Significance of abrupt shifts(s) indicated by at least two out of three change point analysis tools (Figure 5.2.1a)
   b) Stability of the system during a prolonged period (quasi-stable state) (Figure 5.2.1b)
   c) Magnitude of changes in biomass between quasi-stable states (Figure 5.2.1c)

1a) Change point analysis tools
In order to detect statistical significant change points in the biomass of the herring stocks, we applied a multi-model inference approach (Townsend *et al.*, 2014; Samhouri *et al.*, 2017) and used three statistical change point analysis tools (Figure 5.2.1a).
The first tool was the "*changepoint*" R-package (Killick & Eckley, 2013), where we used the binary segmentation ("BinSeg") method on a standardized time series to calculate changes in the mean (Killick & Eckley, 2013). We initially tested the full time series for a change in mean and if a change point was detected, we subsequently split the times-series into two parts, and again conducted the test until the maximum number of change points was reached (Killick & Eckley, 2013). We allowed for a maximum of five change points and used as a penalty, to restrict over fitting, the modified Bayesian Information Criterion (MBIC) (Zhang & Siegmund, 2007) as implemented in the "*changepoint*" package (Killick & Eckley, 2013).
The second tool was the "*strucchange*" R-package which tests for structural changes in a linear regression (Zeileis *et al.*, 2002). We used standardized and differenced time series and analysed changes in the intercept of a linear regression fitted to the data (Zeileis *et al.*, 2002; Bestelmeyer *et al.*, 2011). The best model was evaluated by using the OLS-CUSUM statistics, the BIC and the F-statistics to find significant change points (Bestelmeyer *et al.*, 2011).

The third change point analysis tool was the Bayesian change point analysis ("*bcp*" R-package) implemented with a Markov chain Monte Carlo (MCMC) approximation (Erdman & Emerson, 2007). Here, we extracted the posterior probability of finding a change point and accepted values > 0.5 as probable of having a change in the time series.

We used these three approaches in order to understand better the dynamics of the herring biomass (Townsend *et al.*, 2014; Samhouri *et al.*, 2017) and with that, we find a time range, in which a change occurred (see grey shaded area Figure 5.1 & 5.3; Supplementary Information, Figure S5.1). Our criteria for accepting a change was that that at least two tools find a change

within a 10-year frame, which should be in concordance with the following steps of the analysis (see below). These methods have varying sensitivities in detecting a change point (compare e.g. Figure 5.2.1a stepwise and continuous change), thus having more than one tool indicating a change we avoided overfitting or not detecting a change.

1b) Prolonged period of quasi-stability
When we found those significant changes, we assessed if the stock biomass was in a state of prolonged stability after or before a change in abundance (Figure 5.2.1b) from which we measured the abrupt change in biomass (Fig 5.2.1c). The duration of the quasi-stable state had to be longer than the duration of the change itself (deYoung *et al.*, 2004). In order to be classified as a drastic shift, a change in the herring stock biomass of $\geq 70\%$ had to occur within 10 years, or three generations whichever is longest (cf. IUCN, 2012). Here, we assumed a generation length of 3.5 years (thus, 10.5 years corresponding to three generations), because the majority of herring stocks mature around 3-4 years (Trenkel *et al.*, 2014) and we set the threshold of being accepted as a prolonged quasi-stable state to > 10.5 years.

We used a 5-year moving window linear regression analysis on the time series of stock biomass (scaled to range between 0 and 1 for comparability) and investigated the slopes of those regressions. Since ecosystems and populations are fluctuating constantly (Scheffer *et al.*, 2001; Vert-pre *et al.*, 2013), there is hardly a period of no change (slope = 0) in an ecological time series. Thus, we developed an acceptance level for quasi-stability, where a stable slope should be $\leq 20\%$ of the absolute maximum slope. We explored the sensitivity of setting the acceptance level to 20 % and found an acceptance level of quasi-stability of 10 % to reveal hardly any stable periods and an acceptance level of 30 % did not differ much from the results with 20 % acceptance level (Supplementary Information, Table S5.2). Furthermore, we tested for the effect of varying window sizes (four and eight years, respectively) in the moving linear regression. Overall results did not change significantly by the usage of different window sizes (Supplementary Information, Table S5.2). After these analyses, we remained with a 20 % acceptance level and a 5-year moving window size. We accepted a period of being quasi-stable, if we detected ≥ 7 consecutive stable slopes, which lead to > 10 years of stability, including the years covered through our window size.

1c) Magnitude of change
For these periods of quasi-stability we computed the magnitude of the change in biomass to detect abrupt shifts (Figure 5.2.1c). We calculated the mean of the biomass during quasi-stable periods (plus the four following years, due to the window-size) and related it to biomasses before and after the quasi-stable phase. We considered a shift to be abrupt when the biomass changed by $\geq 70\%$ within three generations, thus within 10.5 years (see IUCN Criteria). Even though the word "catastrophic" suggest a collapse in biomass, in the mathematical sense, a catastrophic shift can also happen to a higher biomass level (Roopnarine, 2008). Thus, we here considered abrupt negative as well as positive changes in biomass.

If all the criteria fitted the stock, we acknowledged a drastic, significant shift in the time series. However, it is not clear based on these analyses, whether the underlying process is a linear

response to a driver that changed discontinuously, a non-linear response to a potentially continuously changing driver or the effect of multiple interacting drivers causing hysteresis (Andersen *et al.*, 2009). In the next step, therefore, we assessed the underlying mechanisms using stochastic CUSP models (Figure 5.2.2).

Step 2: Identification of discontinuity in the response to drivers

Stochastic CUSP model
To test for underlying mechanisms of observed shifts in the stocks, we applied the stochastic CUSP model (Grasman *et al.*, 2009) that builds on catastrophe theory (Thom, 1972), a branch of bifurcation theory, which is able to address discontinuous and nonlinear behaviour of a system. By using the cusp catastrophe, we are able to model discontinuous behaviour with the inclusion of more than one control variable. The stochastic form of the cusp model is implemented into the R-package "*cusp*" (Grasman *et al.*, 2009) and may display catastrophic jumps, bimodality, hysteresis and divergence in the system's behaviour (Jones, 1977). By using two variables, the model results in a 3D-visualization of the system (Petraitis & Dudgeon, 2016). The cusp catastrophe has the canonical form

$$-V(y; \alpha, \beta) = \alpha y + \frac{1}{2} \beta y^2 - \frac{1}{4} y^4 \tag{1}$$

Where y describes the state of the system and α and β are parameters shaping the surface, thus behaviour of the system, if the first derivative is equal to zero (Grasman *et al.*, 2009).

$$-V'(y; \alpha, \beta) = \alpha + \beta y - y^3 = 0 \tag{2}$$

The α-variable causes smooth changes in the state variable until the threshold value with a critical jump will be reached (Jones, 1977; Grasman *et al.*, 2009). The variable β is the bifurcation variable and changes the behaviour of α to the system, determining where the threshold lies. If $\beta > 0$, the trajectory of the system reacting to forcing variables is single sheeted, however when $\beta < 0$, it is triple sheeted, thus three solutions are possible for the position of the systems' state: two stable states and one unstable state (Grasman *et al.*, 2009) . This state is very unlikely to be reached, thus the systems "jumps" between the higher and the lower states and its behaviour becomes unpredictable (bistability).
The catastrophe theory is a deterministic theory, but by including white noise (Wiener process, $dW(t)$), it results into a stochastic differential equation (Grasman *et al.*, 2009) which has the form:

$$dy = \frac{\partial V(y; \alpha, \beta)}{\partial y} dt + dW(t) \tag{3}$$

A density function is then connected with equation (3), which describes the probability density of the system being in a certain state (Grasman *et al.*, 2009). First order polynomial approximations are then fitted to the data by using a maximum likelihood approach (Cobb & Watson, 1980; Grasman *et al.*, 2009). This means, y is the sum of linear functions of the n measured dependent variables $Y_1, Y_2, \ldots Y_n$ and respectively α and β are linear functions of the k measured independent (control) variables $X_1, X_2, \ldots, X_k$ (Grasman *et al.*, 2009).

$$y = w_0 + w_1 Y_1 + w_2 Y_2 + \cdots + w_n Y_n \qquad (4)$$
$$\alpha = a_0 + a_1 X_1 + a_2 X_2 + \cdots + a_k X_k$$
$$\beta = b_0 + b_1 X_1 + b_2 X_2 + \cdots + b_k X_k$$

Here we modelled the state variable y as a smooth transformation of the SSB of herring stocks; the α-variable was a function of fishing mortality (F) because we assumed fishing mortality is the main factor driving the biomass of the herring stocks (Brunel & Dickey-Collas, 2010)br. The fishing mortality data (Supplementary Information, Table S5.1) are in most stocks covering the mature part of the population, thus we chose to do the analyses on the SSB. We modelled the bifurcation variable β as a function of sea surface temperature (SST) with a lag of one year. We calculated the yearly average of the Extended Reconstructed Sea Surface Temperature v4 (ERSST4) (Huang *et al.*, 2015) over the statistical management area for the stock from ICES (International Council of the Exploration of the Sea) and NAFO (Northwest Atlantic Fisheries Convention) (Supplementary Information, Table S5.1).

In addition, we modelled β as a function of cod SSB, also lagged by one year, instead of SST as bifurcation variable on the herring stocks. Here, we wanted to test for possible predation effects of cod on herring, which could, after the collapse of cod in many ecosystems, lead to changes in herring biomass.

A model validation was also conducted for the non-lagged variables of SST and cod SSB, however the lagged version gave better results. Models with or without a lag in the variables were compared with the AIC (Akaike information criterion) and the model with the lowest AIC was selected. The difference between the AIC of the models was ≥ 2 in favour for the model with lagged variable apart for North Sea autumn-spawning herring cusp model with temperature and Georges Bank herring cusp model with cod (Supplementary Information, Table S5.3). However, here, the differences between the AIC was < 2, thus we chose to use the lagged variable.

All calculation were conducted in the R version 3.4.3. (R Core Team, 2016).

Model validation of the stochastic CUSP model
Grasman *et al.,* (2009) suggest as model validation the visual assessment of the bimodality in the cusp area. Furthermore, the check that at least 10 % of the α–β-points should be in the bifurcation area. This number is somewhat arbitrary but we used it in addition to other validation criteria. We chose to validate by the log-likelihood of the cusp model, which should be substantially better than that of a linear model fitted to the data. Furthermore, we used the BIC of the cusp model and compared it with the BIC of a logistic model, where the smaller BIC was chosen as being the better model (Raftery, 1995). Finally, at least one of the respective fitted model parameters $w_1 \ldots w_n$, $a_1 \ldots a_k$ and/or $b_1 \ldots b_k$ should be significant on the 0.05-level (Grasman *et al.*, 2009). Those validation criteria combined indicated to the model selection or rejection of the model.
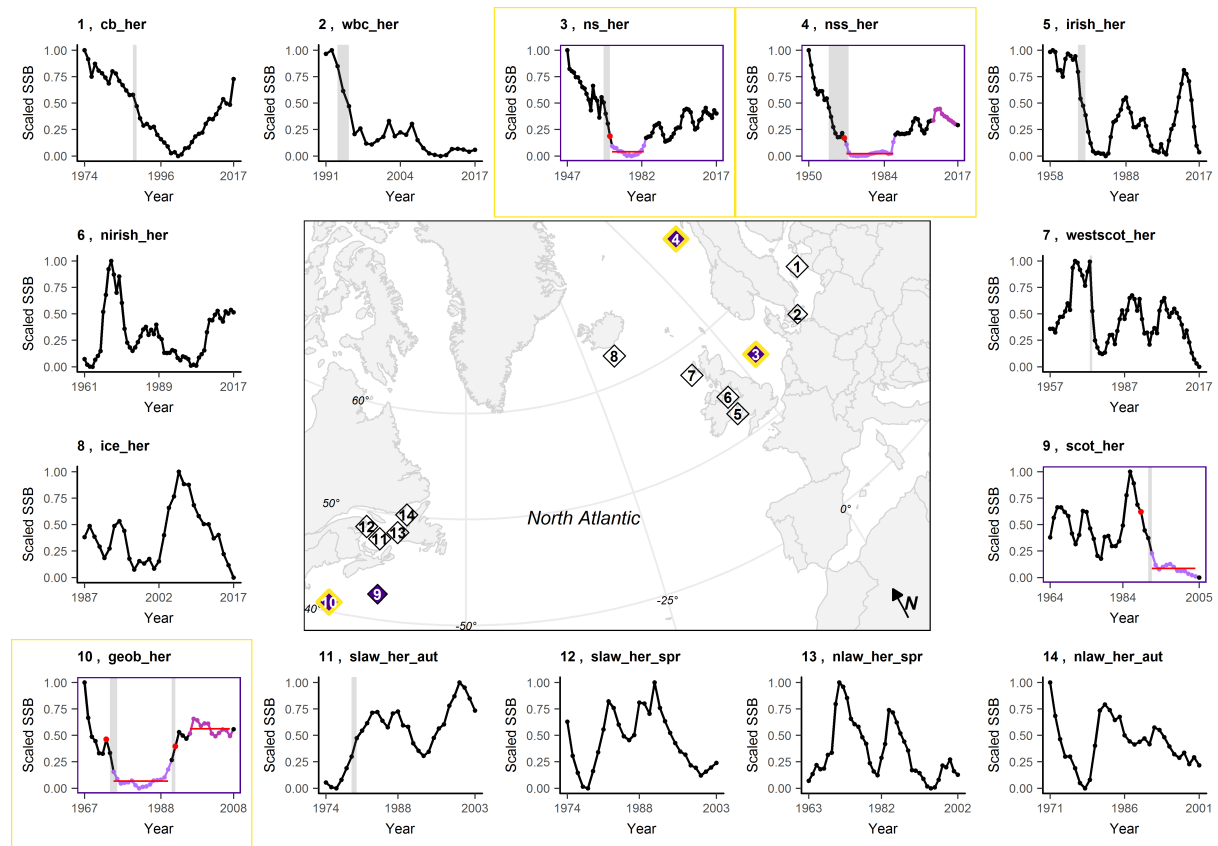
Results

