

# **Management of Atlantic cod (*Gadus morhua* L.) under fu- ture climate change**

Jan Constantin Conradt

## **Dissertation**

with the aim of achieving a doctoral degree at:

Faculty of Mathematics, Informatics and Natural Sciences

Department of Biology, Universität Hamburg

Institute of Marine Ecosystem and Fishery Science

Hamburg, 2023

## **Evaluators**

Prof. Dr. Christian Möllmann, Universität Hamburg

Prof. Dr. Thorsten Blenckner, Stockholm Resilience Center

### Suggested commission for the disputation:

Prof. Dr. Ina Meier (chair), Universität Hamburg

Prof. Dr. Christian Möllmann, Universität Hamburg

Prof. Dr. Thorsten Blenckner, Stockholm Resilience Center

Jun.-Prof. Dr. Flemming Dahlke, Universität Hamburg

Dr. Rüdiger Voss, Christian-Albrechts-Universität zu Kiel

Suggested date of disputation: 15.12.2023

# Contents

Summary	1
Zusammenfassung	4
1. General Introduction	8
2. Chapter I: Robust fisheries management strategies under deep uncertainty	28
3. Chapter II: Safe Operating Space reveals climate-adaptation thresholds for sustainable management of Atlantic cod ( <i>Gadus morhua</i> L.)	49
4. Chapter III: Designing sustainable management strategies for Atlantic cod ( <i>Gadus morhua</i> L.) under deep uncertainty via multi-objective optimization	74
5. General Discussion	98
6. References	115
7. Supplementary material for Chapter I	148
8. Supplementary material for Chapter II	170
9. Supplementary material for Chapter III	196
10. Supplementary references	212
List of abbreviations	218
List of publications	219
Acknowledgements	220
Funding acknowledgements	222
Author contributions	223
Eidesstattliche Versicherung	224

Note on enumeration of figures, tables and equations: a figure- / table- / equation number is composed of the chapter number (in Roman letters, preceded by a „C“), followed by the chapter-specific running index (in Arabic numerals, preceded by a dot). A figure- / table- / equation in a supplementary section has the preceding mark “SI”; the running index is replaced by a composition of a running index enumerating the sections of a chapter-specific supplement and a running index enumerating the figures / tables / equations within that section (two Arabic numerals separated by a slash). Hence, *fig. CIII.1* is the first figure in the third chapter (main section #4 in the overall work), while *fig. SI CII.4 / 1* is the first figure in the fourth section of the supplementary material for Chapter II (main section #8 in the overall work).

References from identical authors / agencies and equal years are letter-indexed independently from each-other in sections 6 and 10

## Summary

Living marine resources are increasingly threatened by combined pressures of fishing and climate change, which put the sustainability of harvesting for yields that can support a fishery at risk. Ocean warming frequently reduces the productivity of commercial fish stocks, aggravating efforts of fisheries management to reverse effects of overfishing incurred through massive buildup of fishing capacity in the 20<sup>th</sup> century. A substantial challenge for management approaches that aim for adaptation to climate change is the lack of comprehensive knowledge on the mechanistic nature of climate effects on the dynamics of harvested populations, especially on their little-observed early life stages. Unexpected management response, e.g. delayed or missing rebuilding dynamics, indicate that stocks react in highly non-linear or discontinuous and long-lasting ways to fishing and climate change; ways that can hardly be anticipated or projected within models. Yet, accounting for such dynamics is important for guiding management decisions, as ignoring them can lead to poor stock condition and fixation thereof and economic hardship for fishers. The present dissertation investigates the impact of deep uncertainty in the relationship between temperature, stock size and recruitment (i.e., early-life-stage- / juvenile survival until entry to the fishery), which partly results from the non-linear stock response to stressors, on the potential for long-term future sustainable harvesting under intensifying future climate change.

To this end, the dissertation adopts the perspective of “Decision-Making under Deep Uncertainty” (DMDU) by performing a large number of model projections under a very large range of uncertain scenarios, defined i.a. by possible stock-environment-recruitment (SR-) relationships and climate scenarios, in combination with a range of harvesting policies. The aim is not to improve model predictive skill or to infer the most “likely” future development but instead to unveil the potential consequences of harvesting policies and ocean warming for stock health. The various SR relationships here are intended to represent the general uncertainty about the SR relationship but especially also different (hypothetical) regimes of stock productivity that might arise from shift-like non-linear stock response to warming and harvesting. Atlantic cod (*Gadus morhua* L.), a fish of high commercial and cultural relevance that was frequently over-fished in the last half-century and displays climate vulnerability and unexpected management response, is chosen as model species.

The dissertation first investigates the impact of deep uncertainty about the SR relationship on the response of a typical moderately over-fished cod stock, the North-Sea cod, to harvesting under future climate change. Procedures developed from the concept of “Robust Decision-



Making” (RDM), a particular analytical approach used in DMDU, are used to explore the existence and properties of harvesting strategies that achieve universal sustainability by maintaining healthy stock size under all deeply uncertain scenarios. It is found that this uncertainty acts equally strong as harvesting on the degree of sustainability, and that no temporally fixed harvesting strategy can attain the objective of continuous future sustainability under climate change under all SR scenarios. A risk analysis is conducted to assess the relative effect of harvesting intensities on future sustainability and economic viability as a surrogate for identifying a fully “safe” policy, finds that these two objectives are related to each-other in a negative trade-off. This relationship shows that higher chances for future sustainable harvesting are likely associated with lower-than-recent profits, at least when aiming for temporally stable harvesting.

The dissertation then adopts this risk-analysis framework for developing “Safe-Operating-Spaces”- (SOS-) concept for sustainable harvesting under climate change of 19 stocks of Atlantic cod inhabiting the eastern- and western-Atlantic shelves and the northerly waters ( $> 60^{\circ}\text{N}$ ). Model simulations are conducted for combinations of various levels of catch, temperature increase and initial stock biomass, resulting in a multivariate map of sustainability risk calculated over SR scenarios. While a fully safe harvesting level is not detected for any stock, the existence and extent of the scenario space yielding  $< 50\%$  risk, i.e. the SOS in the present study, shows distinct patterns between major geographical areas and levels of historical over-fishing: Historically long-term-collapsed western-Atlantic stocks display hardly any SOS, while relatively well-rebuilt northerly eastern-Atlantic stocks appear strongly responsive to harvesting and more southerly eastern-Atlantic stocks additionally display a clear negative climate effect. Initial stock biomass is found to have a profound impact on maximum warming tolerable (i.e. yielding  $\leq 50\%$  risk) for the stock and for harvesting the stock, indicating that building stock reserves could help mitigate future climate effects on many stocks.

Finally, the dissertation develops a heuristic optimization procedure for uncovering sustainable (long-term) harvesting pathways under dynamic ocean warming for the currently depleted Western Baltic cod. The optimization algorithm is designed to respect both conservation- and, with secondary priority, yield objectives. The resulting harvesting trajectories force a quick rebuilding of stock size to sustainable levels and then, by gradually reduce fishing pressure as warming intensifies, maintain sustainable stock size while continuously decreasing catch. Introducing deep SR uncertainty leads to harvesting of similar dynamics but on a much reduced level. Risk of stock decrease to unsustainable levels is kept on a very low level for sev-

eral decades but eventually increases under continuous warming, indicating a cessation of manageability under unfavorable SR scenarios. Risk of missing even a historically modest target yield is, in contrast, continuously comparatively high. Embedding harvesting optimization along with stock monitoring as a recurring procedure within a simulated management pathway, under a true but unpredictable trajectory of changing SR relationships, leads to high stock size and yields. The clear fulfillment of both objectives indicates the combination of uncertainty-conscious long-term harvesting planning, stock monitoring and short-term policy flexibility to be a valuable management approach under future climate change.

The dissertation concludes that Atlantic cod will likely remain manageable under future climate change to a certain degree. Achieving future sustainability will depend strongly on the realized SR relationship(s), the degree of future warming, the degree of stock (re-) building achieved and likely on the severity of historical overfishing. Management strategies most likely to be successful will aim for quickly (re-) building stock biomass and adapt harvesting intensity to realized stock size and with the aim of minimizing long-term conservation risk under a wide-range of future SR scenarios.

## Zusammenfassung

Lebende marine Ressourcen sind zunehmend durch kombinierten Stress aus Befischung und Klimawandel bedroht, was die Nachhaltigkeit der Entnahme von Fängen, die eine Fischerei wirtschaftlich stützen können, einem Risiko aussetzt. Die Erwärmung der Meere reduziert in vielen Fällen die Produktivität kommerziell genutzter Fischbestände, was die Bemühungen des Fischereimanagements, die Effekte der Überfischung, die aus den immensen Vergrößerungen der Fangkapazitäten im 20. Jh. hervorgingen, rückgängig zu machen, erschwert. Eine erhebliche Herausforderung für Managementansätze, die auf Anpassung an den Klimawandel setzen, ist der Mangel an Wissen über die mechanistischen Effekte des Klimas auf die Dynamiken der Fischpopulationen, insbesondere auf die der schwer beobachtbaren frühen Lebensstadien. Unerwartete Reaktionen der Bestände auf Managementmaßnahmen, z.B. stark verzögertes oder ausbleibendes Populationswachstum zum Wiederaufbau eines Bestandes, deuten darauf hin, dass Bestände auf nicht-lineare oder diskontinuierliche und lang-andauernde Weise auf Fischerei und den Klimawandel reagieren. Diese Art der Reaktion kann derzeit von Projektions-Modellen kaum vorhergesagt werden. Der Einbezug solcher Dynamiken ist allerdings von Wichtigkeit für die Lenkung von Managemententscheidungen, da deren Ausblendung zu einer Bestandsreduktion auf geringe Größe und schwierigen wirtschaftlichen Bedingungen für die Fischerei führen oder solche verfestigen kann. Die vorliegende Dissertation untersucht den Einfluss der hochgradigen Unsicherheit in der funktionellen Beziehung zwischen Temperatur, Bestandsgröße und Rekrutierung (d.h. das Überleben der frühen Lebensstadien und juvenilen Fische bis zum Eintritt in die Fischerei) – die sich z.T. aus der nicht-linearen Bestandsreaktion auf Stressoren ergibt - auf das Potenzial für andauernd nachhaltige Bestandsbewirtschaftung unter sich intensivierendem zukünftigem Klimawandel.

Zu diesem Zweck bedient sich die Dissertation der Perspektive des “Decision-Making under Deep Uncertainty” (zu deutsch: “Entscheidungsfindung unter tiefer Unsicherheit”) (DMDU), indem eine große Anzahl an Modellprojektionen unter einer sehr großen Bandbreite an unsicheren Szenarien - definiert u.a. durch mögliche Bestands-Umwelt-Rekrutierungs-(SR)-Beziehungen und Klimaszenarien - für verschiedene Befischungsstrategien durchgeführt werden. Dabei wurde bewusst der Fokus nicht auf die Verbesserung der Vorhersagekraft der Modelle gelegt, oder darauf, die “wahrscheinlichste” zukünftige Entwicklung zu identifizieren, sondern darauf, potenzielle Konsequenzen der Befischungsstrategien und der Ozeanerwärmung für die Bestandsgesundheit als Anzeiger von Nachhaltigkeit aufzudecken. Die verschiedenen SR-Szenarien repräsentieren dabei die generelle Unsicherheit über die SR-

Beziehung, aber insbesondere auch verschiedene Modi der Bestandsproduktivität, die sich aus der verlagerungsartigen nicht-linearen Bestands-Reaktion auf Erwärmung und Befischung ergeben können. Als Modell-Art wird hier Atlantischer Kabeljau (*Gadus morhua* L.) verwendet, ein Fisch mit hoher kommerzieller und kultureller Relevanz, der im letzten halben Jahrhundert vielerorts überfischt wurde und sowohl Klima-Vulnerabilität als auch unerwartete Reaktionen auf Managementmaßnahmen gezeigt hat.

Die Dissertation untersucht im ersten Schritt die Auswirkung der “tiefen Unsicherheit” in der SR-Beziehung auf die Reaktion eines typischen moderat-überfischten Kabeljau-Bestands, des Nordsee-Kabeljaus, gegenüber Befischung unter zukünftigem Klimawandel. Prozeduren, die aus dem Konzept des “Robust Decision-Making” (zu Deutsch: “Robuste Entscheidungsfindung”) (RDM) abgeleitet sind, einer der typischen Analysemethoden im DMDU, werden verwendet, um die Existenz und die Eigenschaften von Befischungsstrategien, die universelle Nachhaltigkeit (d.h. gesunde Bestandsgröße unter allen tief-unsicheren Szenarien) erreichen, zu prüfen. Es zeigt sich, dass diese Unsicherheit einen vergleichbar großen Einfluss auf den Grad der Nachhaltigkeit hat wie die Befischungsintensität, und dass keine einzige Befischungsstrategie das Ziel der dauerhaften zukünftigen Nachhaltigkeit unter Klimawandel erreicht. Eine Risiko-Analyse, die zur Beurteilung des relativen Effekts der Befischungsstrategien auf zukünftige Nachhaltigkeit und ökonomischen Nutzen durchgeführt wird (als Ersatz für die Identifikation einer vollständig nachhaltigen Strategie), zeigt, dass das Erreichen der beiden Ziele einer Trade-Off-Beziehung unterliegt. Dies zeigt, dass eine größere Sicherheit für zukünftige nachhaltige Befischung (wenn ein zeitlich stabiles Befischungsniveau angestrebt wird) wahrscheinlich nur unter Inkaufnahme von geringeren Profiten als denen der jüngeren Vergangenheit erreichbar sein wird.

Im zweiten Schritt wird das Rahmenwerk der Risiko-Analyse zur Entwicklung von “Safe Operating Spaces” (zu Deutsch: “sichere Handlungsräume”) (SOS) für die nachhaltige Befischung von 19 Kabeljaubeständen der west- und ostatlantischen Schelfgebiete und der nördlichen atlantischen Gewässer ( $> 60^\circ\text{N}$ ) unter zukünftigem Klimawandel verwendet. Modellsimulationen werden für Kombinationen aus verschiedenen Fangmengen, Temperaturanstiegsniveaus und Initial-Bestandsgrößen durchgeführt. Hieraus ergibt sich eine multivariate “Karte” des Risikos nicht-nachhaltiger Befischung, wobei das Risiko wieder über die Ergebnisse, die unter unterschiedlichen SR-Szenarien generiert werden, berechnet wird. Wenngleich ein vollständig sicherer Befischungsgrad für keinen der Bestände bestimmt werden kann, zeigen die Existenz und die Charakteristika des Szenario-Subraums, der Ergebnisse mit  $< 50\%$  Risi-

ko umfasst – dieser wird in der vorliegenden Studie als SOS definiert – klar unterscheidbare Muster zwischen größeren geographischen Gebieten und unterschiedlichen Niveaus historischer Überfischung: Die historisch schon seit langem zusammengebrochenen westatlantischen Bestände zeigen keinen oder nur einen minimalen SOS. Die relativ gut erhaltenen nördlichen Bestände im Nordostatlantik reagieren dagegen stark auf den Befischungsgrad, und die südlicheren Bestände im Ostatlantik zeigen zusätzlich einen klaren negativen Klimaeffekt. Die Initial-Bestandsgröße hat in den Simulationen einen erheblichen Einfluss auf den maximalen Erwärmungsgrad, der eine gesunde Bestandsgröße und eine nachhaltige Fischerei (mit  $\leq 50$  % Risiko) ermöglicht. Dies zeigt, dass der Aufbau von Bestandreserven dazu beitragen könnte, zukünftige Klimaeffekte auf viele Bestände abzuschwächen.

Schließlich entwickelt die Dissertation ein heuristisches Optimierungs-Verfahren zum Aufzeigen nachhaltiger (Langzeit-) Befischungs-Pfade unter dynamischer Ozeanerwärmung für den momentan erschöpften Dorschbestand der westlichen Ostsee. Der Optimierungsalgorithmus beachtet dabei sowohl erhaltungs- als auch ertragsorientierte Ziele, wobei ersteres priorisiert wird. Die sich ergebenden Befischungs-Trajektorien forcieren einen raschen Wiederaufbau des Bestands auf ein nachhaltiges Niveau und führen danach, parallel zu einer zunehmenden Erwärmung der Ostsee, zu einer Erhaltung des Bestands auf nachhaltigem Niveau bei gleichzeitig kontinuierlicher Abnahme der Fänge. Die Einbeziehung von tiefer SR-Unsicherheit führt zu einer Befischung mit ähnlicher Dynamik aber auf einem deutlich reduzierten Niveau. Das Risiko einer Bestandsabnahme auf ein nicht-nachhaltiges Niveau wird dabei für mehrere Dekaden auf sehr geringem Niveau gehalten, steigt aber mit zunehmender Erwärmung an, was auf ein Schwinden der Handlungsmöglichkeiten des Fischereimanagements unter ungünstigen SR-Szenarien hindeutet. Das Risiko, selbst einen aus historischer Sicht geringen Zieelertrag zu verfehlen, ist dagegen dauerhaft vergleichsweise hoch. Die Einarbeitung der Befischungs-Optimierung zusammen mit Bestandsmonitoring als wiederkehrendes Verfahren in einen simulierten Managementverlauf, der unter einem wahren aber nicht vorhersagbaren Verlauf wechselnder SR-Szenarien stattfindet, führt zu hoher Bestandsgröße und Erträgen. Die deutliche Erfüllung beider Ziele zeigt, dass die Kombination der Entwicklung von unsicherheitssensitiven Langzeit-Managementplänen mit Bestandsmonitoring und kurzfristiger Entscheidungsflexibilität ein wertvoller Ansatz für das Fischereimanagement unter zukünftigem Klimawandel sein kann.

Die Dissertation zieht die Schlussfolgerung, dass das Management von Atlantischem Kabeljau auch unter zukünftigem Klimawandel bis zu einem gewissen Grad wahrscheinlich mög-

lich sein wird. Dabei wird das Erreichen zukünftiger Nachhaltigkeit stark von der / den eintretenden SR-Beziehungen, dem Niveau der Erwärmung, dem erreichten Niveau des Bestands-(Wieder)-Aufbaus und auch wahrscheinlich vom Grad der historischen Überfischung abhängen. Managementstrategien mit der höchsten Erfolgchance werden auf den raschen (Wieder-) Aufbau von Bestandsbiomasse setzen und werden die Befischungsintensität der realisierten Bestandsgröße und auf das Ziel, das Langzeit-Erhaltungs-Risiko unter einer großen Bandbreite möglicher SR-Beziehungen zu minimieren, hin anpassen.

# 1. General Introduction

## 1.1 Importance of and threats to living marine resources

Globally, living marine resources constitute a major component of human nutrition, especially protein and fatty acids, and fisheries, aside from the aquaculture business, are the primary contributor of making these resources available to humans (FAO, 2022). Demand for aquatic food follows an increasing trend and is expected to further increase until 2030 and beyond, at a rate of 3 % (average 1961-2022), approximately double of that of global population growth (FAO, 2022). While aquaculture is expected to grow strongly in order to support the increasing demand for marine food, fisheries remain an important baseline component for ensuring ready availability of fish and invertebrates for consumption (e.g. Thilsted et al., 2016), as well as providing feed resources for aquaculture (e.g. Boyd et al., 2022). In some lesser-developed / low-income areas of the world, especially island communities, nutrition of the populace is strongly dependent on the availability of seafood (e.g. Kawarazuka & Béné, 2010; Mills et al., 2011). In addition to their importance in providing nutrition, fisheries are also a major provider of employment especially in coastal communities; globally, 600 million people are estimated to make their livelihood directly or indirectly through fishing (FAO, 2022). Furthermore, fishing also has cultural relevance in societies historically built around fish capture, e.g. the Newfoundland cod fisheries (Rose, 2018a). In order to ensure the continued availability of marine resources, fish populations are routinely subjected to scientific assessments integrating catch data with population theory in order to estimate population size and fishing impact on population dynamics and to adjust fishing effort to sustainable levels (Cadima, 2003).

Yet despite the increasing demand for aquatic food and the efforts to understand and regulate fish dynamics, fisheries are confronted with a number of anthropogenic and natural threats: Sustainable fishing is on a decline, with only 64.6 % of all harvested populations being in safe and sustainable limits, compared to a proportion of 90 % in 1974 (FAO, 2022); of those populations inside safe limits, 57.3 % are harvested at maximum sustainable capacity, while only 7.2 % are considered under-fished (FAO, 2022). In addition to (historical) overfishing leading to depletion of populations, lack of knowledge about population ecology is also a contributing factor, with scientific assessments of 18 % of all populations being inconclusive and thus unable to detect potential overfishing (OECD, 2022). Another global threat to living marine resources is global warming caused by climate change, which in many instances is suspected to alter species' habitats and ecological environments (i.e. food webs) (e.g. O'Connor et al., 2009) to a degree that is incompatible with physiological or ecological requirements and can

cause reduced productivity and / or distributional shifts, though large uncertainties about the exact mechanisms and magnitude of effects remain (e.g. Brown et al., 2010; Perry et al., 2005; Brander, 2007). Global ecosystem models predict losses of marine animal biomass of up to, on average, 17 % by 2090-99, as well as major spatial redistribution of resources (Lotze et al., 2019; Tittensor et al., 2021). Lesser-developed countries in particular are expected to suffer from effects of warming (FAO, 2022; Allison et al., 2009), but effects are also becoming apparent and are expected in industrialized nations with well-developed assessment- and management procedures (e.g. Peck & Pinnegar, 2019; Bryndum-Buchholz et al., 2020).

## **1.2 Fishing history of Atlantic cod (*Gadus morhua* L.)**

A major fishery resource that has both suffered from overfishing historically (Rose 2018) and shows signs of sensitivity to climate change (e.g. Brander, 2010; Pershing et al., 2015) is Atlantic cod (*Gadus morhua* L.), a demersal teleost fish spread throughout the Atlantic Ocean in the northern hemisphere. Cod is a strongly-fished species of high commercial value to the European, American and Canadian fishing industries, with many coastal communities having been originally founded exclusively around the purpose of catching and processing cod (Rose et al., 2018). Cod has been fished for millennia (Enghoff et al., 2007), with Norway and in particular the Lofoten area being a particularly prominent and productive long-term historical fishing ground beginning in the 12<sup>th</sup> century (Barrett et al., 2008; Christensen & Nielsen, 1996). Another highly productive area were the Newfoundland waters, which were exploited since the 16<sup>th</sup> century (Lear & Parsons, 1993). The species has since then supported artisanal- (subsistence-) and trade fisheries, with fishing conducted with i.a. hand-lines, hook lines, gill-nets and eventually bottom-trawl nets (Rose et al., 2018). The advent of steam-powered engines at the end of the 19<sup>th</sup> century and further development of motorized engines in the early decades of the 20<sup>th</sup> century led to radical changes in the commercial fishing business: with the construction of freeze trawlers (i.e. trawl ships with capacity for instant freezing of caught fish onboard) and the availability of steam-powered winches (for lifting the trawl net) by the 1950s (e.g. Mansfield, 2010; Heidbrink, 2011), fishing effort and catches reached unprecedented heights (with peak catches of appx. 3.9 Mt in the early 1970s) (Björnsson et al., 2010). Cod thus became a readily-available commodity for the general populace even in areas far from the sea, as well as the catalyst of international conflict for fishing rights and the transformation of relatively primordial societies like that of Iceland to prospering modern nations (Kurlansky, 1997).



Ultimately, the massive increase of fishing effort on the cod populations ultimately proved to exceed their productivity (e.g. Walters & Maguire, 1996; Serchuk & Wigley, 1992), i.e. their capability of replacing removed biomass with reproductive output. For centuries, cod had been perceived to be a quasi-unlimited resource, with fishers usually not being able to make full use of the fish available to them due to limitations to gear and (man-) power (e.g. Huxley, 1883; Homans & Homans, 1858). The increase in effort resulting from the steam-trawl fishery initially resulted in higher catches (e.g. Lear, 1998), purportedly proving that technological limitations had hindered a more extensive utilization of the resource. After peaking in the 1960s to 1980s (depending on the population), however, cod catches decreased at equal levels of effort, and continued to decrease for many years (e.g. Nakken, 1994; Taggart et al., 1994; Hamilton et al., 2004). Catch declines were initially perceived as excessive removals of the accessible standing stock of adult cod rather than reproductive failure; recruitment overfishing (i.e. the reduction of reproductive biomass to levels that cannot produce sufficient offspring for maintaining population size at stable high levels [Hjort, 1914; FAO, 1995]) was not seriously considered to be an issue (Walters & Maguire, 1996). A particularly severe development occurred in the fisheries on cod populations off the eastern Canadian coast, especially in the Northern cod population of Newfoundland, where a multi-national fishery tapping the cod resource had quickly developed by the 1960s, and where, as a consequence of declining catches, the Canadian government extended the country's exclusive economic zone and thus effectively banned non-Canadian fishing vessels from access to the cod (Canada Department of the Environment, 1976). The initial reduction in fishing pressure did lead to a slight increase of catches; however, as was revealed from later stock assessment, population biomass was still severely depleted (Walters & Maguire, 1996). In 1992, the Northern cod, the northern-most and largest Canadian cod population, dropped to unprecedented low levels within a single year, and has not recovered since despite an immediate fishing moratorium (Emery, 1992; DFO, 2022).