Figure 5.1: Map of the North Atlantic showing the distribution of the analysed 14 herring populations indicating their "stock ID" corresponding to the respective plots surrounding the map. The plots surrounding the map show the scaled spawning stock biomass (SSB) of the analysed herring stocks (black dotted, solid line ●━). The purple highlighted parts in the SSB time-series (━●━) indicate periods of prolonged quasi-stability of four of the stocks (see Figure 5.2b). Norwegian spring-spawning and Georges Bank herring stock show two periods of quasi-stability (nss_her: 1967-1988 and 2006-2016; geob_her: 1975-1990 and 1996-2007) indicated by a darker purple colour (━●━). Abrupt shifts by a change in biomass of ≥ 70 % are indicated by a red dot ● and compared to the mean of the prolonged stability period (red line ━━) (see Figure 5.2.1b). The grey shaded areas (▮) in the plots indicate that at least two of the three statistical tools found a change point. **For a detailed view see Figure 5.3 for** North Sea autumn-spawning, Norwegian spring-spawning, Scotian Shelf, and Georges Bank herring and **Supplementary Information, Figure S5.1.** The yellow box around North Sea autumn-spawning herring, Norwegian spring-spawning herring, and Georges Bank herring indicates the valid cusp model (Table 5.1) and the purple box around the stocks indicates a valid change point analysis (Table 5.2, Figure 5.2) (also visible in the purple coloured and yellow lined diamonds in the map).
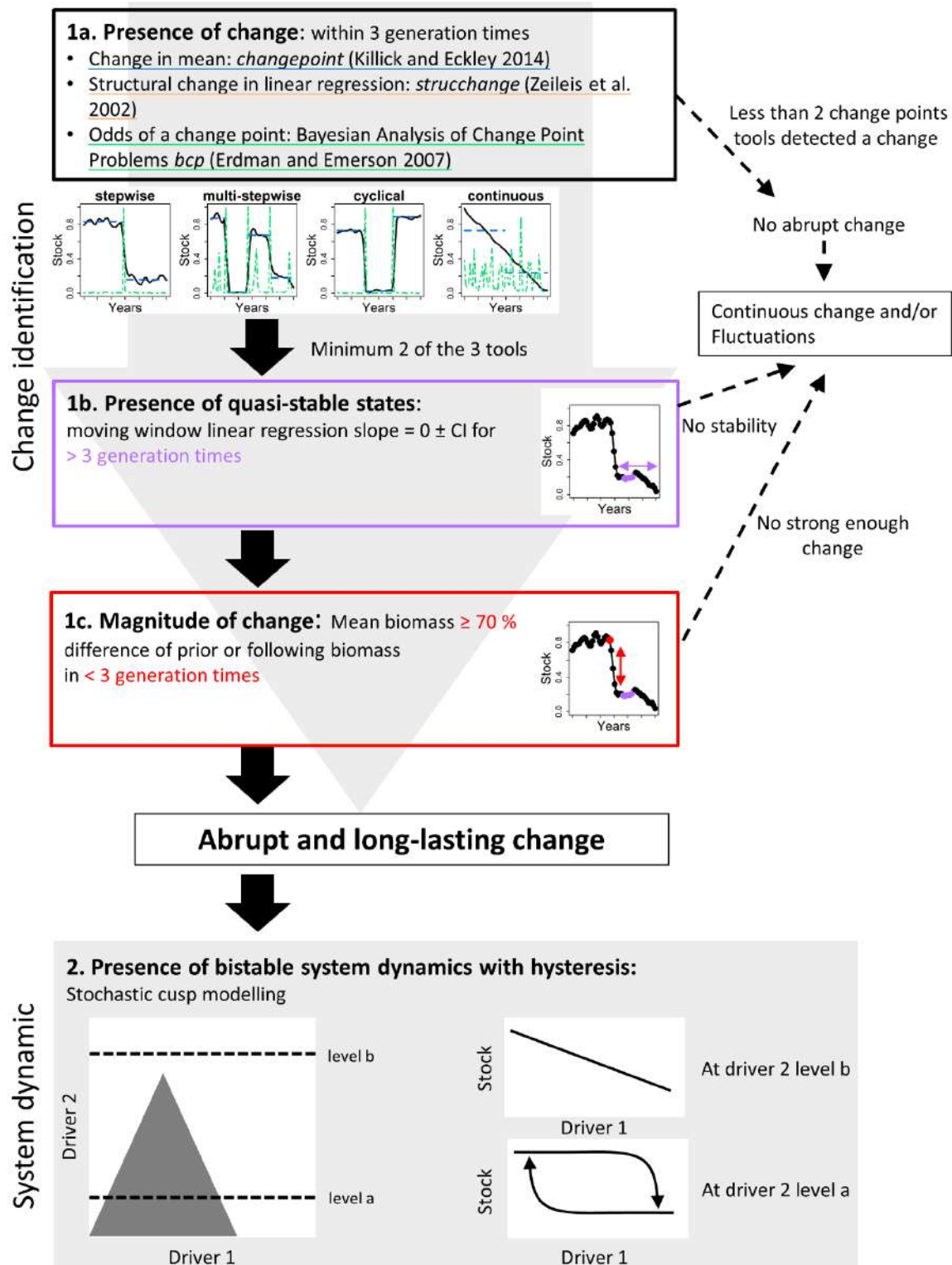
Figure 5.2: The two-step approach how we detected abrupt and long-lasting changes and bistable system dynamics: First was the identification of abrupt and long lasting changes: 1a) The first criteria is the presence of a change in the stock's time series tested with the change point analyses tools. If at least two of the tools indicated a change point within 10 years, 1b) the stocks were further tested for prolonged quasi-stability in the time series for > 3 generations. If this exists 1c) a sudden drop/increase of the biomass by ≥70% compared to the biomass before or after within 3 generations was searched (cf. IUCN, 2012). 1d) If those criteria do not fit the time series we have a continuous change without an abrupt and long-lasting change or fluctuations. The second step includes, when all criteria of 1) are satisfied, the analysis with the stochastic CUSP model, where we detect thresholds and discontinuous behaviour of the stock, depending on the level of the driver variables. The dark triangle shows the bifurcation area, defined by the values of driver 2. Driver 2 (in our case temperature or cod biomass) modulates the response of the system to driver 1 (fishing pressure), either displaying discontinuous dynamics and hysteresis in the area at level a from driver 2, or a linear response at values of driver 2 at level b.

Step 1: Change point analysis

All 14 herring stocks studied showed large interannual biomass fluctuations (Figure 5.1). However, going through the change point analysis displayed in three levels in Figure 5.2.1, reduced the number of stocks to North Sea autumn-spawning, Norwegian spring-spawning, Scotian Shelf, and Georges Bank herring for the further analysis for discontinuous behaviour (Figure 5.2.2).

First level: change point tools:
Only North Sea autumn-spawning, Norwegian spring-spawning, and Georges Bank herring showed clear shifts indicated by all three change point tools. That is, we detected changes in the mean of the biomass ("*changepoint*"), a high probability of a change having occurred ("*bcp*"), and structural changes in a linear regression ("*strucchange*") within a range of 10 years from each other (Figure 5.3). In North Sea autumn-spawning and Norwegian spring-spawning herring, a change occurred within the period of 1964 – 1967 and 1959 – 1968, respectively (Figure 5.3). Georges Bank herring displayed two periods of change: in 1974 – 1976 as well as 1991 – 1992. The "*changepoint*" and "*bcp*" packages identified the second period within one year (1991) (Figure 5.3). Scotian Shelf herring did not show a significant change according to "*strucchange*", but the two other tools found a change point both in the year 1990 (Figure 5.3). In Central Baltic, Western Baltic spring-spawning, Irish Sea, West of Scotland, and Southern St. Lawrence autumn-spawning herring stocks also two change points were identified (Supplementary Information, Figure S5.1). Central Baltic herring showed a change point with the "*strucchange*" package as well, however this change point was not within 10 years of the other two breakpoints identified (Supplementary Information, Figure S5.1). In the remaining stocks, only "*bcp*" detected changes (Supplementary Information, Figure S5.1), thus these stocks did not show abrupt and long-lasting changes, but continuous change and/or fluctuations (Figure 5.2.1).

Second level: Prolonged quasi-stabiliy
The second level of the detection of abrupt and significant changes identified prolonged periods of quasi-stability only in North Sea autumn-spawning, Norwegian spring-spawning, Scotian Shelf, and Georges Bank herring (Figure 5.1 & 5.3). Norwegian spring-spawning herring and Georges Bank herring displayed an additional period of quasi-stability at the end of the time series with a higher biomass state than the previous period (Figure 5.1).

Third level: Abrupt shift in biomass
The third level of the change point analysis (Figure 5.2.1c) detected in all stocks with prolonged quasi-stability periods also abrupt biomass shifts by ≥ 70 % (Figure 5.1). The abrupt shift of North Sea autumn-spawning, Norwegian spring-spawning, Scotian Shelf, and Georges Bank herring resulted in a quasi-stable depleted state. Abrupt changes to the mean biomass of the quasi-stable state happened for the North Sea autumn-spawning and Norwegian spring spawning herring within one year (from 1967 to quasi-stability period in 1968 – 1983, and from 1966 to quasi-stability period 1968 – to 1988, respectively). For the Georges Bank and Scotian Shelf herring the abrupt shift happened within two years (from 1993 to quasi-stability period in

1975 -1990) and three years (from 1989 to quasi-stability period in 1992 – 2004), respectively (Figure 5.1). In the Georges Bank herring stock, the second quasi-stable period with higher biomass shortly after the depletion period was also proceeded by another jump in biomass by > 70 % in 1992 (Fig 5.1).
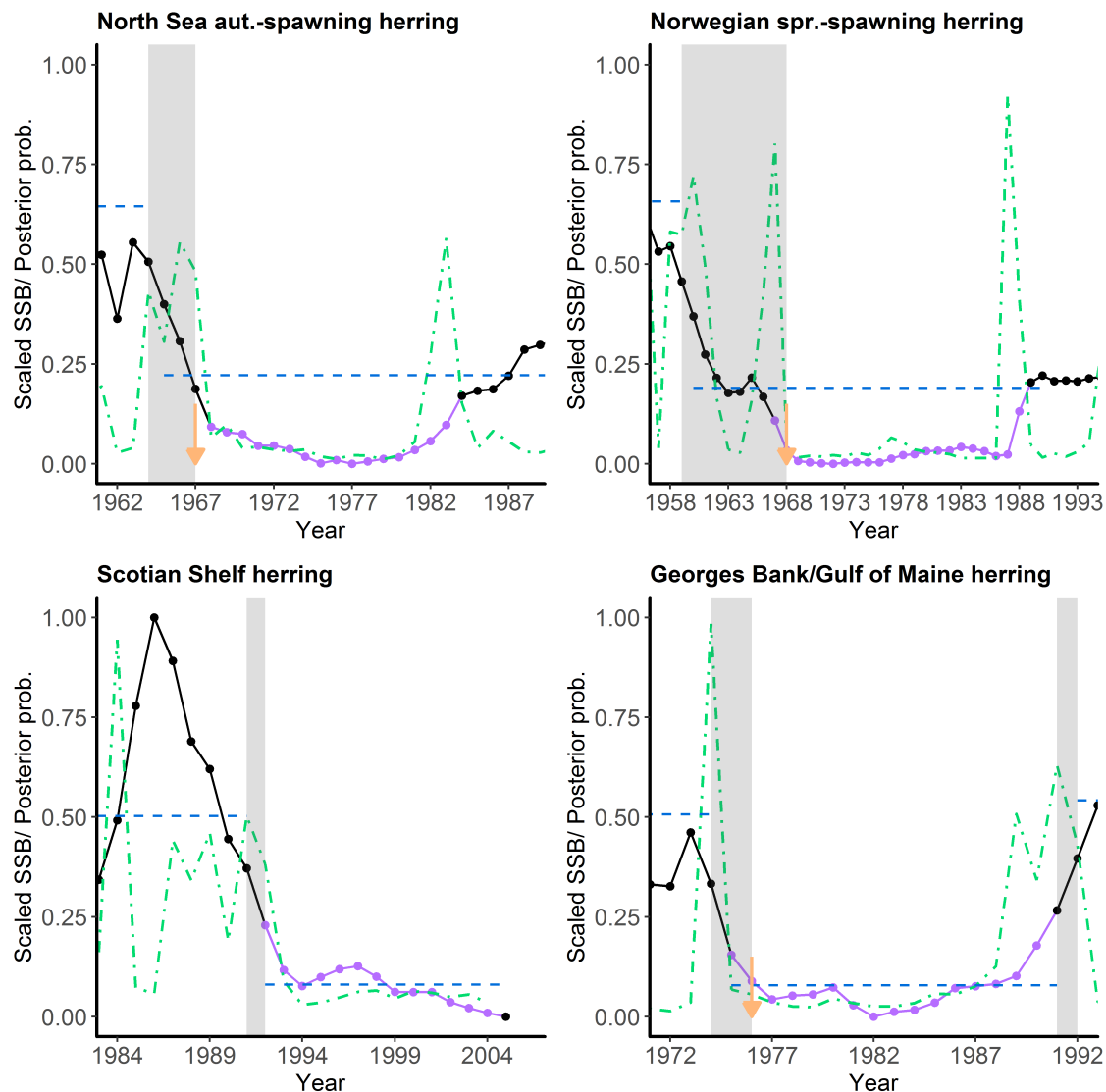

Figure 5.3: The detailed view of the shift identification of North Sea autumn-spawning, Norwegian spring-spawning, Scotian Shelf and Georges bank herring. Here the "changepoint" (dark blue, long dashed line ▬ ·) and the "strucchange" (orange arrow) analyses as well as the posterior probability of the "bcp" analysis (light green, dash-dotted line · · ▬) are indicated. The significant period of change is highlighted in dark grey (▯). Here only the stocks which showed a prolonged period of stability (purple highlighted parts in the SSB time-series (●▬●)) and abrupt shift (Figure 5.1) are displayed. These four stocks qualified for the continued analysis with the cusp model (see Figure 5.2. The change point analyses of the other stocks is displayed in Supplementary Information Figure S5.1.

Step 2 Investigating of system dynamics

Due to the selection for an abrupt and long-lasting change, we tested for discontinuous behaviour in the SSB of North Sea autumn-spawning, Norwegian spring-spawning, Scotian

Shelf, and Georges Bank herring in response to fishing pressure, modulated by temperature or cod biomass.

All the selected stocks apart for the Scotian Shelf herring, and the Norwegian spring-spawning herring in the cusp model with Coastal cod as predator, displayed bimodality in their cusp-area, and had > 10 % of their points in the bifurcation area (Table 5.2). The cusp model was selected over a linear or logistic model because the cusp log-likelihood was larger than the one of the linear model and the BIC of the cusp was always much lower than the BIC of a logistic model. These criteria indicated a better performance of the cusp model for both tested variable combinations, i.e. fishing pressure with lagged temperature or lagged cod abundance (Table 5.2, Figure 5.4 & 5.5). Fishing pressure was in all the cusp models significant. Lagged SST was significant for North Sea autumn-spawning and Norwegian spring-spawning herring, and cod SSB with the Northeast Arctic (NEA) cod stock was only significant for Norwegian spring-spawning herring (Table 5.2). The cusp model results indicated a hysteresis effect of fishing pressure modulated by temperature or predation pressure.

Table 5.2: Validation of the stochastic CUSP model for the four valid stocks from the change point analysis: North Sea autumn-spawning herring (ns_her), Norwegian spring-spawning herring (nss_her), Scotian Shelf herring (scot_her), and Georges Bank herring (geob_her) with either fishing mortality as α-variable and lagged SST as β-variable (denoted as ^{FT} next to the stock's name) or fishing mortality as α-variable and the respective lagged cod SSB as β-variable (denoted as ^{FC}, the * indicating the coastal cod in the Norwegian spring-spawning case). To be chosen over a linear model, the cusp log-likelihood (cusplogLik) had to be higher than the one of the linear model (linlogLik). Furthermore, the coefficient values of $w1$, α and/or β had to be significant at the 0.05 level. The percentage of points in the bifurcation area should be ≥ 10 %. We compared the lagged-variable output with non-lagged models with the AIC (Appendix Table A3 for non-lagged model output). Scotian Shelf herring did not show a valid cusp, since no points were in the bifurcation area.

Stock	cusplogLik	linlogLik	p-value $w1$	p-value α	p-value β	points in bifurcation area [%]	cuspBIC	logisticBIC	Summary model selection	Bimodality in cusp	AIC
ns_her^{FT}	-69.43	-566.08	<0.001	<0.001	0.009	18.84	164.26	1134.36	✓	✓	150.9
nss_her^{FT}	-56.24	-617.54	<0.001	0.01	<0.001	47.76	125.9	1238.56	✓	✓	124.5
scot_her^{FT}	-22.94	-244.5	<0.001	<0.001	0.54	0	68.02	470.13	-	-	57.9
geob_her^{FT}	-27.98	-255.36	<0.001	<0.001	0.3	97.56	78.25	511.45	✓	✓	68
ns_her^{FC}	-55.5	-409.06	<0.001	0.03	0.09	66.04	134.9	832.6	✓	✓	123.1
nss_her^{FC}	-66.8	-621.6	<0.001	0.03	<0.001	31.81	158.8	1246.9	✓	✓	145.6
nss_her^{FC*}	-26.4	-269.14	<0.001	0.054	<0.001	0	73.6	322.1	-	-	64.8
scot_her^{FC}	-10.17	-199.14	<0.001	<0.001	<0.001	8.8	41.49	412.39	-	-	32.3
geob_her^{FC}	1.44	-173.16	<0.001	0.0014	0.41	30	17.51	321.09	✓	✓	9.1

Cusp model with fishing and temperature as driver
North Sea autumn-spawning herring moved from the beginning of the time series in 1951 into the bifurcation area, when temperatures decreased and displayed a discontinuous shift to fishing pressure, which was low (< 0.3). Due to a continuous increase in fishing mortality, which peaked in 1971 with a fishing mortality of 1.3, the stock moved into a quasi-stable state with low biomass (Figure 5.4) and stayed in this state for several years (from 1968 – 1978). Following the depletion years with high fishing pressure, the reduction of the fishing mortality

in the late 1970s and co-occurrence with low temperatures pushed the stock again in the area of instability. Due to a pronounced hysteresis effect at lower temperatures, the increasing temperatures since 1997 in the recovering period linearized the relationship between fishing and SSB and the system was in a quasi-stable state, reaching back to higher biomass (Figure 5.4).

Norwegian spring-spawning herring displayed a similar picture of hysteresis and discontinuity: With decreasing temperatures and at low fishing pressure, the stock moved into the bifurcation area, still with high biomass, but low resilience, meaning its behaviour was unpredictable. The high increase in fishing pressure during the late 1960s and late 1980s however, forced the stock to move outside the bifurcation area and into a low, but quasi-stable state. The continuous low temperatures in the late 1980s, coupled with a decrease in fishing pressure, pushed the system back into an unstable state, followed by an increase in temperature (still at low fishing pressure), which linearized the relationship of fishing mortality and SSB.

Georges Bank herring was not strongly affected by temperature, since it was not significant in the model (Table 5.2), nevertheless the effect of fishing pressure on the SSB was still modulated by temperature. The stock was in the bifurcation area, starting from the beginning of the time series in 1968, over the course of the depletion years starting in 1975 until the recovery (biomass attracted to the higher biomass state) of the biomass starting in 1991. A further increase in temperatures could change the relationship of SSB and fishing (linearize it); however, this lies outside the range of the analysed data (Figure 5.4).

Cusp model with fishing and cod biomass as driver
In the late 1950s as well as the mid 1960s, the low cod biomass < 300 000 t pushed the Norwegian spring-spawning herring in the unstable area (Figure 5.5), indicating the discontinuous shift. Then, the high fishing pressure in the 1970s forced the stock out of the unstable area into a low, but quasi-stable state. However, the low cod biomass in the mid 1970s until late 1980s, which was in most years < 300 000 t, again destabilized the herring stock. A hysteresis effect of fishing pressure on SSB was displayed, when the cod stock strongly increased its biomass after 2001, and the relationship of fishing mortality and herring biomass was linearized (Figure 5.5).