Similar patterns of collapse or severe decline occurred in most other Canadian and U.S. cod populations (Lilly et al., 2008; Murawski, 2005). The eastern Atlantic cod populations also faced declines in the second half of the 20<sup>th</sup> century; however, they did not exhibit patterns of immediate collapse, rather continued declines (Lilly et al., 2008; see also fig. SI CII.9 / 1-2 and stock-assessment reports listed in tab. SI CII.10 / 1), which have nevertheless resulted in population sizes and catches that are only a small fraction of the levels observed in the mid-20th century. Some of these stocks eventually recovered to sustainable levels. A common pattern among several cod populations is recovery failure, i.e. the inability of fisheries man-

agement to return cod biomass to or above sustainable levels despite catch reductions or catch moratoria designed to minimize the percentage of population biomass harvested (Sguotti et al., 2019; Shelton et al., 2006). The lack of (short- to mid-term) effectiveness of catch moratoria is well known in the western Atlantic cod populations since decades, and is attributed to averse ecological and physical conditions that have a particularly severe effect at low population size: influx of particularly cold water (Lilly et al., 2013), as well as increased predation from grey seals (Swain & Sinclair, 2000; Perälä et al., 2022) are thought to limit population growth, as observed through the existence of positive density-dependent effects (Allee effects [Allee et al., 1949; Courchamp et al., 1999]) at low population size (Keith & Hutchings, 2012; Kuparinen et al., 2014). Compared to the western populations, unexpectedly low effectiveness of harvest control, especially with regard to rebuilding measures, is a more recent phenomenon in some of the eastern Atlantic mid-latitude populations (Möllmann et al., 2021; Blöcker et al., 2023a), with statistical evidence pointing to ocean warming resulting from climate change as a main driver, which, in unfavorable combinations with fishing pressure, appears to stabilize depleted cod populations at low levels of productivity (Sguotti et al., 2019).

### **1.3 Biology of cod**

Atlantic cod is a demersal predator species inhabiting the shelf seas of the North Atlantic (fig. CII.1); its geographical range extends from the Celtic Sea (appx. 50 °N) to the Barents Sea (appx. 83 °N) in the eastern Atlantic and from Cape Hatteras (appx. 35 °N) to Newfoundland (appx. 55 °N) in the western Atlantic. Additional populations are located in the northern mid-Atlantic close to Greenland (Cohen et al., 1990; Kaschner et al., 2019). They are found both relatively close to the coast (e.g. the Norwegian coastal population and the “Gulf” and “Banks” populations south to Newfoundland) and farther offshore (e.g. the Barents Sea population), as well as in semi-enclosed (e.g. the Baltic Sea populations) and relatively open seas. They tend to not occur beyond the shelf edge, however (Marteinsdóttir & Rose, 2018). Populations are typically referred to by the management designation of “stock”, which may not equal “true” single reproductive entities (a prime example is the Northern stock comprised of several reproductively distinct subunits [Smedbol & Wroblewski, 2002; Marteinsdóttir & Rose, 2018]). The number of cod stocks varies over time as stocks are divided or united based on improved knowledge or management requirements, but is currently about 27, with 15 occurring in the eastern Atlantic and around Greenland, and the remaining 12 in the western Atlantic. Habitat conditions faced by the different stocks are very variable in terms of temperature and salinity, with mean annual bottom temperatures ranging from 2 °C for the Northern

stock to 11 °C for the Celtic stock (Drinkwater, 2005), and salinity being markedly less than 30 locally in the Baltic Sea (Feistel et al., 2010) (with salinity of as low as 11 required for successful spawning [Westin & Nissling, 1991]), compared to the Atlantic average of 35-38 (Scarborough, 1930). Food-web complexity also differs between stock habitats, with e.g. the Baltic food web being relatively species-poor (Lindegren et al., 2009) and the Barents Sea food web including more species of marine mammals than most other areas (e.g. Wassmann et al., 2006).

Cod prefers depths of up to 600 m (Cohen et al., 1990) and usually resides in proximity to the sea bottom, preferably near structures like reefs (e.g. Tupper & Boutilier, 1995, Flávio et al., 2023) and, especially older ones, near ship wrecks (Lengkeek et al., 2013; Hislop et al., 2015), but occasionally moves off-shelf over open waters for feeding purposes (Ingvaldsen et al., 2017). Most stocks perform annual migrations between wintering grounds, which tend to be located in deeper and warmer water farther from the shore (e.g. Jean, 1964), and feeding- and spawning grounds, with the latter sometimes being located closer to the coast. A prominent example is the Barents Sea cod, which spawn near the Norwegian coast (Olsen et al., 2010). Spawning sites can also be located in more offshore locations, as in e.g. the western Atlantic stocks (e.g. Sundby, 2000). Special physical conditions may also inform spawning-area localization, as is the case in Baltic cod, where higher salinity, only found in deep basins far from the coast, is required for egg development (Kändler, 1944; Nissling & Vallin, 1996). The extent of migration differs between stocks, however, with some exhibiting stronger sedentary behavior (e.g. Jakobsen, 1987). Spawning habitat may sometimes differ from the usually preferred habitat, i.e. may be characterized by coarse soft ground instead of hard structures (e.g. González-Irusta & Wright, 2016). Spawning usually occurs in early spring; the fish aggregate in spawning schools and release pelagic eggs, which develop into planktonic larvae. The larval phase lasts about three months (Froese & Pauly, 2023); after settling, the early juvenile fish then inhabit relatively shallow vegetated areas (Borg et al., 1997). Cod are a rather cold-water-adapted species, but tolerate a relatively broad temperature range of appx. -1.5 to 19 °C (Righton et al., 2010). Temperatures above appx. 15 °C are sub-optimal for growth and are avoided, however (Petersen & Steffensen, 2003; Björnsson et al., 2007; Freitas et al., 2015). Acceptable spawning temperature appears to be limited to 1 to 8 °C (Righton et al., 2010). Temperature limits may also depend on local adaptation in the different stocks (Petersen & Steffensen, 2003).

Cod is mostly a generalist predator; the food spectrum of post-larval specimen includes fish, in particular small pelagics but also other cod, and invertebrates like mollusks and crustaceans (e.g. Daan, 1973; Funk et al., 2021; Bogstad et al., 1994). Invertebrates tend to dominate the diet of younger specimen and fish that of both older ones and that of juveniles prior to the onset of demersal behavior (e.g. Daan, 1973; Lomond et al., 1998). Larval cod prey primarily on larger pelagic copepods and their pre-adult stages, and pre-settlement juveniles on euphausiids and mysids (Heath & Lough, 2007). Specific abundant prey species tend to dominate the diet in some areas and / or years, e.g. Atlantic herring (*Clupea harengus*), capelin (*Mallotus villosus*) and cod in the for adult cod in the Barents Sea (Holt et al., 2019), squid (*Loligo forbesi*) on the Faroe Bank (Magnussen, 2011) and common shore crab (*Carcinus maenas*) in shallow areas of the Baltic Sea (Funk et al., 2020), but this is likely an expression of opportunistic resource utilization rather than of specialization, as cod accepts a very wide range of food (Rose, 2018a). Nevertheless, variability in abundance of a major food source is likely to affect cod population dynamics (Denechaud et al., 2020). Copepods of the genera *Calanus* and *Pseudocalanus* are a major prey items of larval cod (Skreslet, 1989; Beaugrand & Kirby, 2010; Heath & Lough, 2007), but other taxa (e.g. *Acartia*, *Temora*, *Oithona*) are also consumed (Jacobsen et al., 2020). Cod has few natural predators; these include primarily marine mammals like grey seal (*Halichoerus grypus*) (e.g. Lundström et al., 2010; Prime & Hammond, 1990) and minke whale (*Balaenoptera* spp.) (e.g. Flaaten & Stollery, 1996) and seabirds like cormorant (Phalacrocoracidae) (Barrett et al., 1990). Young cod often fall prey to cannibalistic behavior of older co-specimen (e.g. Folkvord, 1991). Cod eggs and larvae are a common food for pelagic forage fish like clupeoids (Sparholt, 1994); reduced predation pressure on larval Southern Gulf of St. Lawrence cod is even suspected to have enabled temporary stock recovery in the 1970s (Swain & Sinclair, 2000).

Variation in natural predation on adult cod does not normally affect stock dynamics in such a noticeable way as fishing when stock size is at healthy levels, but has been suspected to limit the recovery of depleted stocks in some cases (Collie et al., 2013): predation by grey seals on adult cod is suspected to contribute to a lack of rebuilding success in several western-Atlantic stocks, e.g. in the West-of-Scotland stock (Cook & Trijoulet, 2016); relatively strong evidence exists for the Southern Gulf of St. Lawrence cod, where natural aggregation behavior is assumed to exacerbate this effect (Neuenhoff et al., 2019; Swain et al., 2019). Depensation caused by seal predation does not appear to be an universal issue, however, as it is regarded to be of low importance for the also depleted Northern, Gulf of Maine and Georges Bank stocks (DFO, 2019; Northeast Fisheries Science Center, 2013). Decreased abundance of adult cod

can lead to an increase in pelagic forage fish through a loss of so-called natural “cultivation” of these species, increasing predation on eggs and larvae and reinforcing cod decline (e.g. Walters & Kitchell, 2001). This negative effect has been suggested to occur in e.g. Southern Gulf of St Lawrence (Swain & Sinclair, 2000), and, as a general driver of population dynamics, in the North Sea (Fauchald, 2010) and Baltic cod (Köster & Möllmann, 2000). Predation is, however, not the only potential cause affecting cod stock recovery: alternative, additional or also interactive effects to predation include e.g. ocean warming (Winter et al., 2019), changes to prey size distribution (van Leeuwen et al., 2008) and delayed fisheries management adaptation (Pershing et al., 2015; Möllmann et al., 2021).

#### **1.4 Climate effects on cod**

Ocean warming, as caused by climate change, affects adult and juvenile fish, including cod, in a variety of direct and indirect ways (Pörtner & Peck, 2010), including behavior alterations (diel vertical migration [Freitas et al., 2015]) condition and mortality especially of embryos and spawners (Dahlke et al., 2020), faster growth and reduced maximum size (Ipkewe et al., 2020), and reduced habitat (Huserbråten et al., 2019). In cod, the recruitment of juvenile fish to the fished component of the stock appears to be positively related to temperature in stocks inhabiting waters closer in temperature to the lower end of the acceptable range, while the relationship is negative in stocks inhabiting waters at the higher end of habitat-temperature range (Planque & Frédou, 1999; Drinkwater, 2005). Average stock age may modify the temperature-recruitment relationship, though, with an apparent increased climate sensitivity at lower stock age (Ottersen & Holt, 2022). The changes in pre-recruit mortality with temperature may have multiple causes, as early pre-recruit life history in general is subject to a large number of drivers (Ottersen et al., 2014). These include changes in food availability for early larvae (Hjort, 1914), which may be the result of altered phenology of prey species related to warming waters (Durant et al., 2007), as well as increasing physiological stress forcing increased allocation of resources for homeostasis as opposed to growth (especially at above-optimal temperatures and / or unsuitable food abundance) (e.g. Arula et al., 2015; Dodson et al., 2018; Pankhurst & Munday, 2011) and thus prolonging the period of high vulnerability to predation (Cushing, 1975; Robert et al., 2023). Warming also affects the adult- and egg life stages of cod, with increased and unavoidable physiological stress decreasing cod condition (Orio et al., 2022; Receveur et al., 2022), an effect suspected to also impact reproductive output negatively e.g. through reduced gametogenesis (Dahlke et al., 2022). Reduced egg quality may impact egg survival, e.g. in the Baltic Sea, where lower-quality eggs from stressed

spawners may lack sufficient buoyancy to keep them from sinking into denser but oxygen-depleted waters (Nissling & Vallin, 1996; Hinrichsen et al., 2016). In addition to warming, less direct effects of climate change like altered predator-prey interaction (Köster et al., 2005) and ocean acidification can be detrimental to survival of early life stages (Frommel et al., 2011), the latter i.a. through tissue damage, particularly in combination with other detrimental factors like warming and reduced food availability (Cominassi et al., 2020).

Climate change is not only expected to yield negative outcomes for cod: ocean warming has the potential to improve habitat conditions for the standing stock of adult cod especially in colder areas like the Barents Sea, where temperature increase is expected to lead to an extension of feeding habitat (Kjesbu et al., 2014) (experimental work indicates that cod in the wild are food-limited [Dutil and Brander 2003]) and an increase in individual growth rate and reproductive output, reducing predation mortality and density-dependent limitations of population growth and thus potentially allowing for larger fisheries yields (Holt & Jørgensen, 2014). However, increased growth through improved physiological performance may be offset by negative climate effects on prey abundance particularly in lower-latitude stocks (Rogers et al., 2011) and (future) loss of spawning-habitat even in higher-latitude stocks (Dahlke et al., 2018). Cod is expected to increasingly occupy other more northward areas as well, e.g. the northern Greenland waters and waters north of Newfoundland; migration patterns are expected to be affected as well, especially by retreating sea ice extent (Drinkwater, 2005). Northward shifts of spawning grounds in a likely effect of warming (Sundby & Nakken, 2008). Also of importance are interacting and multi-faceted effects of ocean warming and interaction with biological and anthropogenic drivers, as observed in the Northern cod, where a relatively recently commenced rebuilding is attributed to warming having both a positive effect on the cod and the abundance of its primary prey species, capelin, as well as to minimal fishing pressure (Rose & Rowe, 2015).