For the North Sea autumn-spawning and the Georges Bank herring stock, cod SSB is not significant and thus had not a strong effect on the herring biomass. However, cod biomass was still modulating the effect of fishing on herring SSB, which led to the display of hysteresis (Figure 5.5). North Sea autumn-spawning herring showed hysteresis at high cod SSB, whereas for the Georges Bank herring, the hysteresis effect of fishing was more pronounced at low cod biomass and the stock managed to jump to higher biomass levels (Figure 5.5). The high cod SSB at the beginning of the time series in 1979, stabilized the relationship of fishing pressure on the herring SSB, leading to a low, quasi-stable state.
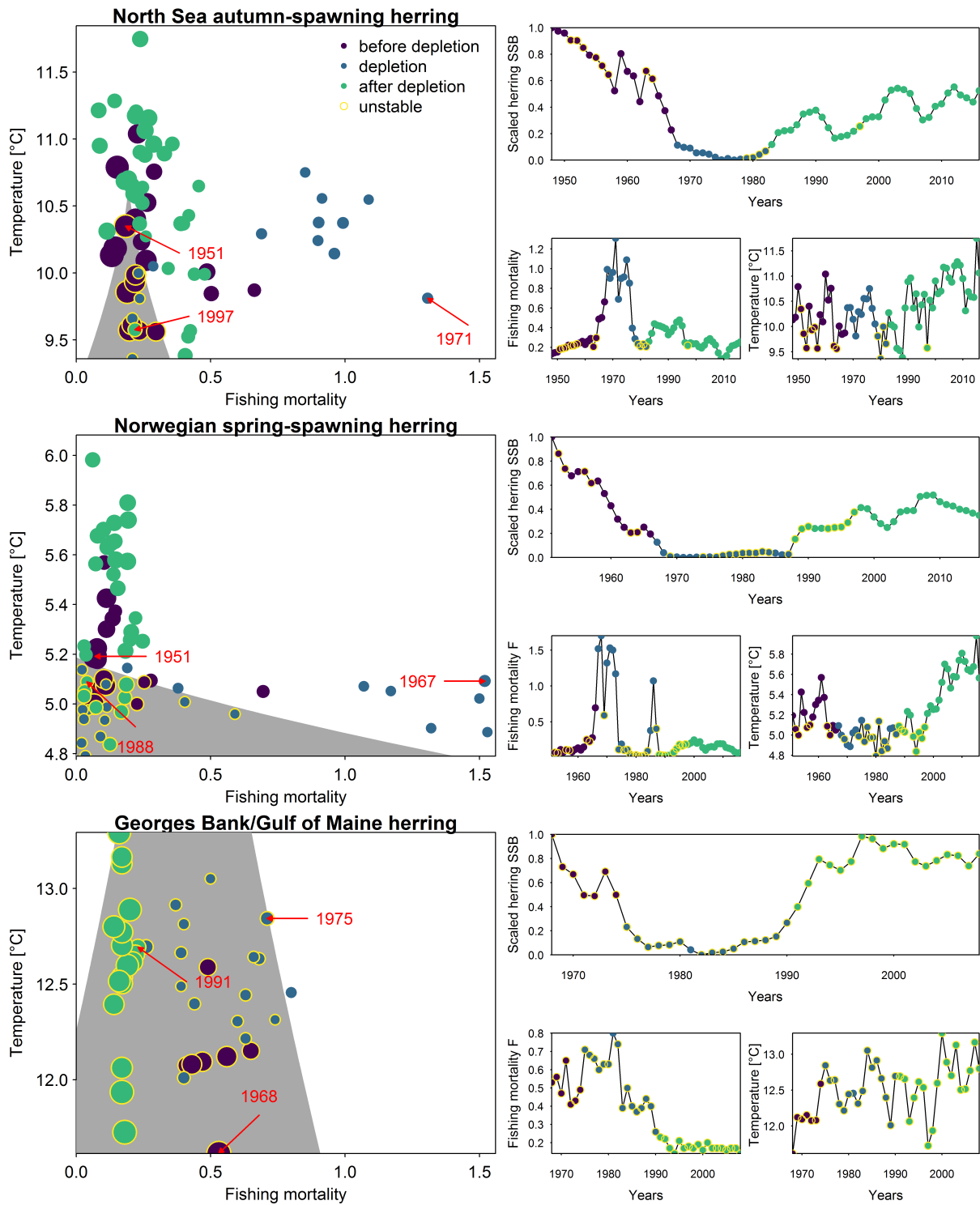
Figure 5.15: The cusp model for the valid North Sea autumn-spawning herring, Norwegian spring-spawning herring, and Georges Bank herring complex (according to Table 5.2) with fishing mortality and 1-year-lagged temperature as pressure variables. The grey area in the plots in the left column shows the bifurcation area ( ), thus the unstable area, points in this area are marked with a yellow lining. The colours indicate the different periods of the stock, purple before the depletion, blue for the period of depletion and green for the period following depletion (recovery). Some years, which display changes in the variables are indicated with an arrow in red, further information is found in the text. The dots are the scaled biomass, the larger one dot, the larger the biomass and thus a high state of the stock. On the right side, the scaled SSB is visualized with the same colour scale as in the bifurcation plot, as well as the fishing mortality and temperature.
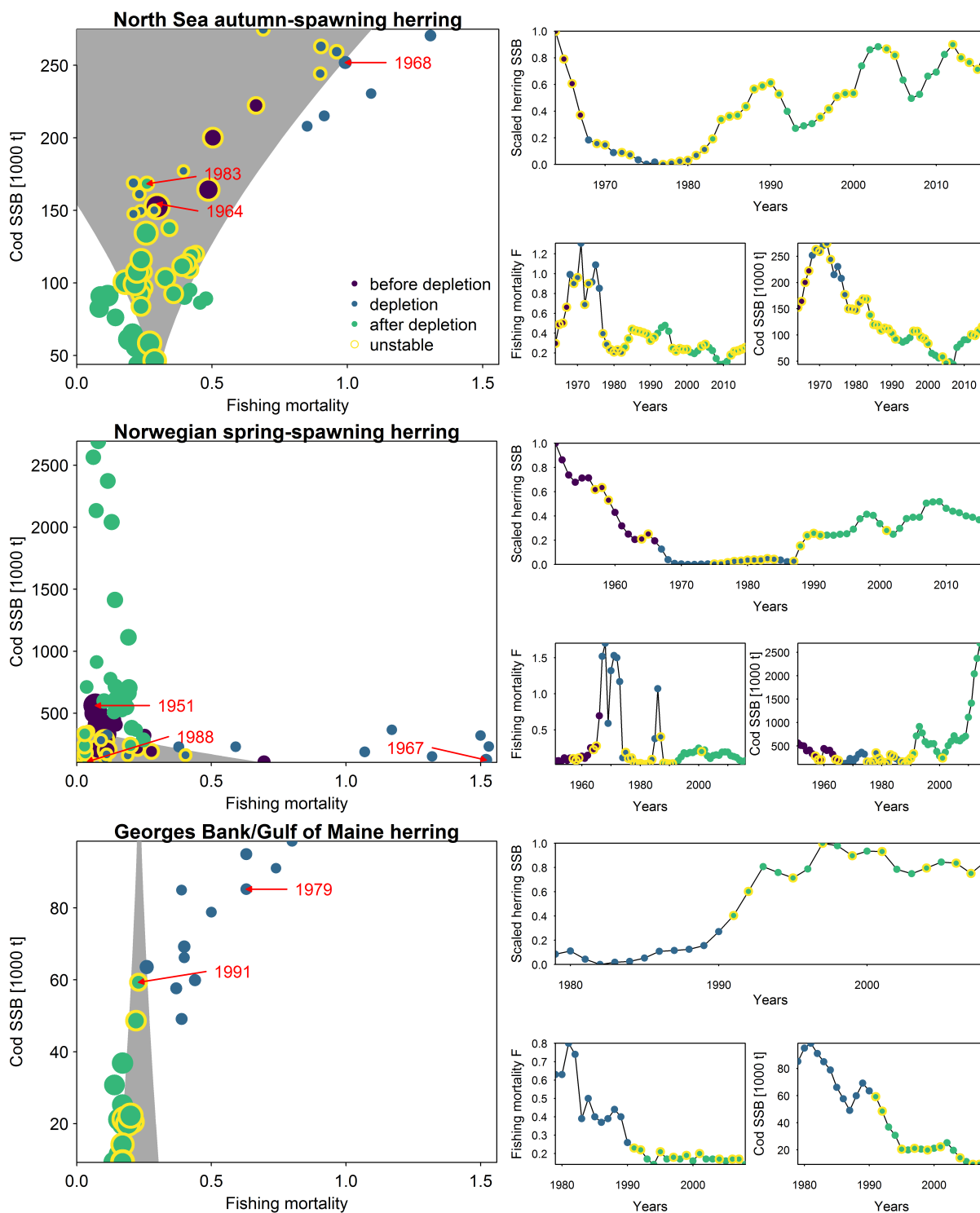
Figure 16: The cusp model for the valid North Sea autumn-spawning herring, the Norwegian spring-spawning herring and the Georges Bank herring complex (according to Table 5.2) with fishing mortality and 1-year-lagged cod

SSB as pressure variables. The grey area in the plots in the left column shows the bifurcation area ( ), thus the unstable area, points in this area are marked with a yellow lining. The colours indicate the different periods of the stock, purple before the depletion, blue for the period of depletion and green for the period following depletion (recovery). The respective first year of a period is indicated with an arrow. The dots are the scaled biomass, the larger one dot, the larger the biomass and thus a high state of the stock. On the right side, the scaled SSB is visualized with the same colour scale as in the bifurcation plot, as well as the fishing pressure and cod SSB. The Georges Bank cod stock data started in 1979, thus the period before the depletion of the herring stock is excluded from the analysis

Discussion

Catastrophic shift in the herring stocks

Of the 14 herring stocks, all with large biomass fluctuations only North Sea autumn-spawning, Norwegian spring-spawning, and Georges Bank herring stock satisfied our criteria of the change point analysis for an abrupt and long-lasting shift and the validity of the cusp model (Figure 5.1).

All the herring stocks, apart for the Northern Gulf of St. Lawrence autumn-spawning, were at least in some periods fished with relatively high fishing pressure (Appendix Figure A3) and the temperature increased in the analysed period (Boyd *et al.*, 2014), which could have had the potential of catastrophic shifts (Dickey-Collas *et al.*, 2010; Essington *et al.*, 2015). The herring stocks seem, since most of the stocks fluctuated strongly and bounced quickly back after disturbances (Figure 5.1), resilient to these changes and can recover after strong impacts fairly fast (Hutchings, 2000). The Georges Bank herring stock even returned to a higher biomass state when fishing mortality was decreased.

Still, fishing in combination with environmental drivers or species interactions can cause a discontinuous response of the stock biomass to fishing as was shown in the cusp analysis of North Sea autumn-spawning and Norwegian spring-spawning herring and Georges Bank herring stock. In both North Sea autumn-spawning herring and Norwegian spring-spawning herring, lower temperatures destabilized the stock. The low temperatures during the depletion period kept the Norwegian spring-spawning herring in an unstable state (Figure 5.4). Warmer temperatures positively affect Norwegian spring-spawning herring SSB and productivity (Toresen & Østvedt, 2008; Ottersen *et al.*, 2013). Higher temperatures could have contributed to a faster recovery of the herring stock, when fishing pressure was low (Figure 5.4), since the stock was during the depletion period mainly in an unstable state. In the cusp model an increase in temperature stabilized the SSB in the North Sea autumn-spawning herring, however, the recruitment success is depending on rather colder temperatures (Ottersen *et al.*, 2013) . Thus, a further increase in temperature due to climate change could be a limiting factor in the full recovery of the stock and quite deleterious, since warm waters will lead to high growth, but shorter lifespan and low weight (Brunel & Dickey-Collas, 2010).

The North Sea and Georges Bank herring and cod stocks experienced both strong depletions, however the herring stocks a few decades earlier than the cod stock, when herring gained higher biomass again. North Sea and Georges Bank cod had their highest level of SSB in 1971, and 1980 respectively (Figure 5.5), in years, when the respective herring stock was depleted. Both cod stocks declined since their maximum, which may have allowed the herring stocks to increase their biomass again. The successive strong decline in both species are in concordance to the ecosystem changes described by Möllmann and Diekeman (2009), where the overfishing of large predators lead to increases in the small-pelagic fishes. Even though the effect of cod on herring in our model is not significant, it is still visible that high North Sea and Georges Bank herring biomass did not co-occur with high cod biomass (Figure 5.5). In the case of the Norwegian spring-spawning herring and NEA cod it seemed the stocks were more driven by the same external conditions, most likely temperature, which leads in colder years to lower

herring and cod abundances (Rouyer *et al.*, 2011). Here, predation of cod might be low, since the adult stocks overlap only during the spawning migration of the NEA cod to its spawning grounds along the Norwegian Coast. However, in general, other predators, next to fishing, might be more important and influence the herring biomass more strongly than cod biomass (Overholtz & Link, 2006).

The faster recovery of the herring stocks after high fishing pressure and stock depletion, compared to many other overfished stocks such as Gadidae (Hutchings, 2000) could be due to the difference in fishing impacts on the adult stock and the number of fish remaining, once the stocks are depleted. Herring has the characteristic to form shoals, contract their habitat, and with that is still able to effectively reproduce (Beverton, 1990). Both the North Sea autumn-spawning herring as well as the Norwegian spring-spawning herring experienced strong recruitment overfishing and with that, decreases in the population's age structure (Dickey-Collas *et al.*, 2010; Rouyer *et al.*, 2011). This can erode the resilience of the stock and contribute to their collapse (Anderson *et al.*, 2008; Rouyer *et al.*, 2011). The strong fishing pressure over several years had the potential to lead to long-lasting population changes (Dickey-Collas *et al.*, 2010). Yet, for both North Sea autumn-spawning and Norwegian spring-spawning herring stocks, the genetic diversity was not severely affected and it seems no fisheries induced evolution to earlier maturation, but rather a plastic response to increased pressure, was triggered (Engelhard & Heino, 2004). Reducing the fishing pressure allowed the stocks to regain their former population structure with the contribution of a few good years of recruitment, supporting the rebuilding of the stock as seen from the Norwegian spring-spawning herring (Toresen & Østvedt, 2008).

Methodological considerations

The chosen criteria of a stock undergoing a catastrophic shift were quite conservative, since only four stocks satisfied the criteria of an abrupt and long-lasting change (Figures 2.1 & 3). However, after our test of the sensitivity of our chosen criteria, we are confident to have identified the main patterns in the herring stocks with our criteria, since North Sea autumn-spawning, Norwegian spring-spawning, Scotian Shelf, and Georges Bank herring, showed the same results in a vast majority of the sensitivity analyses (Supplementary Information, Table S2).