### **1.5 Fisheries management and stock assessment**

Harvesting of extensively fished fish stocks underlies politically-imposed limitations that aim at maintaining a stock at levels generating maximum productivity. A fundamental assumption about the dynamics of fish stocks is the existence of such a level that will lead to maximum stock reproduction under equilibrium ecosystem- and environmental conditions. The general relationship between stock size and its productivity is dome-shaped, meaning that an intermediate stock size (reduced from maximum abundance by harvesting) can generate maximum stock productivity (Gordon, 1954; Schaefer, 1991). Lower stock levels lack the reproductive

resources necessary to generate large levels of offspring; compensatory effects like increased difficulty of finding spawning mates are assumed to be an additional constraint (Allee et al., 1949; Courchamp et al., 1999). Productivity at larger stock levels is limited by constraints put by ecological carrying capacity (Beverton & Holt, 1957) and sometimes negative density-dependent effects like cannibalism (e.g. Pereira et al., 2017; Bogstad et al., 1994). The target of current fisheries legislation in Europe, the United States of America and Canada is to either rebuild or maintain stocks maximum productive levels (depending on their status) (European Union, 2013; U.S. Department of Commerce, 2007; Government of Canada, 2019; NAFO, 2017), as maximum productivity enables maximum catches that are being replaced by annual stock growth; this principle is known as managing for Maximum Sustainable Yield (MSY) (Chapman, 1949; Maunder, 2008). (The Canadian legislation does not explicitly require rebuilding to MSY levels, however [J. Hutchings in Cheney, 2019]). The principle of management-by-MSY has been criticized for lack of consideration of the fact that maximum productivity changes in a non-equilibrium environment (Travers-Trolet et al., 2020) - among other reasons including the impossibility of achieving MSY-level catches in a complex ecosystem (Larkin, 1977; Steele et al., 2011). However the adoption of more advanced management policies that integrate environment dynamics is often still constrained by ambiguity on how to deal with uncertainties in the response of stocks to environmental change (Skern-Mauritzen et al., 2016), as well as i.a. structural-administrative constraints to management implementation (Holsman et al., 2019).

Successful fisheries management requires proper statistical estimation of stock size. Fisheries management relies heavily on stock assessments, which is essentially the fitting of a population model including a catch process on commercial catch data and systematized survey catch data (i.e. accounting for homogeneous spatial coverage) from research surveys (Gunderson, 1993). Catch samples are subjected to age determination, i.e. the “reading” of age rings deposited in the otoliths (calcareous deposits in the inner ear of fishes), in order to estimate the age composition of the catch and the stock. They are also analyzed for individual weight and spawning maturity (e.g. National Research Council, 1998). Natural mortality, the instantaneous rate of natural population decrease primarily through predation, can be inferred from e.g. multi-species stomach analyses, tagging-recapture studies, with the estimation performed e.g. as part of fitting the assessment model (Maunder et al., 2023), but is often treated to be constant over ages and / or years due to a lack of data (Punt et al., 2021). The population model, or assessment model, yields time series of estimated age-specific abundances of fish in the stock, as well as of its spawning biomass (SSB) (the product of abundance, individual age-

specific weight and maturity rate, summed over all age classes) and of the age-specific fishing mortality that the stock is subjected to. Fishing mortality is the instantaneous rate of decrease of a cohort of fish caused by fisheries removals, and is thus a metric that expresses catch as a function of stock (that is, the same amount of catch can result in different fishing mortalities for stocks of different sizes). Initial cohort size (i.e., recruitment) and fishing mortalities are parameters in the population model are fitted in order to achieve a close match between predicted and observed catches (e.g. Cadima, 2003), and thus depend on accurate catch reporting and validity of model assumptions regarding biological stock characteristics (Schnute & Richards, 2001; Punt, 2023).

Management success is defined by both SSB and fishing mortality (the latter is usually averaged over the most strongly selected age classes); SSB should be above the precautionary reference point (typically termed  $B_{PA}$ ,  $B_{upper}$  or “upper stock reference” depending on assessment agency; hereafter termed “ $B_P$ ”) and fishing mortality should be at or below the level yielding MSY in the long term, termed  $F_{MSY}$  (ICES, 2021a, DFO, 2006; US Department of Commerce, 2007; NAFO, 2004; Rosenberg & Restrepo, 1996). A common consensus is that  $F_{MSY}$  should be treated as a limit rather than target, given that the MSY concept tends to be simplified and does not account for variability and uncertainty (Larkin, 1977; Mace, 2001). Fishing mortality is generally treated as a controllable variable that is achieved by constraining catch to an upper limit, the total allowable catch (TAC) (e.g. Beddington & Rettig, 1984). Attaining a desired fishing mortality can fail when the TAC decided by policy-makers exceeds scientific advice or catches exceed TAC (Da Rocha et al., 2012), or when the estimate of stock size turns out to have been over-estimated in retrospect, a result of assessment error often related to inadequate assumptions about or knowledge of the stock (e.g. Mohn, 1999). When SSB is below  $B_P$ , which indicates an increased risk of the stock further declining to levels that lead to reproductive failure (below the limit reference point), target-F is usually set to a level markedly lower than  $F_{MSY}$ . In ICES areas, this level is proportional to the ratio of SSB to  $B_P$  (ICES, 2021a). When SSB is below the limit reference, the fishery is often closed due to the imminent danger of reproductive failure of the stock (ICES, 2021a). In a small number cases, where effects of a distinct environmental driver on the stock are clearly understood, the annual magnitude of that driver also informs the formulation of target-F or catch limit (Bentley et al., 2021), though this principle has failed on occasion when effect direction changed from expectation informed by historic data (Free et al., 2022).



Management planning is usually conducted by projecting the stock into the future for a very limited number of years (often 1-2); the expected development of SSB over time under various candidate fishing-mortality scenarios is used to guide the advice on the target  $F$  (and resulting TAC) for the next year (the one following the year in which the assessment is conducted) (Cadima, 2003). Biological parameters (e.g. individual weight, maturity) are usually fixed to present values in such a projection (Cadima, 2003). Unlike with the retrospective assessment model, where annual recruitment is estimated deterministically, recruitment needs to be predicted within a forecast. It is usually assumed that recruitment strength is related to SSB in the previous year (or earlier, if recruitment age is  $> 1$ ), as the amount of offspring produced puts a baseline limit to the number of fish that can survive to recruitment age (Beverton & Holt, 1957). SSB-recruitment relationships are, however, often weak due to the multiplicity of factors that can affect survival from the egg stage to recruitment age (Subbey et al., 2014), prompting a frequent use of SSB-independent random sampling methods (e.g. random-walk techniques) for short-term projections (e.g. Van Beveren et al., 2021).

The general relationship between SSB and recruitment is usually represented by a saturation-like function, where recruitment initially increases linearly with SSB but levels off at higher levels of SSB, reflecting limitations set by the ecological carrying capacity of a given system (this carrying capacity can vary strongly between stocks of the same species [MacKenzie et al., 2003]); this functional relationship is known as the Beverton-Holt equation (Beverton & Holt, 1957). Alternatively, recruitment may decrease again at higher SSB due to negative density-dependent effects, e.g. cannibalism (e.g. Sparholt, 1994), which is common in Atlantic cod (e.g. Folkvord, 1997); this process is formulated in the Ricker equation (Ricker, 1954). Environmental drivers are, like density dependence, typically considered to act on an exponential scale (Ricker, 1975; Hilborn & Walters, 1992). SSB and recruitment data from the stock assessment may not fit the Ricker- or Beverton-Holt models well, and data- rather than mechanism-informed surrogates like catastrophe-theory-based cusp models, state-space reconstructions (Sguotti et al., 2020) and neural networks (Arregui et al., 2006) have been explored as alternatives to account especially for highly non-linear dynamics. Environmental factors are rarely incorporated especially in applied management due to the spuriousness of environment-recruitment relationships (Myers, 1998; Punt et al., 2014; Haltuch et al., 2019). The incorporation of environmental information into assessments of gadoid fishes in particular was found to be unfruitful (Basson, 1999), potentially a result of their relatively long pre-recruit phase (Haltuch et al., 2019). Nevertheless, environmental drivers, including climate-

related drivers, are strongly assumed to affect recruitment (e.g. Szuwalski et al., 2015, Plagányi et al., 2019).

Recruitment uncertainty in its basic form is usually considered as simple random – albeit partially large – deviations from a unique underlying functional relationship (Cadima, 2003). Recent developments in the dynamics of several commercially-fished stocks indicate, however, that recruitment uncertainty can also be interpreted as the existence of multiple recruitment *regimes*, where similar driver levels generate recruitment of strongly varying magnitudes depending on the regime (e.g. Britten et al., 2015; Szuwalski et al., 2019). Statistical analyses indicate that climate-related variables and other, more direct anthropogenic activities such as eutrophication act in conjunction to cause regime shifts (Rocha et al., 2015; Sguotti et al., 2019). In cod, temperature and fishing pressure appear to increase the likelihood of such switches between alternate regimes of the relationship between fishing pressure, environmental drivers and recruitment (Blöcker et al., 2023b). Each recruitment regime can be represented by a uniquely parameterized SR relationship (Szuwalski et al., 2019). Statistical evidence indicates that such a set of SR relationships or breakpoint-defined SR relationships are likely better descriptors of stock dynamics than a singular SR relationship both in stocks with high natural stock fluctuation (forage fish [Szuwalski et al., 2019]) and in stocks with fishing-triggered regime shifts (Blöcker et al., 2023a). Exact mechanisms behind regime shifts are often uncertain and / or case-specific (e.g. food-web perturbations by invasive species in the Black Sea [Daskalov et al., 2007]). Allee effects affecting population growth rate have been suggested as one possible partial mechanism in regime-like recruitment dynamics (Tirronen et al., 2022). A lack of comprehensive knowledge on clear and case-independent mechanisms describing regime shifts, however, makes the shifts difficult to anticipate or predict (Hastings & Wysham, 2010).

Stock assessments and short-term projections are conducted on an annual basis (Cadima, 2023), while an evaluation of assessment methodology and assumptions about stock biology and ecology are conducted every three to five years in so-called benchmark assessments (ICES, 2023a). Annual stock assessments can be rejected when quality checks, e.g. sensitivity tests, are not passed, especially when strong patterns of retrospective error (Mohn, 1999), which are indicative of a flawed perception of a stock (i.e., a flawed model configuration), become apparent (Punt et al., 2023). This event triggers an *inter*-benchmark assessment in stocks under ICES advice jurisdiction, wherein model assumptions, e.g. about natural mortalities, are critically checked (ICES, 2023a). Benchmark assessments are also an occasion for re-

calculating SSB- and F-related reference points (ICES, 2023a), as both are based on available assessment output data (Cadima, 2003), which are extended by additional assessment years. Stock assessments result in *advice* on TAC given by a scientific agency (ICES in Europe, DFO in Canada, NOAA in the U.S., NAFO on the western-Atlantic shelf), which is requested by national (governments of Canada and the U.S.) or multi-national agencies (i.a. European Union in conjunction with the governments of non-EU states). Advice based on fisheries biology is considered alongside social and technical aspects in the decision on the final TAC; where biologically-informed advice disagrees with e.g. socio-economic factors considered, final TAC may be higher than advised (Carpenter et al., 2015). After agreement, TAC is split into catch units that can be bought and traded by fishers, so-called Individual Transferable Quotas (ITQs) (Grafton, 1996).

## **1.6 Management Strategy Evaluation**

While stock assessment and advice guide imminent management action, long-term management aims are formulated in management strategies defined by harvest-control rules (HCRs), which are effectively different principles of exploiting a healthy, non-endangered stock (Punt, 2010). HCRs can include removal of a fixed (historical) catch, application of a fixed harvest rate or maintaining a fixed stock biomass (the latter two leading to variable catches) (e.g. Deroba & Bence, 2008). Common evaluation criteria for assessing a HCR include the effectiveness of stock conservation (magnitude of stock biomass), magnitude and temporal stability of catch, and trade-offs between these (e.g. Smith, 1994). HCRs are typically simulation-tested in the modeling exercise of Management Strategy Evaluation (MSE), a relatively novel framework that seeks to guide fisheries management in a more holistic, perspective-oriented way than stock assessments that only do short-term projections for guiding imminent management action (Smith, 1993; Smith et al., 1999; Punt et al., 2016). The aim of MSE is to critically assess the overall implications of implementing a specific HCR over time, in order to evaluate a candidate management strategy. To this end, MSE sets up a number of operating models that represent plausible “ground truths” of stock dynamics. Projections are performed with these models, and an assessment model is used to estimate the “true” dynamics (using output from the operating models that has been altered with random error), and simulated TACs are set based on the HCR and (possibly) assessment-model output (e.g. Sainsbury et al., 2000). MSE is thus used to investigate both the skill of stock assessment to identify the true stock dynamics, and the effectiveness of harvest-control rules to maintain the stock at sustainable levels. Operating models differ in their assumptions about ecological processes, e.g. re-

recruitment, and the selection of operating models corresponding to these scenarios usually follows expert judgment on scenario plausibility. (Punt et al., 2016). Selection and weighting of system scenarios is a primary constraint to the implementation of MSE in practice (Punt, 2017). However, it has been recognized that reporting of even low-probability scenarios is important in stakeholder interaction when strategy performance deteriorates considerably under these scenarios (Holland, 2010; Rademeyer et al., 2017).