We set the generation length for the herring stocks at 3.5 years, which is rather short for especially the Norwegian spring-spawning herring (ca. 6.5 years) (Ottersen *et al.*, 2013). In our analysis, the stock's SSB declined within one year (Figure 5.1) and the duration of the prolonged stability is 22 years long, thus the stock, even with a longer generation time, would still fit into our definition of the prolonged period of quasi-stability (3-times the generation time). With this, it is visible how drastic this decline was for the Norwegian spring-spawning herring (Toresen & Østvedt, 2008). We acknowledge that the analysis might look different with the usage of different change point detection tools and approaches, which are available in great amounts (for some examples on further change point detection tools see e.g.(Andersen *et al.*, 2009; Bestelmeyer *et al.*, 2011; Möllmann & Diekmann, 2012)), which might detect regime shifts (with its various definitions) in more herring stocks. However, we are confident that our

combination of methods and analyses steps, found long-lasting, significant and catastrophic shifts, but also detected different behaviours of SSB changes such as fluctuations (e.g. Northern Irish herring stock) and gradual decline (e.g. Central Baltic herring stock, followed by a gradual increase).

In the cusp model, it is important to identify and understand the underlying mechanisms driving the system (Roopnarine, 2008), however one can assume the drivers, which might lead to discontinuous, catastrophic behaviour, if the system shows e.g. catastrophic transitions, stable states and hysteresis (Roopnarine, 2008; Grasman et al., 2009). We tested our herring stocks for abrupt and long-lasting changes with periods of prolonged quasi-stability, indicating catastrophic behaviour, thus excluding stocks, which might show a false positive in the cusp validity. We deliberately chose as modelling variables those drivers that are known to have a key effect on herring (Beverton, 1990; Link et al., 2009; Brunel & Dickey-Collas, 2010) in order to explore the discontinuous behaviour of the stocks. However, in the case of the Scotian Shelf herring (Figure 5.1), it is likely that we missed the key variables to which the stock does respond in a discontinuous manner. Nevertheless, since we wanted to have an overall comparison between the stocks, we did not explore this any further in this study. For some of the stocks, the available time series was too short, in order to potentially find drastic changes, for example the Icelandic herring, where a collapse was reported in 1957 (Beverton, 1990) and which seems to have a strong decline in recent years again (Figure 5.1). In addition, the Western Baltic spring-spawning herring stock is still on a declining path, so it would be interesting to follow the development of these stocks.

Conclusion

In conclusion, from our study and as seen from other studies on small pelagic fish, herring stocks are susceptible to disturbances and might fluctuate strongly, but are able to recover fast and thus might show a high resilience (Folke, 2016). Herring stocks seem to be able to reverse population effects of strong fishing pressure. This might indicate that herring, in contrast to other relatively long-lived fish species such as cod (Anderson et al., 2008; Rouyer et al., 2011), might be more sustainable to harvest, since it seems with reasonable precautionary fishing pressure, the integrity of the herring stocks can be preserved. The cusp model gives an opportunity to develop a safe operating space for the fisheries (Carpenter et al., 2017). We show here that the previous experience of the stock, the limits of the bifurcation area (see Figure 5.4 & 5.5) can indicate where to set management efforts to decrease the fishing mortality to a safe level and with that avoid the occurrence of hysteresis. Here, climate change and species interactions, like here illustrated through the interaction with cod were modulating the hysteresis effect of fishing on stock biomass. Due to the uncertainty in productivity regimes, which might not necessarily depend on the abundance of the stock (Vert-pre et al., 2013), it is important to fish small pelagics in regard to their importance in the ecosystem with an precautionary approach and have suitable reference points for their management.

Supplementary Information Chapter 5

Supplementary Information Text

<u>Data</u>

The spawning stock biomass and the fishing mortality used for the 14 herring stocks and 13 cod stocks were collected from various sources, mainly stock assessments. For Norwegian spring-spawning and Northern Irish herring stocks, as well as for Kattegat, Western Baltic, and Norwegian coastal cod two assessments were used in order to prolong the time series (Table S1). One high fishing mortality value in the year 1968 (> 3 (ICES 2006)) for the Norwegian spring-spawning herring seemed unrealistically high in relation to the noted fishing mortalities from Toresen and Ostevedt (2008). This high value was replaced with the value given in Toresen and Ostevedt (2008) for the year 1968 after comparisons with their other fishing mortalities for the period covered (mean difference of 0.02). The fishing mortality they found for 1968 (1.7) is still the highest, as well as the one noted in the stock assessment of ICES. The range of fishing mortality and temperature experienced by the stocks is illustrated in Figure S5.2.

<u>Reasoning for generation lengths for herring</u>

The Atlantic herring mature 2-6 years, however the majority at 3-4 years (Trenkel *et al.*, 2014). Thus, we use the mean 3.5 years as our generation lengths. Thus, one generation lengths is longer than the first breeding individual (IUCN 2012) and shorter than the oldest breeding individual (maximum ages up to 20, but mostly 12-14 years (Trenkel *et al.*, 2014) so it can count as one generation (IUCN 2012). With this, the change in the stock has to happen within 3-generations, thus ≤ 10.5 years and the prolonged duration of the stability should be > 10.5 years. The assumption of this generation length can be short for some of the stocks, however there were no stocks, where this lead to changes in the result (see discussion main text). The analysis takes its cues from the IUCN criteria of an endangered species, where an abrupt change of 70 % has to happen within three generations or ten-years, whichever is longest, thus even if herring stocks might show shorter generation times than 3.5 years, the 10 year threshold would still be valid.

<u>Sensitivity to moving window size and acceptance level of being stable</u>

The stocks, which showed significant change points within 10 years (Figure S5.1, Figure 5.3 main text), were further investigated for prolonged quasi-stability. We chose to do our analysis with the use of a 5 year-window size for calculating the slope of a linear regression and used an acceptance level of 20 % of being stable (calculated from the absolute maximum slope of the respective time series). However, since this choice might have influenced our results, we tested also a 4-year moving window, an 8-year moving window with acceptance levels of 10 %, 20 % and 30 % respectively. The 10 % acceptance level was quite a restrictive choice and only North Sea autumn-spawning, Norwegian spring-spawning herring and Scotian Shelf

herring showed periods of prolonged quasi-stability. The 30 % acceptance level included many random fluctuations in the stock, however often the periods were not long enough (results not shown). For the 5-year moving window, at least seven consecutive slopes of the linear regressions had to fall within our confidence band of being stable, in order to achieve > 10 years. Accordingly, for the 4-year moving window it had to be at least eight consecutive years and for the 8-year window at least four years. We find especially with the 8-year moving window some additional stable periods. However, then in the next step, finding an abrupt shift in the biomass within 10 years (Figure 2.1c, main text), only gives two additional stocks: Irish Sea and South St. Lawrence autumn-spawning herring (Table S5.2, Figure S5.2). However, both stocks did not fit into the cusp criteria, thus they do not show bistability (results not shown). Otherwise, the results obtained with a 20 % acceptance level and a 5-year moving linear regression did not differ from the results obtained with other threshold or window sizes (Table S5.2).

Supplementary Information Table

Table S5.2 Overview over the herring stocks and their corresponding cod stocks, which are used in the cusp-model analysis and the available years of data we had for the SSB, fishing mortality was often shorter and then in the cusp analysis, data was cut at that year. The overlapping years of the herring and cod stocks were used. Temperature data was available for all used years. The source indicates from which report, or contact person, the data was collected. SAM – State-space assessment model, TSA – Analytical age-based assessment (time series analysis), XSA – Extended survivor analysis, SPA – Sequential population analysis, SCA – Statistical catch at age, VPA – Virtual population analysis

[1] Stocks that in the last year failed the assessment

[2] Stocks where, in order to have longer time series, we mixed old assessments and new ones, after checking for same trends and stock dimensions

Region	Stock	Short name	NAFO/ICES management area	Available years	Source
Western Baltic	Kattegat cod[1,2]		IIIa, 21	1971-2015	ICES/WGBAFS, SAM stock assessment model, Johan Lövengren
	Western Baltic cod[2]		22-24	1970-2016	ICES/WGBAFS, SAM stock assessment model, Margit Eeron
	Western Baltic spring-spawning herring	wbc_her	22-24	1991-2017	ICES Stock Assessment Database. Copenhagen, Denmark. ICES. [accessed 25.10.2017]. http://standardgraphs.ices.dk
Eastern Baltic	Eastern Baltic cod[1]		25-32	1966-2016	
	Central Baltic herring	cb_her	25-29,32 (without Gulf of Riga, 28-1)	1974-2017	WGBFAS Report 2017, Table 4.2.15, 4.2.20,
North Sea	North Sea cod		IV, IIIa(N), VIId	1963-2016	ICES/WGNSSK, TSA stock assessment model, Alexander Kempf
	North Sea autumn spawning herring	ns_her	IV, IIIa, VIId	1947-2017	HAWG Report 2017, Table 3.6.3.12, 3.7.12
Irish Sea	Irish Sea cod		VIIa	1968-2017	ICES/WGCSE, SAM stock assessment, Colm Lordan
	North Irish Sea herring	nirish_her	VIIa(N)	1961-2017	HAWG Report 2017, Table 7.6.3.12, ICES stock assessment 2014, accessed 17.2.15
Celtic Sea	South Irish Sea herring	irish_her	VIIa(S), VIIghjk	1958-2017	HAWG Report 2017 (ICES 2017a), Table 6.6.2.4
Celtic Sea and West of Scotland	West of Scotland cod		VIa	1981-2017	ICES/WGSCE, TSA stock assessment, Rui Catarino
	Celtic Sea and West of Scotland herring	westscot_her	VIa(combined), VIIbc	1957-2017	HAWG Report 2017 (ICES 2017a), Table 4.6.12
Barents Sea/Norwegian Sea	Northeast Arctic cod		I, II	1946-2016	ICES/AFWG, XSA stock assessment, Gjert Endre Dingsør
	Coastal cod[2]		I, II	1984-2016	ICES/AFWG, Survey SSB and F from VPA, Gjert Endre Dingsør

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	Norwegian spring spawning herring[2]	nss_her	I, II, V	1950-2016	WGWIDE Report 2017 (ICES 2017c) Table 4.5.1.4, ICES Stock Assessment Database 2014. Copenhagen, Denmark.
Iceland	Iceland cod		Va	1955-2016	ICES/NWWG, Forward based statistical catch at age model, Einar Hjörleifsson
	Iceland summer spawning herring	ice_her	Va	1987-2017	NWWG Report 2017 (ICES 2017b), Table 11.3.2.5
South of Gulf of St. Lawrence	South of St. Lawrence cod		4TVn	1971-2016	DFO, SCA assessment model, Doug Swain
	South of St. Lawrence spring spawning herring	slaw_her_spr	4T	1974-2007	RAM legacy database, Version 3.0, accessed 10.01.2018 (Ricard et al. 2012)
	South of St. Lawrence autumn spawning herring	slaw_her_aut	4T	1974-2007	RAM legacy database Version 3.0, accessed 10.01.2018 (Ricard et al. 2012)
North of Gulf of St. Lawrence	North of St. Lawrence cod		3Pn4Rs	1974-2015	DFO, SPA assessment model, Claude Brassard
	North of St. Lawrence spring spawners	nlaw_her_spr	4R	1963-2002	RAM legacy database Version 3.0, accessed 10.01.2018 (Ricard et al. 2012)
	North of St. Lawrence autumn spawners	nlaw_her_aut	4R	1971-2003	RAM legacy database Version 3.0, accessed 10.01.2018 (Ricard et al. 2012)
Scotian Shelf	Eastern Scotian Shelf cod		4VsW	1970-2010	DFO, VPA (Swain and Mohn 2012)
	Scotian Shelf herring	scot_her	4VWX	1964-2005	RAM legacy database Version 3.0, accessed 10.01.2018 (Ricard et al. 2012)
Georges Bank	Georges Bank cod		5Z	1978-2016	NOAA; Age structured model, Loretta O'Brien
	Georges Bank/Gulf of Maine herring	geob_her	5Z, 5Y	1967-2008	Shepherd et al. (2009), Table 18

Table S5.3: Overview of the periods which fit the criteria of a prolonged quasi-stability (Figure 5.2.1b main text) for an acceptance level of 10 %, 20 % and 30 % and 4-year, 5-year and 8-year moving window size for the linear regression. Only stocks are shown, which satisfied the first criteria of a significant change indicated by at least two change point analysis tools (Figure S5.1; Figure 5.2.1a, Figure 5.3 main text) and at least one long enough period of stability. The analysis of the slope needed to indicate 8, 7 and 4 consecutive stable years respectively, for 4-year, 5-year and 8-years sliding to reach > 10 years of stability. If the stocks indicated a sudden shift to or from the prolonged quasi-stability the period is indicated, as well as the year in which the ≥ 70 % biomass shift compared to the mean in the stable period occurred. If there is more than one period, the shift and years are indicated with the respective number in () behind the year.

stock	period 1	period 2	period 3	period 4	period 5	sudden shift	year of 70% jump	acceptance level	moving window size
wbc_her	1995-2001					no		20%	8-year
wbc_her	1996-2005					no		30%	4-year
wbc_her	1995-2009					no		30%	8-year
ns_her	1968-1978					yes	1967, 1985	10%	5-year
ns_her	1968-1979					yes	1967, 1984	20%	4-year
ns_her	1968-1979					yes	1967, 1985	20%	5-year
ns_her	1968-1976					yes	1967, 1985	20%	8-year
ns_her	1968-1980					yes	19,671,985	30%	4-year
ns_her	1968-1979					yes	1967, 1985	30%	5-year
ns_her	1953-1958	1967-1977	1984-1987	1989-1993	2003-2009	yes(1:4), no(5)	1968(1), 1966(2), 1988(2); 1981(3); 1981(4)	30%	8-year
nss_her	1968-1984					yes	1967, 1988	10%	4-year
nss_her	1968-1983					yes	1967, 1988	10%	5-year
nss_her	1968-1980					yes	1967, 1988	10%	8-year
nss_her	1968-1984					yes	1967, 1988	20%	4-year
nss_her	1967-1984	2006-2012				yes(1), no(2)	1966(1), 1989(1)	20%	5-year
nss_her	1967-1981	1994-1999				yes(1,2)	1966(1), 1989(1); 1987(2)	20%	8-year
nss_her	1967-1985	2006-2013				yes(1), no(2)	1966(1), 1989(1)	30%	4-year
nss_her	1967-1984	2006-2012				yes(1), no(2)	1966(1), 1989(1)	30%	5-year
nss_her	1966-1982	1987-2000	2003-2009			yes(1,2), no(3)	1965(1), 1990(1); 1986(2)	30%	8-year
westscot_her	1999-2003					no	NA	20%	8-year
westscot_her	1975-1982	1984-1992	2001-2011			no	NA	30%	4-year
westscot_her	1974-1977	1985-1988	1999-2005			no(1:3)	NA	30%	8-year
irish-her	1958-1962					yes	1975	20%	8-year
irish-her	1958-1963	1973-1976	1988-1991	1996-2000		yes(1,2), no(3,4)	1975(1), 1968(2)	30%	8-year
scot_her	1993-2001					yes	1990	10%	4-year
scot_her	1967-1970	1992-1996				no(1); yes(2)	1989 (2)	10%	8-year
scot_her	1992-2001					yes	1989	20%	4-year
scot_her	1992-2000					yes	1989	20%	5-year
scot_her	1967-1970	1992-1997				no(1), yes(2)	1989 (2)	20%	8-year

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scot_her	1992-2001			yes		1989	30%	4-year
scot_her	1992-2000			yes		1989	30%	5-year
scot_her	1966-1971	1974-1977	1991-1997	no(1,2), yes(3)	1988(3)	30%	8-year
geob_her	1976-1987			yes	1973, 1992	20%	4-year
geob_her	1975-1986	1996-2003		yes(1,2)	1973(1), 1992(1); 1989(2)	20%	5-year
geob_her	1976-1981			yes	1974, 1992	20%	8-year
geob_her	1975-1987	1996-2004		yes(1,2)	1973(1), 1992(1); 1989(2)	30%	4-year
geob_her	1975-1986	1996-2003		yes(1,2)	1973(1), 1992(1); 1989(2)	30%	5-year
geob_her	1975-1983	1993-2000		yes(1,2)	1973(1), 1992(1); 1989(2)	30%	8-year
slaw_her_aut	1980-1983			yes		1977	20%	8-year
slaw_her_aut	1980-1984			yes		1977	30%	8-year

"πάντων γὰρ ὅσα πλείω μέρη ἔχει καὶ μὴ ἔστιν οἷον σωρὸς τὸ πᾶν"
"The totality is not, as it were, a mere heap, but the whole is something besides the parts"

Aristotle, Methapysics

CONCLUSIONS

Understanding the recovery mechanisms and potential of our marine resources is fundamental to apply effective management measures and to unravel how the ecological but also socio-economic system will react. In this thesis, I investigated the recovery potential of 20 Atlantic cod stocks under climate change applying a range of methodologies to unravel non-linear discontinuous dynamics. These methods range from the basic change point analysis to the more sophisticated wavelet transform, and to two non-parametric models, the stochastic CUSP model and the Empirical Dynamic Modelling. I applied these methods to the biomass and the recruitment of single stocks in order to understand cod stocks dynamics and their drivers, namely climate change and fishing pressure; important information to incorporate into management.

Linear or non-linear?

In this thesis, I show that Atlantic cod stocks present non-linear dynamics. Non-linear discontinuous dynamics and chaos are pervasive in marine systems and can interest different compartments of the marine ecosystems, from single stocks, to a full trophic level or even the entire ecosystem (Chapter 1) (Beaugrand, 2004; Möllmann & Diekmann, 2012; Vasilakopoulos & Marshall, 2015; Morse *et al.*, 2017). Applying a range of non-linear methods, I show that non-linear, state-dependent dynamics can be detected in cod stocks not only at a biomass level, but also in the recruitment process and the stock-recruitment mechanism (Chapter 2,3 and 4). Some stocks presented a higher degree of linearity compared to others, having either recruitment described by the linear Ricker model, or not showing catastrophic dynamics in their biomass (Chapter 2 and 4). However, all the stocks presented non-linearity at least in one trait, thus suggesting that non-linear dynamics might be more the rule then the exception in cod stocks. Indeed, these types of dynamics have been detected for multiple species, from large top predators such as salmon, to small pelagic fishes (Vasilakopoulos *et al.*, 2014; Perretti *et al.*, 2015; Ye *et al.*, 2015; Deyle *et al.*, 2018; Munch *et al.*, 2018), and can also be confirmed by the trophic cascade reported in previously cod-dominated ecosystems (Frank *et al.*, 2005; Casini *et al.*, 2008a; Minto & Worm, 2012; Steneck & Wahle, 2013).

Detecting non-linear dynamics is fundamental for management, since they can jeopardize the management measures in place resulting in management failures and societal issues (Chapter 1) (Blenckner *et al.*, 2015b; Levin & Möllmann, 2015). The methods applied in this thesis, proved to be efficient methods to detect true discontinuous dynamics in the time series of fish

stocks. For instance, the stochastic CUSP model was applied to both cod and herring, species that show different life history traits, i.e. in the generation time. Herring presented more linear dynamics compared to cod, indicating that this method is able to discern between different dynamics and is efficient in detecting abrupt changes of the populations (Chapter 5). The presence of non-linearities and abrupt changes indicates a decreased resilience of the system (Holling, 1973; Scheffer *et al.*, 2001; Beisner *et al.*, 2003) Applying the methods used in this thesis to multiple species will help to understand their dynamics and their resilience, and thus will help to apply more efficient and specific management measures in order to favour the sustainable use of the stocks (Hutchings, 2000; Standish *et al.*, 2014; Vasilakopoulos & Marshall, 2015; Ye *et al.*, 2015). The consideration of multiple traits of fish populations, such as growth, maturity, spatial components, could also lead to more robust and more reliable resilience assessments (Vasilakopoulos & Marshall, 2015). Using 20 stocks from all over the North Atlantic, it was impossible to consider all these traits here, however the strong agreement between my results derived from the various, innovative methods and different population characteristics (biomass and recruitment) allows to confirm that cod stocks present non-linear, state-dependent dynamics.

Non-linear dynamics are often caused by the cumulative impacts of multiple drivers on the marine environment (Doak *et al.*, 2008; Maxwell *et al.*, 2013; Halpern *et al.*, 2015). Here, I investigated the effects of two drivers, fishing and climate change, which are believed to be the most relevant stressors for marine ecosystems and populations, and to act in additive or synergistic ways (Lehodey *et al.*, 2006; Anderson *et al.*, 2008; Kirby *et al.*, 2009; Perry *et al.*, 2010; Planque *et al.*, 2010; Halpern *et al.*, 2015). Two stressors are synergistic if the effect of the two stressors combined is greater than the sum (addition) of the two single effects (Boyd & Brown, 2015). The application of the stochastic CUSP model allowed for the first time the full disclosure of the mechanism of interaction between these two drivers (Chapter 2,5 and 4). The model showed that while fishing pressure is the driver controlling the population dimension, climate change induces hysteresis, lowering the resilience of the populations and reinforcing the effects of fishing. This is a key information for management, because it identifies threshold values of drivers which should not be crossed in order to maintain the population safe and stable (Rockström *et al.*, 2009; Standish *et al.*, 2014; Carpenter *et al.*, 2015). It also highlights the need to move towards a more precautionary approach when dealing with marine systems under climate change (Costanza *et al.*, 1998; Grafton & Quentin Grafton, 2010; Blenckner *et al.*, 2015b; Levin & Möllmann, 2015). My thesis confirms the primary importance of these two drivers not only for cod stocks but also for herring, and move an additional step forward identifying their synergistic effect.

Investigating at a stock level, I did not consider the mechanisms through which climate change and in particular warming affect cod (Pörtenr & Farrell, 2008; Pörtner & Peck, 2010). Temperature can have an effect on cod populations acting directly on growth, fertility or mortality, or indirectly through predator-prey switches, changes in currents and habitat degradation (Brander, 1995; Brander *et al.*, 2001; Beaugrand *et al.*, 2003; Stige *et al.*, 2006; Wang *et al.*, 2014; Huebert *et al.*, 2018). Moreover, temperature increase can also induce population movement towards deeper waters and northern areas, thus potentially altering the

structure of entire ecosystems and of the socio-ecological systems relying on them (Perry P.J. Low, J.R. Ellis, J.D. Reynolds *et al.*, 2005; Dulvy *et al.*, 2008; Pinsky *et al.*, 2018). Finally, here I considered global indices while spatially resolved indices may be more relevant. Indeed, the main stressors might have a more local effect and be more specific for each population, i.e. anoxic areas in the Baltic Sea (Bates *et al.*, 2018; Reusch *et al.*, 2018). A more detailed understanding of the drivers and mechanisms at a local scale could be important to integrate in order to understand the consequences of climate change in specific areas and adapt the local management measures accordingly.

To recover or not to recover? That is the question!

The presence of non-linear, discontinuous dynamics has an important effect on the recovery of stocks (Chapter 1) (Beisner *et al.*, 2003; Levin & Möllmann, 2015; Vasilakopoulos & Marshall, 2015). In my thesis, I show that the majority of cod stocks is still in a very depleted state, even after more than 20 years of management (Chapter 2). A property of a system presenting non-linear dynamics is hysteresis, being the delayed or absent return of the system to previous conditions after the removal of the stressor (Chapter 1) (Scheffer *et al.*, 2001; Scheffer & Carpenter, 2003; Bestelmeyer *et al.*, 2011). The stochastic CUSP model detected hysteresis in almost all the Atlantic cod stocks, thus explaining the failed recovery (Chapter 2). Indeed, even if fishing pressure was delayed or removed in some areas, the presence of hysteresis delayed or hindered completely the recovery of cod stocks, highlighting the importance of detecting these types of dynamics in management (Folke *et al.*, 2004; Levin & Möllmann, 2015; Selkoe *et al.*, 2015). In this thesis, I referred to recovery as an increase towards historical biomass level, even if multiple definitions of recovery could be used and more parameters should be evaluated to have a comprehensive view of cod stocks recovery (Lotze *et al.*, 2011; Vasilakopoulos & Marshall, 2015). Nevertheless, the application of multiple methods and the consideration of different population mechanisms allowed me to understand the recovery potential of cod stocks, which varies depending on geographical areas.