Long-term stock projections are limited in predictive precision by fundamental uncertainty about the recruitment process and in particular about stock response to climate change and the stability of environmental effects (Subbey et al., 2014; Myers, 1998; Szuwalski & Hollowed, 2016). Efforts have been made to design management strategies that are reactive to non-linear stock behavior, i.e. to switches between productivity regimes (phases of higher or lower recruitment), including MSE simulations with assessment models accounting for environmental effects (King et al., 2014; Szuwalski & Punt, 2013). However, these have generally shown little improvement over classical, non-environmentally-conscious MSE, due to the difficulty of recognizing the onset of novel recruitment regimes precisely from simulated data. This difficulty is primarily caused by large within-regime recruitment variability, which hinders the exact recognition of regime onset, as well as the often short time series of recruitment data linked to a particular regime, which limits the fitting of a regime-specific SR relationship and thus productivity estimation (Szuwalski & Punt, 2013). Reactive HCRs that scale exploitation with stock depletion with the aim of maintaining healthy SSB may instead account for limited knowledge, but are reliant on accurate estimates of stock size (Carruthers et al., 2014) and can probably not prevent beginning depletion in the first place. In the absence of models that can reliably predict regime shifts and / or (non-linear) stock response to environmental drivers, it has been suggested to aim for robustness to uncertainties instead in HCR design by limiting catches and regularly check for the emergence of reliable environmental indicators (Skern-Mauritzen et al., 2016). Resulting stock “buffers” are intended to reduce the risk of overfishing in face of uncertainty, i.e. when stock response to climate change is more severe than expected; however, they do incur the risk of foregone yield (Lauck et al., 1998; Free et al., 2022).

### **1.7 Decision-Making under Deep Uncertainty**

The problematic of model projections of limited skill has become apparent especially in the treatment of uncertainties by decision-makers: the linkage between prediction and decision-making can lead to flawed decisions, as potentially detrimental consequences under events

that have a low probability but are not impossible according to a model (of limited skill) remain un-assessed and / or deliberately ignored by policy-makers (Pielke et al., 2000). Similarly, policy-makers might react with delaying action or inaction in anticipation of “better” projections and lack of knowledge on how to deal with model uncertainty, respectively (Lemos & Bood, 2010). An emerging approach termed Decision-Making under Deep Uncertainty (DMDU) therefore suggests to focus research more on the decision-making aspect rather than on the development of universal models with high predictive accuracy and precision (Marchau et al., 2019a), especially when the latter tends to increase complexity and requirements for model development and thus postpones availability of finalized model projections (Pielke et al., 2000). Deep uncertainties are a class of uncertainty characterized by difficult- or impossible-to-quantify scenario probabilities, which are common in systems of high stochasticity and limited mechanistic knowledge (Walker et al., 2013), such as in (harvested) complex ecosystems (Hadjimichael et al., 2019). Deep uncertainties are thus distinguished from so-called “shallow” uncertainties characterized by narrow probability distributions and general low ambiguity in overall trends (Marchau et al., 2019a). Deep uncertainties are recognized to exist and pose a major challenge in the management of ecosystems, and an “a-priori” assessment of policies under multiple scenarios and policy flexibility are suggested as a potential resolve to delayed management action resulting from after-the-fact recognition of policy failure (Schindler & Hilborn, 2015; Hilborn & Peterman, 1995). DMDU proposes to evaluate multiple management strategies for performance under multiple possible (model-based) system descriptions or to evaluate the potential for adopting or altering strategies under uncertain and / or temporally changing conditions (e.g. Kwakkel et al., 2016a).

DMDU research has yielded a set of procedures for the assessment and refinement of management strategies under (deeply) uncertain model projections, including Dynamic Adaptive Policy Pathways (DAPP) (Haasnoot et al., 2013) and Robust Decision-Making (RDM) (Lempert et al., 2003; Lempert et al., 2013; Lempert et al., 2019), with the intention of improving the utilization of models by policy-makers and other stakeholders. DAPP seeks to define and evaluate pathways of management decisions, where external drivers trigger the adoption of a new management strategy once the previous strategy fails to achieve management targets (Haasnoot et al., 2019). RDM, on the other hand, seeks to stress-test management strategies for their robustness against a wide range of (temporally constant) scenarios (a procedure termed “exploratory modeling” [Bankes, 1993]) and investigate strengths and weaknesses of these strategies (Lempert, 2019). No switching between strategies over time is tested here, as strategy robustness to changing conditions is also investigated (Kwakkel et al., 2016b). Data-

mining algorithms and visualization tools are used to analyze management outcomes, e.g. to identify primary drivers or to determine the properties of successful and unsuccessful strategies (or combinations of strategies and uncertain scenarios) (e.g. Kwakkel, 2017). In applied usage of RDM, these tools are utilized to isolate a successful, i.e. robust-to-uncertainty, management strategy, or to iteratively redefine the analysis by focusing on identified critical scenarios and eventually identify limitations to strategy adaptation (e.g. Groves et al., 2019; Vaghefi et al., 2021). RDM does not constrain scenario selection via plausibility assessment or weighs results according to probabilities (Lempert et al., 2013), as according to the DMDU principle, the existence of an irreducible deep uncertainty should favor an “assumption-consequence” analysis of policies over plausibility analyses (Bankes, 1993).

As of today, the DMDU approaches are both used in practical applications and in theoretical experiments (Stanton & Roelich, 2021). Existing applications typically aim for improving uncertainty identification, management advice and stakeholder interaction: a prominent implementation is that for planning flooding management under climate-change-induced sea-level rise or heavy rainfall (e.g. Webber & Samaras, 2022; Babovic et al., 2018). For example a dynamic-adaptation approach (close to DAPP) was incorporated to design monitoring- and communication schemes for flood-protection planning in the Netherlands (Bloemen et al., 2019). RDM is starting to being used experimentally for policy planning related to water trade in the Colorado River Basin, given uncertainties about future hydrology and water demand (Smith et al., 2022). Other applications of DMDU methodologies include i.a. economic management of ski resorts under climate change (implementation of DAPP and RDM [Vaghefi et al., 2021]), planning for traffic infrastructure under uncertainties related e.g. to future costs and demographics (Song et al., 2017) and planning for electric infrastructure under uncertainties related to climate change and associated extreme events and consumer behavior (Brockway et al., 2022). Within the field of fisheries management, implementation of DMDU approaches has been suggested (Hadjimichael et al., 2020; Wainger et al., 2021), but especially RDM has, to the author’s knowledge, so far not been implemented for management evaluation. A common challenge encountered in implementing DMDU approaches is the requirement of relatively large computational resources, forcing the adoption of simplified models (Webber & Samaras, 2021), while a common limitation to the practical implementation of DMDU appears to be a limited consideration of decision context (i.e. organizational requirements, individual preferences) by DMDU analysts (Stanton & Roelich, 2021). Nevertheless, while a concrete “field implementation” of DMDU can be challenging, the bridging of domains of researchers and politicians achieved by DMDU-based studies can already generate

an increased sensitization for decision-making-related research communication and for uncertainty consideration in making political decisions (*sensu* Marchau et al., 2019b).

## 1.8 Safe Operating Space

While DMDU and particularly RDM address the impact of model uncertainty and knowledge gaps in policy-making by stress-testing strategy candidates against every conceivable scenario, a concept technically similar in style is frequently employed to investigate system response to management under different intensities of (a) natural driver(s): the so-called Safe Operating Space (SOS) for ecosystems (Scheffer et al., 2015). Given a mapping of the response of a component-of-interest of a natural system, e.g. an ecosystem, to two or more interacting drivers, the SOS is that region in the mapping where that objective component is in a desirable state. The driver variables are usually a set of natural variables, often related to climate change, e.g. temperature, and anthropogenic activity, e.g. water extraction from a lake (Green et al., 2017) or fishing (e.g. Carpenter et al., 2017), and the response variable is often a metric describing the conservation status of the objective component, e.g. ecosystem community composition (Green et al., 2017). The intensity range of the natural driver usually reflects the observed or anticipated range under a future scenario; the similarity to RDM lies in the “testing” of a large range of policies under a large range of possible magnitudes of the natural driver(s). The SOS concept is founded in the theoretical framework of “planetary boundaries” that established thresholds in stressor variables on the Earth System that, when crossed, would likely lead to irreversible alterations of its functioning (Rockström et al., 2009). The SOS concept translates that framework for localized, applied management questions, and the SOS boundary is often understood as the set of multivariate conditions where a natural system rapidly changes from a desirable into an undesirable state (Scheffer et al., 2015; Steffen et al., 2015). The SOS is thus intended as an analytical tool for management evaluation and -information, as it enables to distinguish relatively easily between well- and poorly-performing policies given a distinct natural state (e.g. Carpenter et al., 2015). The requirement for describing a driver-response mapping and the SOS (possibly) contained therein is thus a set of observations or model predictions for every combination of driver variables.

The SOS concept is relatively novel to environmental management; example implementations include wetland management (response of wetland ecosystems to water extraction and nutrient loading, with the SOS characterized by unaltered community composition of wetland fauna and flora) (Green et al., 2017), the identification of western Mediterranean fishing areas vulnerable to combined fishing-, biogeochemical- and climate effects (where the SOS is char-

acterized by low cumulative impacts) (Ramírez et al., 2021), identification of thresholds to anthropogenic impacts on coral reefs (where the SOS is characterized by healthy corals dominating the reef) (Norström et al., 2016) and management of inland fisheries (with stock biomass or catch as objective) (Carpenter et al., 2017; Hansen et al., 2019; Ofir et al., 2022). SOS designs differ relatively notably from case to case, with the number of driver variables ranging from the typical two to up to four (Carpenter et al., 2017), and with SOS definition based both on observed data (i.e. a purely statistical analysis) (Ramírez et al., 2021) or model simulations (Ofir et al., 2022). Constraints to defining a SOS and managing a system to remain within the SOS noted include relatively high monitoring effort on the study system, requirement of sufficient data and / or process understanding and requirement for flexible and quick-acting structures for policy design and -enforcement among multiple stakeholders (Carpenter et al., 2017; Green et al., 2017).

## **1.9 Motivation and outline of the thesis**

As described above, the fisheries on Atlantic cod face a highly uncertain future due to the strong stochasticity in the relationship between stock biomass, environmental drivers and recruitment, i.e. the primary source of productivity of a fish stock. The overall objective of this dissertation is thus to assess the potential for sustainable exploitation of Atlantic cod (*Gadus morhua* L.) under future climate change, i.e. in the time-frame from the present until the end of the century and considering the climate scenarios presented by the Intergovernmental Panel on Climate Change (IPCC). To this end, numerical population models coupled with climate-sensitive stock-recruitment functions are utilized to project stock response to fishing and climate change in a manner similar to that used in Management Strategy Evaluation (MSE). The deep uncertainty inherent in the relationship between spawning-stock biomass, environmental drivers and recruitment and the limitations it poses for long-term management planning, is explicitly addressed by incorporating multi-model approaches based in part on the Robust-Decision-Making (RDM) framework, in particular various risk-assessment methodologies.

In **Chapter I**, my co-authors and I expand on the problematic of the uncertain SR relationship for making reliable stock projections, utilizing the North Sea cod stock as a case study. We implemented the exploratory-modeling approach from the RDM framework and tested a large range of management policies against a large range of stochastically sampled SR relationships under two climate scenarios using a numerical population model (with a climate-sensitive SR function predicting recruitment) and a coupled economic model projecting fisheries profit. We investigated the impact of deep uncertainty and the drivers of model outcomes by em-



ploying the techniques of scenario discovery (to investigate the existence and properties of sustainable and uncertainty-proof policies) and feature scoring (to identify main drivers of sustainability). Finally, we performed a risk assessment to evaluate the potential of sustainability failure of each policy, and compared these “sustainability risks” against risk of missing target profit to check for potential trade-offs between stock conservation and economic gain.

In **Chapter II**, my co-authors and I expand on the RDM-informed risk assessment from Chapter I by conceptualizing a risk-based safe operating space (SOS), with harvesting, sea-surface temperature (SST) and initial stock biomass as driver variables, and with the risk of SSB, calculated over simulations conducted with a variety of SR relationships, being below the precautionary reference level as response variable, with risk being equal to or lower than a target level as the objective defining the SOS. We conducted “open-end” model simulations under every combination of driver values from specific pre-defined ranges, and so generated a risk map over drivers for each of 19 cod stocks (covering the full range of geographic distribution), as a basis for determining the SOS. We investigated the relationship between SOS size and target-risk level, as well as the existence and extent of the SOS at 50 % risk level and its direction with respect to SST (indicating the SST response of the stocks) for each stock and compared the stocks with respect to geographic location and historic stock development. We also investigated the catch potential within the SOS with respect to SST and initial biomass in order to determine the degree of climate mitigation possible by aiming for higher stock-conservation aims.

In **Chapter III**, my co-authors and I combine the DMDU approach with the mathematical optimization of a harvesting time series under projected ocean warming. We optimized for maintaining stock biomass in biologically safe levels and for attaining target catch, with priority for the former objective. We optimized both under a single stock-recruitment relationship (i.e., no uncertainty) and under a multitude of possible SR relationships (i.e., conditions of deep uncertainty) and investigated the impact of increasing warming and the effect of considering deep uncertainty on optimized fishing effort and on the chance for sustainable management over time. Further we employed the optimization approach within a simulated management trajectory to investigate the potential of combining uncertainty-sensitive optimization with regular stock monitoring for generating viable SSB and catches.

The work is concluded by a general discussion consolidating the insights obtained from all three chapters and addressing the overall question of the manageability of Atlantic cod under future climate change.