Among the Atlantic cod stocks North-East Arctic cod and Iceland are the biggest stocks and can be found in a very healthy state (Chapter 2,3 and 4). In particular, North-East Arctic cod is at its largest population size since the last 60 years. These stocks reside at their northern distribution limits, thus at the edge of their possible physiological distribution and far from their thermal optima (Pörtner *et al.*, 2008; Butzin & Pörtner, 2016). Warming is thus beneficial for these stocks and therefore an increase of temperature can have positive effects on both adult and larvae (Drinkwater, 2005). At the moment, the populations are in a such high state that recruitment is rather low, due to the strong density dependent effects (Chapter 3 and 4). These two stocks present also peculiar types of dynamics and never really showed collapses, but before the 1990s, were mostly in a depleted state due to the cold temperatures (Chapter 2 and 3). For all the remaining stocks, warming and climate change, on top of fishing pressure, resulted in negative effects on both biomass and recruitment, as also shown in many other studies (Chapter 2 and 4) (Brander, 2005; Drinkwater, 2005; Stige *et al.*, 2006; Butzin & Pörtner, 2016).

In this thesis, I show that the recovery potential of cod stocks varies between stocks in west and in the east Atlantic. These stocks present dissimilarities concerning life history traits, environmental conditions and exploitation history (Rätz & Lloret, 2003; Pörtner *et al.*, 2008; Wang *et al.*, 2014; Frank *et al.*, 2016). Western stocks (i.e. Canadian and USA stocks and Greenland) present more fragile life history traits and tend to be exposed to more variable environmental conditions (Köster *et al.*, 2013). The Stochastic CUSP model highlighted that western stocks are less resilient and more unstable compared to eastern stocks, indicating that the former might be more difficult to recover. However, all the stocks present non-linear discontinuous dynamics and recently also the eastern ones present a decreased resilience due to the increase of the water temperature (Chapter 2).

After many years, some stocks showed small signs of recovery due to a spike in recruitment during a year with favourable environmental conditions, in combination with efficient management measures (Chapter 3). Recruitment in this thesis is thus identified as an important mechanism to start population recovery, as also seen in other studies (Myers *et al.*, 1995; Hutchings & Rangeley, 2011; Kuparinen *et al.*, 2014). However, in stocks residing in the south and central areas of the North Atlantic, recruitment is negatively influenced by warming (Brander, 2005; Stige *et al.*, 2006). Thus even if recovery is theoretically possible, the productivity of most of the population will likely stay low under global changes, as also shown in another study (Drinkwater, 2005). Also in this case differences between eastern and western stocks can be detected. The stock-recruitment relationship showed discontinuous and catastrophic dynamics in western stocks pointing out their lower resilience compared to the eastern ones (Chapter 4). Moreover, recruitment in the East seemed more affected by local conditions (i.e. temperature), while in the West responded more to large scale climatic fluctuations (i.e. Atlantic Multidecadal Oscillation) (Chapter 4), indicating that these stocks might experience more fluctuating environmental conditions, again stressing on their higher instability (Pörtner *et al.*, 2008; Köster *et al.*, 2013; Botero *et al.*, 2015).

The main finding of this thesis is that Atlantic cod stocks recovery potential in the central and southern North Atlantic is low since the stocks present discontinuous dynamics and hysteresis and since climate change has a negative effect on the adults and the larvae of these stocks (Figure 10, Chapter 2, 3 and 4) (Brander, 1995; Drinkwater, 2005; Pörtner *et al.*, 2008). Stocks in the Northwest Atlantic appear even more vulnerable compared to stocks in the Northeast, confirming that important differences exist depending on the geographical areas (Rätz & Lloret, 2003; Pörtner *et al.*, 2008).

Of course, there might be different outcomes in nature. Local environmental conditions and the presence of subpopulations inside the stocks can have an impact on recovery and were not considered in this thesis (Smedbol & Wroblewski, 2002; Reiss *et al.*, 2009). Also the evolutionary potential of cod and its capacity to adapt to climate change documented in various fish populations were ignored (Hoffmann & Sgrò, 2011; Crozier & Hutchings, 2014; Botero *et al.*, 2015). The temperature increase in southern areas, especially if outside the thermal niche of cod, could lead to a complete migration of cod populations northwards (Engelhard *et al.*, 2014; Kortsch *et al.*, 2015). Consequently, an increase of the stocks in northern areas is

theoretically possible. The disappearance of cod from the south will confirm the failed recovery highlighted in this thesis. Indeed, the stocks will not reside anymore in their "traditional" areas leading to repercussion on the entire socio-ecological system (Pinsky *et al.*, 2018; Selden *et al.*, 2018).
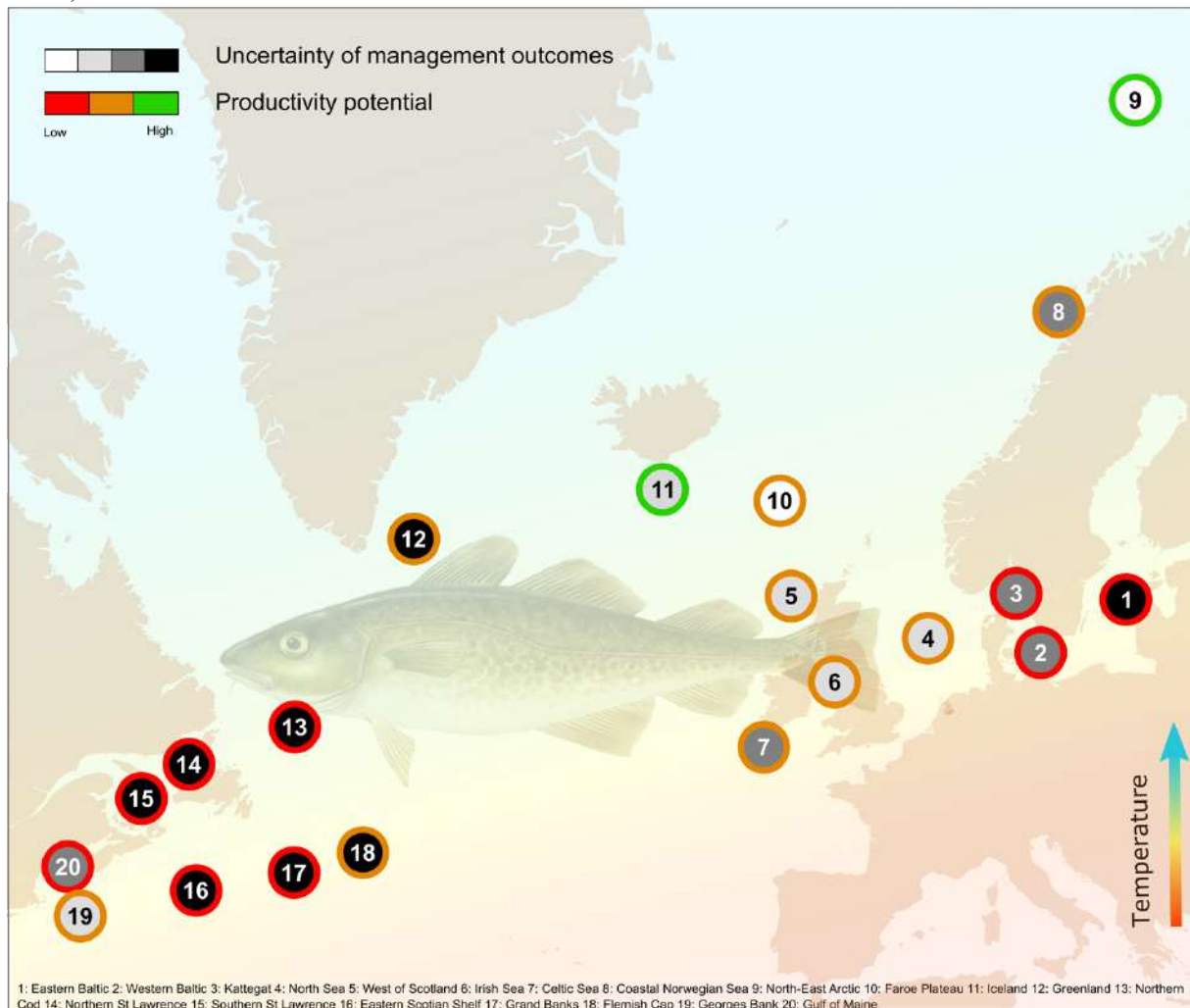

Figure 10: Synthetic figure of main thesis results framed in a management perspective (produced by Xochitl Cormon).

This thesis stresses that the detection of non-linear dynamics is fundamental for management, to i) understand the resilience of the system, ii) identify the drivers and their thresholds necessary to maintain the system in a high and stable state, iii) understand the mechanisms that could favour the system´s recovery (Standish *et al.*, 2014; Blenckner *et al.*, 2015a; Carpenter *et al.*, 2015; Levin & Möllmann, 2015). The methods applied here proved extremely good in unravelling non-linear dynamics. The definition of resilience and of reference points in management could be done using a combination of the methods applied in this thesis, in particular the stochastic CUSP model (Chapter 2) (Selkoe *et al.*, 2015; Hunsicker *et al.*, 2016). Management intervention in some cases requires knowledge of the mechanisms of collapse and recovery, which was achieved here with the wavelet analysis (Chapter 3). Modern management in some areas such as USA and Australia, already uses multiple model frameworks to increase the robustness of the management measures, therefore the multi-model approach applied in this

thesis could also be applied and improve management efficiency(Chapter 4) (Punt *et al.*, 2013; Levin & Möllmann, 2015; Punt *et al.*, 2016).

Finally, these methods seemed also able to give indications of non-linearity before they occur. For instance, the stochastic CUSP model did not fit well to Gulf of Maine and Faroe cod stock data. However, the models still indicated that even though the stocks are at present in a stable state with linear dynamics, future temperature changes might induce discontinuous dynamics and thus abrupt collapses (Chapter 2). This of course could be important for management to anticipate possible undesired surprises, and to confirm results from other indicators like the early warning signals (Dakos *et al.*, 2008, 2017; Kefi *et al.*, 2013). The presence of discontinuous dynamics and the low resilience of many stocks can highlight areas in which management outcomes are more uncertain and where more adaptation options are needed (Figure10). To develop more flexible management approaches and to be ready to adapt to unforeseen changes the methods applied in this thesis can help to move towards more integrative ecosystem based management (King *et al.*, 2001).

Consequences of the failed recovery of Atlantic cod stocks

Here, I show that Atlantic cod stocks might not be able to recover in the future years due to climate change, and thus that many ecosystems will permanently lose their dominant predator. This could lead to huge repercussion both from an ecological but also socio-economic perspective (Hutchings & Myers, 1995; Haedrich *et al.*, 2000).

The consequences of the depletion of southern and central Atlantic cod stocks can be already seen in various ecosystems, both in the East and West Atlantic (Frank *et al.*, 2005; Österblom *et al.*, 2007; Casini *et al.*, 2008a). Atlantic cod is a top predator of marine food-webs (Link *et al.*, 2009) preying mainly on forage fish and benthos at an adult stage, and on plankton at a juvenile stage (Hanson & Chouinard, 2002; Beaugrand *et al.*, 2003; Minto & Worm, 2012). The theory suggests that the removal of an apex predator, i.e. "trophic downgrading, can lead to major shifts in the full ecosystem based on 3 pillars: i) the so-called trophic cascade, ii) the presence of alternative stable states and iii) the connectivity in food-webs (Estes *et al.*, 2011). This can already be seen in different ecosystems where cod collapsed, such as in the Eastern Scotian Shelf (Frank *et al.*, 2011). The disappearance of cod led to a release of its predation pressure on its preys and to a strong trophic cascade with consequent increase of forage fishes but also macroinvertebrate animals, i.e. crustaceans (Frank *et al.*, 2005; Jordán, 2009; Ellingsen *et al.*, 2015; Malhi *et al.*, 2016; Ichii *et al.*, 2017). This led to the instauration of an alternative new state, which, if cod stocks will fail to recover in the future, has to be considered the new and permanent state (Estes *et al.*, 2011). In some areas, the new system is characterized by a restructured trophic chain, where the food-web becomes less homogeneous and present greater variation of species and abundances. Thus, with the increase of the heterogeneity, resilience and resistance may decline, leading to less stable and novel ecosystems (Ellingsen *et al.*, 2015).

The decline and disappearance of cod brought also huge socio-economic repercussions (Myers *et al.*, 1996; Haedrich *et al.*, 2000; Xu *et al.*, 2013; Quaas *et al.*, 2016). Especially in Canada where a fishing moratoria was established, thousands of fishermen lost their job, leading to the disappearance of many fishing villages and consequent social issues (Kurlansky, 2009). To adapt to the disappearance of cod, in many areas fishermen have changed their target resources, moving towards substitutes (Steneck *et al.*, 2011). This adaptation required some years but was favoured also by the increase of other species such as forage fish or macroinvertebrates consequent to the trophic cascade (Frank *et al.*, 2005; Conway & Shaw, 2008). For instance, in Maine, many fishermen have switched towards more advantageous resources such as lobsters or crustaceans (Steneck *et al.*, 2011, 2013). The market is so prosperous that at the moment there is no will to have cod back in the ecosystem, since the new business is far more valuable. However, this opens many questions about the sustainability of fishing down marine food-webs and what will happen if the lobster will also be gone (concept called "gilded trap") (Steneck *et al.*, 2011). Of course, social conflicts are present; indeed, some fishermen are winners (the ones who changed their business or who already had licences for the emergent species) and some losers (the ones who continued to fish for cod).

The loss of key-stone species or apex predators, such as cod, is often coupled with climate change and other anthropogenic stressors, and thus the consequent changes in biodiversity, ecosystem structure and functioning are not always easy to explain or predict (Estes *et al.*, 2011; Ellingsen *et al.*, 2015). The loss of cod could just result in the increase of forage fish and thus a downgrading of the food-chain or could open up new niches in the ecosystem and favour the entering or the establishment of new species from other areas (i.e. southern). An example is the projected increase of spiny dogfish as new regulator of the food-web in Gulf of Maine after the collapse of cod due to fishing and climate change (Selden *et al.*, 2018). The new predator could help the ecosystem to maintain a similar structure and thus, the entrance of new species could act as buffer mechanism and increase the system´s resilience (Selden *et al.*, 2018). Therefore, the consequences of apex predators' loss may vary between areas and ecosystems and are not easy to understand and predict due to the complexity of the food-webs and the multiple anthropogenic pressures acting on them. Similarly, it is not entirely clear whether the decline of cod is completely negative from a socio-economic point of view, and whether the new states are less or more desirable economically.

In the Northern areas, i.e. Barents Sea and Iceland, cod populations present really high abundances. The stocks in the north are projected to increase and likely to expand even further north. In this case cod will become the "colonizer" species of new food-webs as it is happening in the Arctic. The Arctic food-web is in general quite simple, and the entrance of cod can completely change its structure rendering it more heterogeneous and thus decreasing the resilience and stability of the system itself, with important repercussions on its functions (Blanchard, 2015; Kortsch *et al.*, 2015). The very high abundances of cod especially in the Barents Sea have hugely changed its world market. Indeed, even if depleted, cod is still one of the main requested species by the public (Quaas *et al.*, 2016). At the moment, the entire world cod market is dominated by the Barents Sea cod, and thus looks very different compared to the

market some decades ago (Figure 11) (Sguotti *et al.*, 2018). This of course raises concerns about the market resilience and the capacity of the new cod market to absorb stresses (Richter & Dakos, 2015). Moreover, a single stock-dominated market can have important repercussions on the management and the fishing activities for cod in other areas, thus potentially influencing the recovery of the stocks. Socio-economic factors were just very weakly touched in this thesis, however, a comprehensive analysis on the impact of the market on the recovery of cod stocks, and an analysis of the social components of the systems would improve our understanding on cod stocks dynamics and especially recovery. The socio-ecological system should be analysed as a whole and should be maintained within a safe space, defined by management (Färber *et al.*, 2018) (Rockström *et al.*, 2009; Carpenter *et al.*, 2015, 2017)
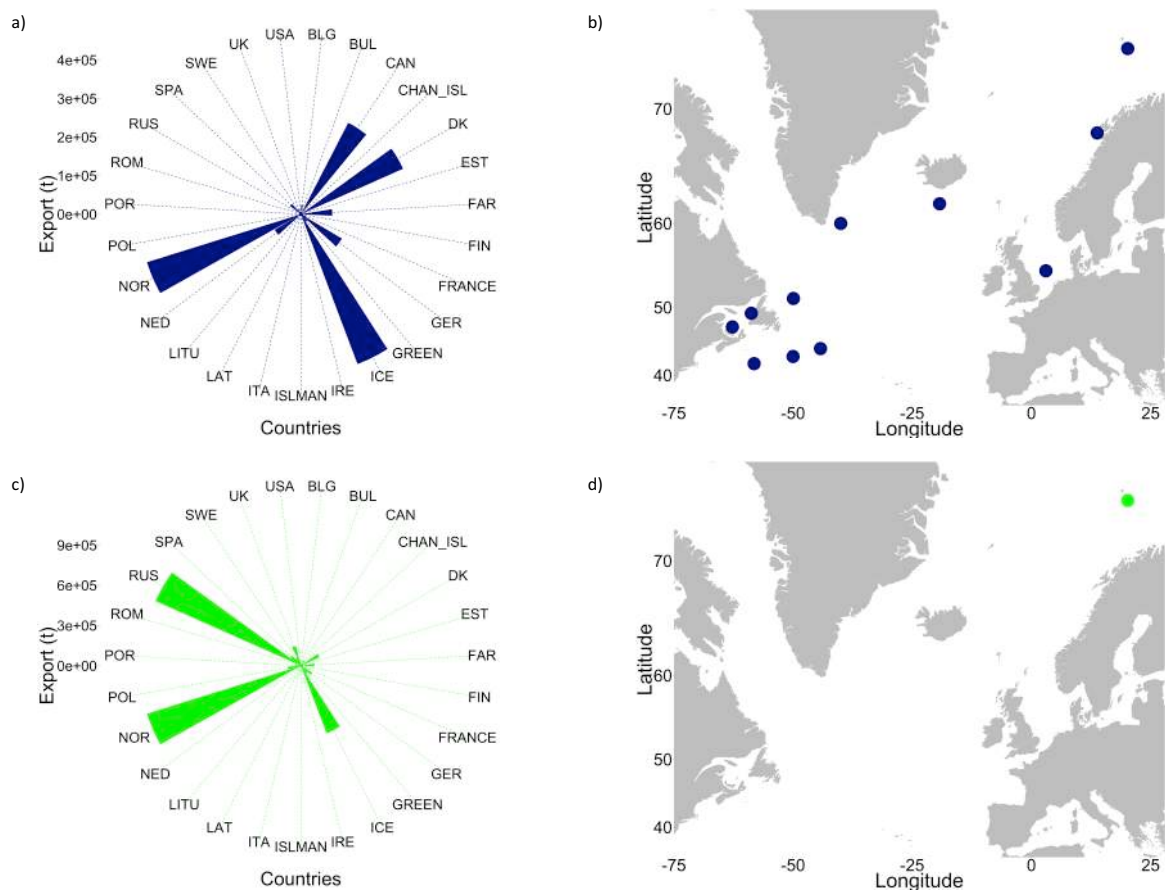

Figure 11: Snapshots of Atlantic cod market in the 1970s and 2010s. a,c) Export per countries respectively in the 1970s and 2010s. b,d) Stocks which mainly served the market respectively in the 1970s and 2010s.

The hypothesised failed recovery of Atlantic stocks could lead to some socio-economic and ecological repercussions, difficult to fully estimate and predict. The adaptation towards a world with less cod has already started in some areas and therefore can give an indication of what will happen in the future if the recovery would be hindered (Frank *et al.*, 2011; Steneck & Wahle, 2013; Selden *et al.*, 2018). Adaptation is the only way in which society and management can handle the future changes of marine ecosystems (Allison *et al.*, 2009; Kates *et al.*, 2012; Ogier *et al.*, 2016). If we want to be able to feed the planet and secure livelihoods for humans, we need to apply adaptive and flexible management which can adjust to the projected global changes (Merino *et al.*, 2012; Sale *et al.*, 2014). In this context, the ecosystem based

management, considering the systems as a whole, is trying to move towards this direction (Long *et al.*, 2015). The inclusion of non-linear, discontinuous dynamics in this management framework is important to avoid ecological surprises and requires the utilization of non-traditional models and the reformulation of some management practice (Osterblom *et al.*, 2010; Levin & Möllmann, 2015; Selkoe *et al.*, 2015; Ye *et al.*, 2015; Deyle *et al.*, 2018). Even if the change of management practices might be scary or with unknown outcomes, we need to move towards a new, more flexible and more adaptive management to be able not only to cope, but also to adapt and take advantage of the present and future global changes (Creighton *et al.*, 2016).

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LIST OF PUBLICATIONS

Published Articles

Sguotti C., Cormon X. (2018) Regime Shifts – A Global Challenge for the Sustainable Use of Our Marine Resources. In: Jungblut S., Liebich V., Bode M. (eds) YOUMARES 8 – Oceans Across Boundaries: Learning from each other. Springer, Cham

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In review or submitted

Sguotti C, Otto SA, Frelat R, Langbehn TJ, Plambech Ryberg M, Lindegren M, Durant JM, Stenseth, NC, Möllmann C (2018) Catastrophic dynamics limit Atlantic cod recovery. *In review at Proceedings of the Royal Society B.*

Sguotti C, Otto SA, Cormon X, Werner KM, Deyle E, Sugihara G, Möllmann C (2018) Non-linearity in stock-recruitment relationships of Atlantic cod: insights from a multi-model approach. *In review at ICES Journal of Marine Science.*

Färber L, **Sguotti C**, Durant JM, Langangen Ø, Otto SA, Möllmann C (2018) Detection of discontinuous behaviour causing shifts in North Atlantic herring stocks. *Submitted to Fish and Fisheries.*

Plambech Ryberg M, Behrens J, Brander K, **Sguotti C**, Nielsen A, Lindegren M (2018) Shifting importance between external climate -related factors and internal density-dependent processes regulating North Atlantic cod (*Gadus morhua*) growth throughout ontogeny. *Submitted.*

In Preparation

Sguotti C, Frelat R, Cormon X, Otto SA, Möllmann C. Coupling and decoupling of spawner biomass and recruitment explain Atlantic cod collapse and recovery.

Reports

ICES 2017. Report of the Working Group on the History of Fish and Fisheries (WGHIST), Lysekil, Sweden

ICES 2016. Report of the Working Group on the History of Fish and Fisheries (WGHIST), Copenhagen, Denmark

Sessions chaired at conferences

Cormon X, **Sguotti C**, Möllmann C, Hunsicker M (2018) "Tipping points complex nature and implications for marine socio-ecological systems management", ICES Annual Science Conference, 24-27 September 2018, Hamburg, Germany

Sguotti C, Cormon X (2017). "Ecosystem dynamics in a changing world: regime shifts and resilience in marine communities", YOUMARES 8, Kiel, Germany, 13.- 15. September 2017

Presentations and Posters

Sguotti C, Möllmann C, Richter A (2018) "Teleconnection of Atlantic cod stocks in the world market", talk at ICES Annual Science Conference, 24-27 September 2018, Hamburg, Germany

Sguotti C, Otto S, Cormon X, Frelat R, Möllmann C (2018) "Linear or non-linear? Understanding the effect of climate change on Atlantic cod recruitment", talk at the 4th International Symposium on the Effects of Climate Change on the World's Oceans (ECCWO), Washington DC, 2-8 June2018

Sguotti C, Frelat R, Otto S, Plambech M, Lindegren M, Möllmann C (2017). "The failed recovery of Atlantic cod stocks ", talk at the 3rd PICES/ICES Early Career Scientists Conference, Busan, South Korea, 30. May - 2. June 2017

Färber L, Schuch E, **Sguotti C**, Winter AM, Durant J, Möllmann C, Richter A (2018) "When good enough is optimal. Defining the safe operating space of a fishery on the brink of collapse". Poster at at ICES Annual Science Conference, 24-27 September 2018, Hamburg, Germany

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Funding

Prof. PhD Myron A.Peck
Institute for Marine
Ecosystem and Fisheries
Science
Olbersweg 24, D-22767-
Hamburg
Tel +49 4042 838 6602
Fax +49 4042 838 6618
myron.peck@uni-
hambugr.de

Universität Hamburg
Biozentrum Klein Flottbek
Studienbüro Biologie
z. H. Frau Sült-Wüpping
Ohnhorststr. 18
22609 Hamburg

Dear Frau Sült-Wüpping

I have briefly reviewed the thesis "North Atlantic cod recovery under climate change and exploitation pressures, a non-linear approach" written by Camilla Sguotti. The thesis is written in English. As a native English speaker, I can attest that the writing (grammar and syntax) is acceptable. The English writing is of sufficient quality to move forward with the submission and review process.

Sincerely,

Prof. Myron A. Peck

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.

Hamburg,   Camilla Sguotti