## 2. Chapter I: Robust fisheries management strategies under deep uncertainty

Jan Conradt<sup>1\*</sup>, Steffen Funk<sup>1</sup>, Camilla Sguotti<sup>1,2</sup>, Rudi Voss<sup>3,4</sup>, Thorsten Blenckner<sup>5</sup>, Christian Möllmann<sup>1</sup>

<sup>1</sup>Institute of Marine Ecosystem and Fishery Science, Universität Hamburg, Hamburg, Germany

<sup>2</sup>Department of Biology, University of Padova, Via Bassi, Padova, Italy.

<sup>3</sup>German Centre for Integrative Biodiversity Research (iDiv), Leipzig, Germany

<sup>4</sup>Center for Ocean and Society (CeOS), Christian-Albrechts-University Kiel, Kiel, Germany.

<sup>5</sup>Stockholm Resilience Centre, Stockholm University, Stockholm, Sweden

\*Principal author

### 2.1 Abstract

Fisheries worldwide face uncertain futures as climate change manifests in environmental effects of hitherto unseen strengths. Developing robust management strategies requires reliable projections of stock response to climate change under different exploitation levels. Unfortunately, model-based management strategy evaluation is severely limited by large uncertainties in the recruitment process, as the required stock-recruitment relationship is usually not well represented by data. An alternative is to shift focus to improving the decision-making process, as postulated by the Decision Making under Deep Uncertainty (DMDU) framework. Robust Decision Making (RDM), a key DMDU concept, aims at identifying management decisions that are robust to a vast range of scenarios and uncertainties. Here we employ RDM to investigate the capability of North Sea cod to support a sustainable and economically viable fishery under future climate change. We projected the stock under 40000 combinations of exploitation levels, emission scenarios and stock-recruitment parameterizations and found that model uncertainties and exploitation have similar importance on model outcomes. Our study revealed that no management strategy exists that is fully robust to the uncertainty in relation to model parameterization and future climate change. We instead propose a risk assessment that accounts for the trade-offs between stock conservation and -profitability under deep uncertainty.

**Key words:** North Sea cod, deep uncertainty, long-term projections, climate change, robust decision-making, management strategy evaluation

## 2.2 Introduction

Fisheries worldwide face uncertain futures as climate change manifests in environmental effects of hitherto unseen strengths (Lotze et al., 2019; Tittensor et al., 2021). Developing climate-resilient management strategies requires reliable projections of how fish stocks respond to the effects of climate change under different degrees of exploitation. Model-based projections of marine social-ecological systems including fisheries are however notoriously impeded by uncertainty about key ecological processes (Hill et al., 2007; Payne et al., 2016; Szuwalski & Hollowed, 2016). Such uncertainty often arises from limitations in the understanding of their intricate mechanisms and their relationships to physical variables like temperature. Resulting simplified models reflect a general consensus about the most basic mechanisms, e.g. models describing larval dispersal contain well-known hydrodynamic processes but not poorly-understood effects of larval behaviour (e.g. Pineda et al., 2009). In fisheries science, a major challenge is the prediction of the strength of the incoming year-class as a basis for setting future fishing opportunities for the industry (Haltuch et al., 2019; Collie et al., 2021). Because this “recruitment” process is the result of a multitude of complex biological processes, e.g. growth-rate variability (e.g. Houde, 1987; Lomartire et al., 2021) and physical processes, e.g. larval drift (e.g. Nilssen et al., 1994; Macura et al., 2019; Tiedemann et al., 2021), prediction of the number of incoming offspring is usually based on the assumption that the size of the mature population, the spawning stock biomass (SSB), is the main predictor (Myers & Barrowman, 1996). The nature of mechanisms that go beyond this most basic assumption, such as the importance of environmental variability or the role of feedback effects of recruitment on SSB (Szuwalski et al., 2019), are subject to debate (e.g. Basson, 1999; Haltuch et al., 2019). Hence, lacking ecological understanding and limited data quality and quantity cause the existence of multiple interpretations about the responsible factors and the functional forms of these “stock-recruitment” (SR) relationships.

The inability to agree on the mechanisms behind critical processes in a dynamic system is a key characteristic of the theoretical concept of “Deep Uncertainty” (Walker et al., 2013). In the decision-making literature, Deep Uncertainty (DU) is considered to be the strongest level of uncertainty (e.g. Courtney, 2001; Walker et al., 2003). DU is characterized by situations in which experts are unable to find intellectual consensus on the mechanisms behind system processes, where a quantification of uncertainty (e.g. in the form of probability distributions) is not possible, or where unpredictable events are known to occur (Marchau et al., 2019). With respect to forecasting this means that the number of scenarios to be considered would be large

and not necessarily limited to a few discrete instances. In contrast to DU, lower levels of uncertainty are characterized by either the possibility to predict probabilistically (i.e. based on probability density or on different levels of plausibility) or by the possibility to formulate a low number of discrete, equally plausible futures (Marchau et al., 2019).

DU is increasingly considered in projections of management systems expected to become severely affected by climate change, e.g. in water management (Bloemen et al., 2019) and ski resorts (Vaghefi et al., 2021). However, modeling of ecological systems and population modeling tends to ignore the existence of this strong uncertainty level. For example, Management Strategy Evaluation (MSE), an extended version of modeling fisheries systems under various candidate management strategies, usually performs projections under several scenarios that are assigned a plausibility rank. This rank is based on expert knowledge, and the scenario outcomes are weighted based on plausibility in order to assess the vulnerability of the management strategy candidates (Punt et al., 2016). Within MSE, but also in stock projections in general, recruitment of fish stocks is often projected via statistical parameter estimates of the SR model to which residuals from the observations are added randomly (e.g. Blamey et al., 2021). The usage of the mean SR model parameter estimates often assumes that recruitment uncertainty can be characterized by probability. Such an approach can be considered as an example of an “expected-utility framework”, characterizing decision-making approaches where scenarios are assigned subjective probabilities (Lempert, 2019)

Yet there are clear indications that working with plausibilities and probabilities have limitations in applied modeling, because it is often difficult to find consensus on the plausibility of a certain scenario (Punt et al.; 2016). Consequently, fish stock dynamics are likely subject to higher levels of uncertainty than currently recognized. Furthermore, such uncertainty is not simply due to lacking knowledge, but of ambiguous nature that is symptomatic to DU problems, and may lead to poor decision-making caused by narrow-focused analyses (Lempert et al., 2004). Howell et al. (2013) recognized this problem, considered uncertainties in their population projections as “unquantifiable”, an attribute of DU, and proposed a wide range of scenarios to perform MSE with. Schindler & Hilborn (2015) characterized the ignorance of DU as a major concern in long-term planning of ecosystem management, including fisheries management, and advocated to widen the range of uncertainty considered and the development of strategies robust against it.

The science of dealing with such high-level uncertainties, formally known as “Decision-Making under Deep Uncertainty” (DMDU), has seen the development of a number of con-

cepts that address the difficulty in performing precise projections from a practical, management-based point-of-view (Marchau et al., 2019). The most popular of these is the exploration-based “Robust Decision Making” (RDM) used to analyze and stress-test candidate management strategies (Lempert et al., 2003; Lempert et al., 2013). Other DMDU approaches are Dynamic Adaptive Planning (Walker et al., 2001; Walker et al., 2019) and Dynamic Adaptive Policy Pathways (Haasnoot et al. 2013), which focus on specifying rules for decision adaptation over time or the prior formulation and evaluation of alternative decision routes.

Common to all DMDU approaches, but to RDM in particular, is the proposition to shift emphasis from improving model predictions to improving management decisions (Lempert, 2019). This proposition is based on the observation that improving predictions often involves increasing model complexity, which in turn increases the number of uncertain factors, and that better predictive capability does not necessarily result in better decision-making (Pielke et al. 2000). The aim of RDM is thus to increase an understanding about the consequences of management actions under a large spectrum of possible scenarios, and to help define a management strategy that achieves the desired outcomes under DU, i.e. is robust to a multitude of different but equally possible futures (Lempert & Popper 2005). To this end, RDM employs the generation of a large number of model projection runs for each candidate management strategy. Each run represents one uncertain scenario; these scenarios can include discrete scenarios, such sampled from a continuous range or a combination thereof. Results from these runs are then aggregated and investigated using e.g. Machine-Learning or visualization tools to i) determine the importance of uncertain parameters in achieving management objectives (exploratory modeling), ii) determine conditions under which a candidate strategy fails or succeeds (scenario discovery) and iii) unveil potential trade-offs between multiple objectives (Lempert et al., 2013). Understanding yielded from these analyses is often used to update management strategy candidates, which are then again subjected to modeling under the same range of uncertain scenarios. Once the RDM analyses are completed, a candidate strategy that fulfils the desired outcomes to the greatest extent possible under the largest number of scenarios is chosen for implementation (Lempert et al., 2003).

The consideration of DU and the usage of DMDU methods have been explicitly proposed for fisheries management (Hadjimichael et al., 2020; Wainger et al., 2021), though RDM has as yet not been put into applied use in the research field. Here we apply the RDM framework to uncover robust management strategies for North Sea cod (*Gadus morhua* L.) under future climate change. North Sea cod is one of Northern Europe’s most valuable ground-fish stocks,

yielding a landings value of approximately 7 billion US\$ (1986-2010), with potential economic value under more effective management estimated as approximately 19 billion US\$ (Villasante et al., 2013). While historically it was a highly productive resource with catches up to 550 kt estimated for the 1980s (Blanchard et al., 2005), North Sea cod is currently in a low productive state which yields annual catches of 40-50 kt only (ICES, 2021b). The low productive state of North Sea cod is the result of phases of severe overexploitation in the second half of the 20th century and failed rebuilding attempts in the early 21st century (Rose et al. 2018; Hutchings & Reynolds, 2004) which may be the result of climate-driven state shift of productivity (Sguotti et al., 2019) via a negative effect of temperature increase on recruitment (Sguotti et al., 2020; Blöcker et al., 2023a). With temperature increase expected to continue, and climate effects projected to lead to biomass decreases globally (Lotze et al., 2019; Tittensor et al., 2021), and reorganizations of ecosystems in general (Sguotti et al., 2022a; Sguotti et al., 2022b), sustainable future management is becoming both more complicated and more necessary. Nevertheless, given its economic importance, rebuilding and maintaining North Sea cod is of high importance for the fisheries involved.

We here applied the RDM approach to a simplified MSE-like management-strategy-testing to quantify the potential for both ecologically and economically sustainable management given uncertainties in the recruitment process and the future course of climate change, and to characterize sustainable management strategies. We formulated the results of our study in a risk analysis and trade-off-mapping framework that allowed us to illuminate the potential of sustainably managing North Sea cod under DU.

### **2.3 Methods**

Our study follows robust decision making (RDM) protocols (NRC, 2009; Lempert et al., 2013; Lempert, 2019) that consist of A) identification of the decision-making problem and of decision alternatives, B) specification of the system structure, i.e. the model used to simulate the effects of management decisions, C) identification of system uncertainties, D) development of (potentially conflicting) management objectives, and E) exploratory modeling (EM) (fig. CI.1). EM comprises multiple model projections followed by a multi-way analysis of the simulation results with respect to management objectives (Lempert, 2019).

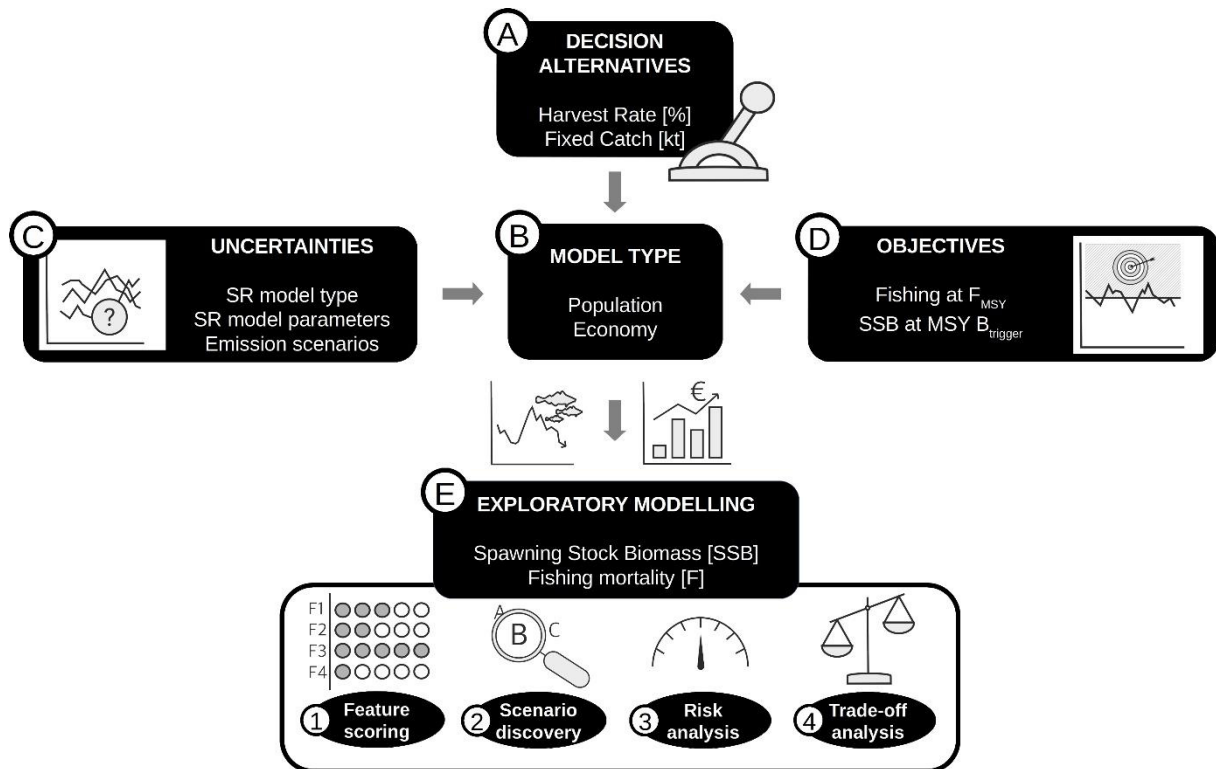


Figure CI.1 Study design according to Robust Decision Making (RDM) protocols. (A) the specification of decision alternatives, i.e. fisheries management strategies according to harvest rates and fixed catch levels; (B) the model system consisting of coupled population and economical components; (C) uncertainties affecting the success of management strategies, i.e. stock-recruitment (SR) model types and parameterization as well as emission scenarios; (D) management objectives that management strategies will be evaluated against; (E) exploratory modelling and analysis of model projection outcomes (SSB, fishing mortality [F]), including (1) evaluation of the relative importance of management measures and uncertainties for achieving objectives (feature scoring), (2) identification of combinations of management measures and uncertainties that achieve objectives (scenario discovery) and (3) evaluation of the risk of exploitation levels not achieving sustainability and profitability objectives (risk analysis), and (4) evaluation of trade-offs between exploitation levels as well as sustainability and profitability objectives (trade-off analysis).

### 2.3.1 Decision alternatives

The decision-making problem in the context of planning long-term fisheries management implies finding exploitation strategies that maintain the stock in a safe biological state while yielding acceptable profits for the fishers who depend on the stock for income (Walters & Martell, 2005). The optimal decision, in accordance with RDM theory, would achieve these aims under a large variety of assumptions about future recruitment dynamics and independent of the future development of climate change (Lempert et al., 2003). We here considered two exploitation metrics, i.e. i) constant catch in tonnes of fish stock biomass, and ii) constant harvest rate, i.e. a fixed ratio of catch to stock size. Both metrics are used as regulatory metrics in fisheries management to maintain or achieve a safe biological level, but have different advantages and disadvantages (Deroba & Bence, 2008; Restrepo & Powers, 1999). Constant catch rules theoretically provide stable catches, but may lead to excessive exploitation rates at low stock sizes. In contrast, catches equal to a fixed proportion of the current stock size (es-



entially reflecting constant fishing mortality) are more responsive to fluctuations in stock size (Free et al., 2022). In our analysis, decision alternatives for each model run were maintained as constant values over all projection years to investigate the long-term viability of each exploitation level.

### **2.3.2 Model system**

We projected the stock dynamics of North Sea cod for the period 2030 – 2100 using an age-based single-species population model (Allen, 1975) where cohorts of equal-aged fish are subject to decrease over time due to fishing, i.e. catch or harvest rate translated to fishing mortality ( $F$ ), and natural mortality (due to predation and other causes). SSB is calculated as the number of fish per age-class, their age-specific weight and maturity rates. The stock is replenished annually by recruits (age individuals) depending on both the amount of SSB and on environmental pressures. We employed SSB – recruitment (SR) models that include the effect of sea-surface temperature (SST) on offspring production (SI CI.2, SI CI.3). As a major environmental driver, temperature is frequently applied in the modeling of future management of fisheries (e.g. Serpetti et al., 2017) and in the design of SR models in particular (Subbey et al., 2014).

Our population model of the North Sea cod stock is coupled to an economic model that computes future profits for the fishery (Schenk et al., 2023). Profits are based on revenues derived by assigning specific market prices to fish of specific weight, as well as costs. Costs increase with catch, due to e.g. increased requirements for storage capacity and work power. Further details on the population- and economic models are given in the appendix (SI CI.1, SI CI.6, SI CI.7).

Historical stock data for North Sea cod were obtained from the ICES (International Council for the Exploration of the Sea) Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK; ICES, 2021b). SST observation data for fitting the SR models were retrieved from the NOAA Extended Reconstructed Sea Surface Temperature (ERSST) dataset, version 5 (Huang et al., 2017). SST projection data were obtained from a regional ocean model (Peck et al., 2020), and were bias-corrected against the ERSST data (simple mean bias correction; Maraun, 2016). Pricing data were obtained from the German federal office for agriculture and food (BLE, 2020).

### 2.3.3 Uncertainties

The relationship between SSB, environmental pressures and recruitment is usually subject to strong uncertainty due to the large number of unobserved physical and biological processes involved and the often low amount of high quality data. We hence conducted our RDM analysis around several recruitment scenarios, which were defined by three sources of uncertainty:

*Functional form of the SR relationship* – The relationship between SSB, environmental pressures and recruitment is most commonly modeled via the Ricker (Ricker, 1954) and Beverton-Holt (Beverton & Holt, 1957) relationships or their environmentally-sensitive extensions (Ricker, 1975; Hilborn & Walters, 1992). Both models describe initially positive linear effects of SSB, a negative exponential effect of SSB reflecting population and ecosystem capacity limitations and resulting in either asymptotic (Beverton-Holt) or decreasing recruitment (Ricker) at high SSB, and a negative exponential effect of SST (eq. CI.1; see also SI CI.2, SI CI.3). The high degree of unexplained recruitment variability and lack of recruitment data for very high levels of SSB makes the “true” underlying functional form often unclear (Patterson et al., 2001). We hence performed our stock projections with both SR models to account for this ambiguity.

$$R_{t+1} = N_{t+1,1} = e^{-\gamma E_t} \frac{\alpha SSB_t}{1 + \beta SSB_t}$$

$$R_{t+1} = N_{t+1,1} = \alpha SSB_t e^{-\beta SSB_t - \gamma E_t}$$

Equation. CI.1: Environmental Beverton-and-Holt (Hilborn & Walters, 1992) (top) and Ricker (1975) (bottom) stock-recruitment-model equation. The strength of the positive linear effect of SSB on recruitment is given by  $\alpha$  (recruitment increases with increasing SSB). The limitation of recruitment (or its reduction) through SSB is parameterized by  $\beta$  (ecosystem carrying capacity or other density-related effects like cannibalism). The strength of environmental pressure on recruitment is described by  $\gamma$ . R = recruitment, N = population number, SSB = spawning-stock biomass, E = environmental variable

*SR model parameterization* – SR models only describe very basal assumptions about the effects of SSB and environmental pressures on recruitment, and often fit the data poorly, resulting in wide confidence ranges of parameter estimates (Pineda et al., 2009; Subbey et al., 2014). In addition to unexplained processes that modify the basal “true” SR relationship, the existence of a singular continuous SR relationship for a given stock itself is challenged by observed “low-recruitment regimes” (ICES, 2021c) and statistical evidence for highly non-linear or discontinuous SR dynamics (Sguotti et al., 2020). We here considered a wide array of continuous SR relationships defined by parameter values sampled from the standard-error

range of the statistical estimates (SR equations were re-arranged and logarithms of SSB-related parameters were fitted to avoid sampling biologically meaningless negative parameter values; SI CI.2.3, supplementary table SI CI.2 / 1). We considered the standard-error range as an estimate of the range of possible SR relationships with equal probability (we traded in homoscedasticity on the current recruitment time series for covering potential future SR relationships). SR relationships most notably and strongly differed in maximum attainable levels of recruitment (SI CI.5).

*Future development of climate change* – The future of climate change depends primarily on current and future mitigation measures to reduce carbon emissions (van Vuuren et al., 2011). Multiple future pathways of future carbon emissions, the Representative Concentration Pathways (RCP), have been lined out and used to force global and regional climate models that simulate future climate development on a spatial scale (Moss et al., 2010). Naturally, implementing climate mitigation measures is not in the purview of fisheries management. Future warming, i.e. an increase of SST, is thus an uncertainty for future recruitment and stock development. We forced the cod population model with projected North Sea SST data for the RCP4.5- and RCP8.5 emissions scenarios, i.e. a “middle-of-the-road” mitigation- and a “business-as-usual” scenario, respectively, through the recruitment process (negative effect of SST on recruitment). These scenarios correspond to different degrees of future SST increases, with increases above the observed maximum occurring more frequently and with a larger magnitude in the latter (SI CI.4). Data were obtained from a North Sea regional ocean model (Huang et al., 2017).

#### **2.3.4 Objectives**

Fisheries management in the European Union applies the Maximum Sustainable Yield (MSY) framework that proposes that under a distinct level of  $F$  (i.e.  $F_{MSY}$ ) a stock in safe biological limits can maintain a high level of average catch quasi-indefinitely (ICES, 2019). Accordingly the MSY concept is the basis against which the International Council for the Exploration of the Sea (ICES) evaluates exploitation and stock status, and gives advice on total allowable catch (ICES, 2019; ICES, 2021d). Management reference points for this approach are the target  $F$ ,  $F_{MSY}$ , that theoretically generates MSY, and a precautionary limit biomass level (typically termed  $B_{PA}$  by ICES; here termed  $B_D$ ) that is used to readjust  $F$  at too low biomasses. While both higher and lower  $F$  levels will generate lower average yield, exceeding  $F_{MSY}$  also puts the stock at risk of decreasing population numbers and  $F_{MSY}$  is therefore considered a limit to be avoided (Mace, 2001). We considered both reference points, i.e. achieving  $F \leq$

$F_{MSY}$  and  $SSB \geq B_P$  as objectives in our stock simulations. MSY reference points were set to those currently used in the stock assessment of North Sea cod, i.e.  $F_{MSY} = 0.28$  and  $B_P = 97.8$  kt (ICES, 2021b).

### 2.3.5 Exploratory modeling

Exploratory Modelling (EM) was conducted by projecting the North Sea cod stock under multiple combinations of uncertain scenarios and management decisions via the climate-forced population model. We initialized the stock in 2030 with a SSB equaling the present  $B_P$  (and corresponding stock numbers, which follow the distribution over age classes estimated for 2018 [ICES, 2021b]). We thereby assume a successful rebuilding of the presently depleted cod stock until the starting year of the simulation. 40000 projection runs were conducted consisting of 200 random schemes of SR model parameterizations and climate scenarios, (separate sets of runs for Ricker- and the Beverton & Holt) as well as 100 random management decisions of constant catches and harvest rates (ranges defined based on initial trial simulations; SI CI.10). Evaluation of projection outcomes was based on procedures commonly applied in EM analysis:

*Feature scoring* – We first evaluated the importance of the various uncertainty factors and the management measures for achieving the management objectives using gradient boosting regression trees (Friedman, 2001). We defined the target regression variable as the number of years in which both management targets, i.e.  $SSB \geq B_P$  and  $F \leq F_{MSY}$ , have been met, and values of the SR parameters and climate scenarios as predictors. Separate regression analyses were performed for each of the Ricker- and the Beverton & Holt SR models.

*Scenario discovery* – In a second step we identified out of all projection runs the successful scenarios where both management targets, i.e.  $SSB \geq B_P$  and  $F \leq F_{MSY}$ , were met for the entire projection period. Subsequently, we explored the combinations of constant catch or harvest rate and uncertain factors that characterize these successful projections.

*Risk and trade-off analysis* – We eventually assessed the risk that different exploitation levels (constant catch levels or harvest rates) will not successfully achieve management objectives. We calculated *sustainability risk* as the risk of  $F \geq F_{MSY}$  (indicating over-fishing [Mace, 2001]) and  $SSB \leq B_P$  (indicating vulnerability to reproductive failure), and additionally *profitability risk*, reflecting the risk of profit being less than the average profit over the years 2000 to 2018, which is a relatively stable level (i.e. c. 50 million € (model hindcast, see SI CI.8)). Risks were calculated as the percentage of projections not meeting at least one of either sus-

tainability objective or not meeting the profitability objective by the total amount of projection data for each management measure.

### **2.3.6 Software**

All population and economic modelling as well as data analyses were performed in Python (van Rossum, 1995). Sampling of uncertainties and decisions in the population model was conducted using the Monte-Carlo sampler of the “EMA Workbench” package for EM tasks (Kwakkel, 2017). Boosting regression tree analysis was conducted using the “GradientBoostingRegressor” function (with default settings) of the Scikit-Learn package (Pedregosa et al., 2011). Visualizations were performed in R (R Core Team, 2020) using the “tidyverse” package (Wickham et al., 2016) and in Python using the “matplotlib” package (Hunter, 2007).

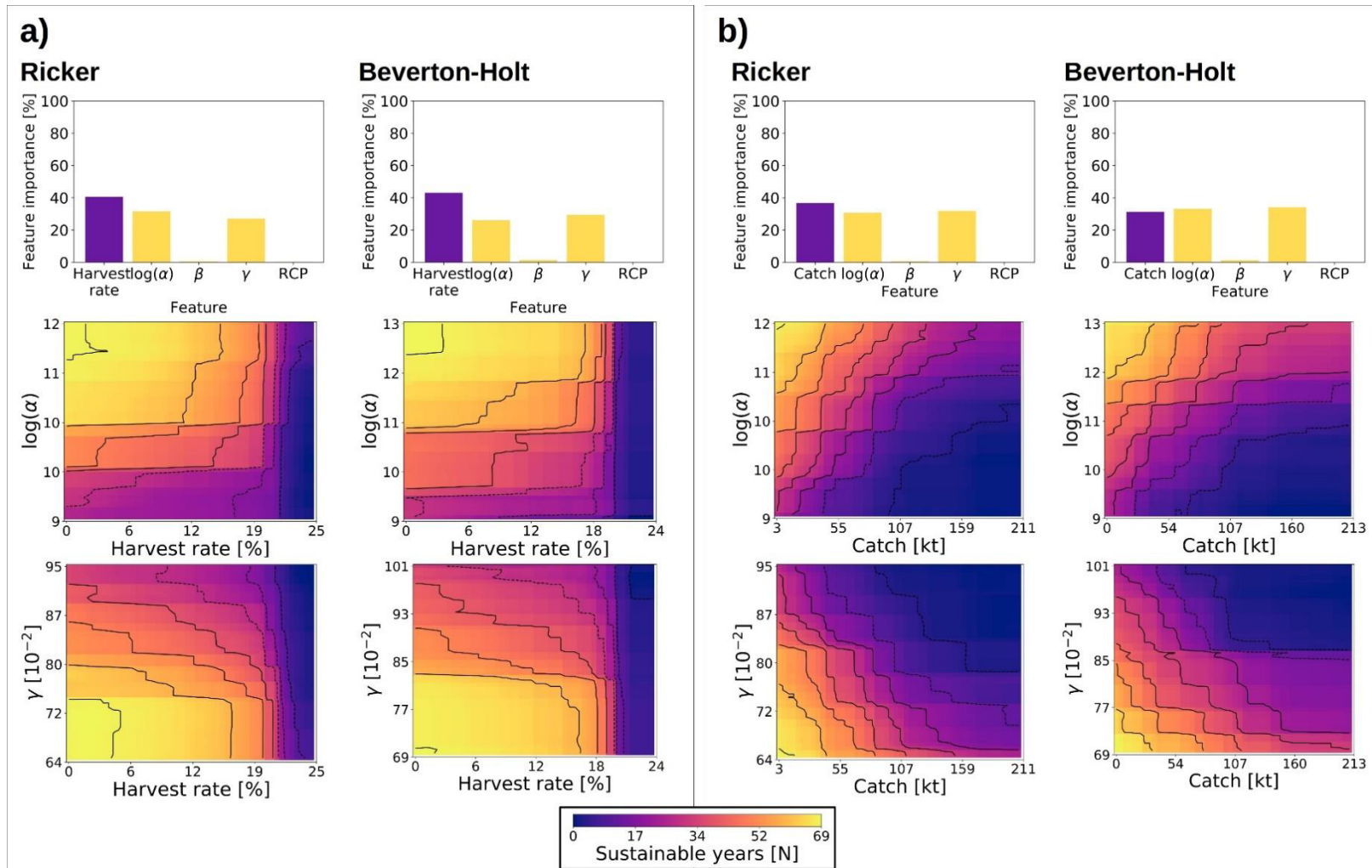


Figure CI.2: Importance of management measures and uncertainty effects – Results of boosting-regression-tree analysis of projections with Ricker and Beverton-Holt SR-models under harvest rate (**a**) and fixed catch scenarios (**b**); individual effects (upper row) and interactions between management measures and the stock-size-related SR parameter  $\log(\alpha)$  (middle row) and the temperature-related SR parameter  $\gamma$  (lower row). Lighter color in interaction plots denotes higher number of sustainable years (i.e. years with  $SSB \geq B_p$  and  $F \leq F_{MSY}$ ). RCP = climate scenario (representative concentration pathway)

## 2.4 Results

### 2.4.1 Feature scoring

Feature scoring using boosted regression trees revealed that although exploitation pressure is generally the dominating factor for management success in our simulations of North Sea cod dynamics (except for the combination of the Beverton & Holt model and constant catch), uncertainty in SR model parameters  $\log(\alpha)$  and  $\gamma$  is of similar importance (fig. CI.2). Our simulations also showed that the realized climate scenario as well as the strength of the density-dependence in the stock (the  $\log(\beta)$  parameter in SR model) are likely of minor importance for management success (the number of years in which sustainability objectives are achieved) of North Sea cod. Partial effect plots demonstrate that management success of any of the harvest control rules is dependent on high values of  $\log(\alpha)$  (describing the positive effect of SSB on recruitment) and low  $\gamma$  (describing the magnitude of the negative effect of higher SSTs on recruitment) independent of SR model type. In harvest-rate-based management strategies two-dimensional threshold dynamics are clearly visible (fig. CI.2a). Thresholds occur between lower and higher management success in relation to  $\log(\alpha)$  and  $\gamma$  values, but especially at c. 20% harvest rate to 100% management failure (i.e. zero sustainable years). In contrast, a constant-catch harvest control rule resulted in a more transitional interaction with SR parameter uncertainties (fig. CI.2b). Management with harvest rate resulted in a larger safer space of relatively high management success. However, that space is not defined by management strategies alone but also by uncertainty in the SR-model parameterization, in both harvest-control rules.

### 2.4.2 Scenario discovery

Scenario discovery revealed that neither a constant catch nor a harvest rate was identifiable that met the sustainability targets over the entire simulation period. Minimum constant catch (0.4 kilo-tonnes) and harvest rates (0.02 %) resulted in 68 and 70 % successful scenarios, respectively. We found successful scenarios at constant catches  $< 75 \cdot 10^3$  tonnes and harvest rates  $< c. 18\%$ , with a frequency depending strongly on  $\log(\alpha)$  and  $\gamma$  parameters (fig. CI.3), a pattern already shown by feature scoring. The highest numbers of successful scenarios were discovered at the lowest catch- and harvest rate levels, but decreased with decreasing  $\log(\alpha)$  and increasing  $\gamma$  values. However, the effect of varying  $\log(\alpha)$  and  $\gamma$  on the occurrence of successful scenarios is stronger in the constant-catch harvest control rule (fig. CI.3a,b) compared to the harvest rate strategy (fig. CI.3c,d) that provided a

broader safe range of management measures. Successful scenarios are furthermore largely independent of climate scenario and functional form of the SR relationship.

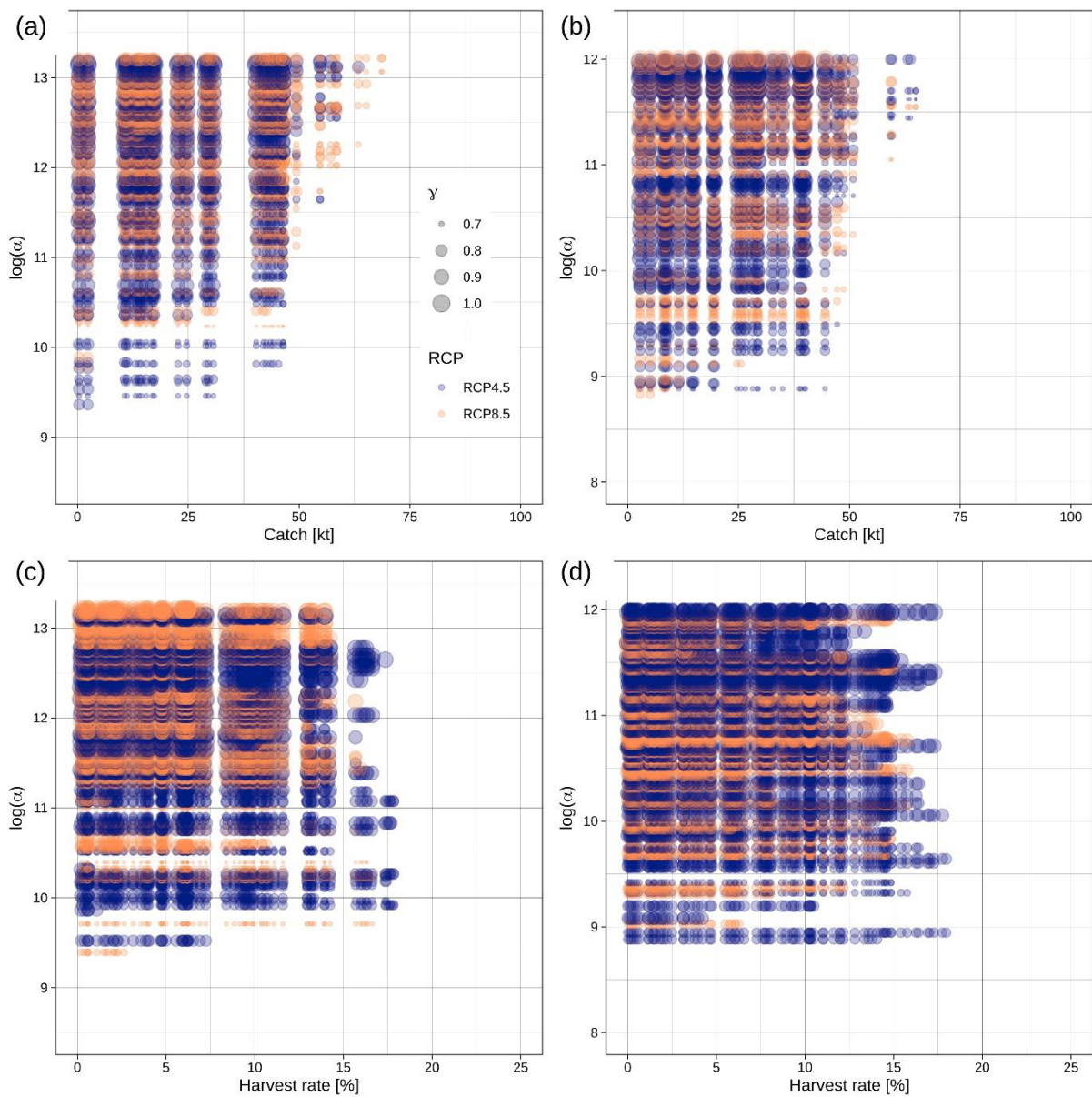


Figure CI.3: Occurrence of successful scenarios in the policy-uncertainty space – The space is defined by harvest intensity (catch or harvest rate) and the three SR parameters ( $\log(\alpha)$ ,  $\log(\beta)$  [axis not shown] and  $\gamma$  [shown as dot size]). Successful scenarios are defined as projections with  $SSB \geq B_P$  and  $F < F_{MSY}$  in all projection years. Results are shown for Beverton-Holt (a,c) and Ricker (b,d) SR models under total catch (a,b) and harvest rate (c,d) scenarios as well as emission scenarios RCP4.5 (blue) and 8.5 (yellow).  $\log(\alpha)$  and  $\gamma$  (represented by dot size) are SR model parameters.

### 2.4.3 Risk and trade-off analysis

Our scenario discovery exercise revealed no completely safe levels of catch and harvest rate for North Sea cod given the uncertainty in SR model parameterization. As a consequence every level of a management measure would bear a degree of risk not achieving the sustainability objectives. We hence assessed the risk that different levels of harvest rates and fixed catches



would have on achieving management objectives. In addition to *sustainability risk*, we developed an economic risk metric, i.e. *profitability risk* that indicates the probability that different levels of harvest rates and fixed catches would have to not achieve average recent historical profits. By these metrics we explored the trade-off between risk of not achieving sustainability and the risk of the fishery not operating in a profitable way.

We found sustainability risk for North Sea cod to slowly increase to 50% towards a harvest rate of c. 20% for both mid- and end-of-century periods, the earlier period however starting from a lower risk level. (fig. CI.4a). Afterwards sustainability risk increased faster, approaching 100% at harvest rates of c. 25%. Applying a constant catch harvest control rule would result in a relatively linearly increasing sustainability risk for both periods peaking at c. 80% at a catch of 200 kt (fig. CI.4b). Profitability risk decreased continuously with increasing harvest rate levelling off at about 50 % (with a slight downward offset for the first period) at the harvest rate causing 100 % sustainability risk (fig. CI.4c). In contrast, profitability risk decreased abruptly with increasing constant catch from c. 40 kt towards c. 60 kt. From that catch level on profitability risk increased linearly with increasing catch to the peak level causing maximum sustainability risk (fig. CI.4d); the increase is likely related on an increase in scenarios that lead to eventual stock collapse and thus to the termination of fishing (SI CI.11).

Our trade-off analysis for harvest rate management strategies revealed an initial rapid decrease of profitability risk (from 100 to c. 50-55 %) and a less strong increase in sustainability risk (fig. CI.4e) with increasing harvest rates until c. 18 %. With a further increase in harvest rates sustainability risk increases rapidly while profitability risk remains constant. An initial steep decrease in profitability risk and an increase in sustainability risk with catches up to c. 63 kt is also found for constant-catch management strategies (fig. CI.4f). However, in contrast to harvest rate management, both risks increase in parallel with further increasing catches. Overall both risks are lower for the mid-century compared to the end-of-century period.

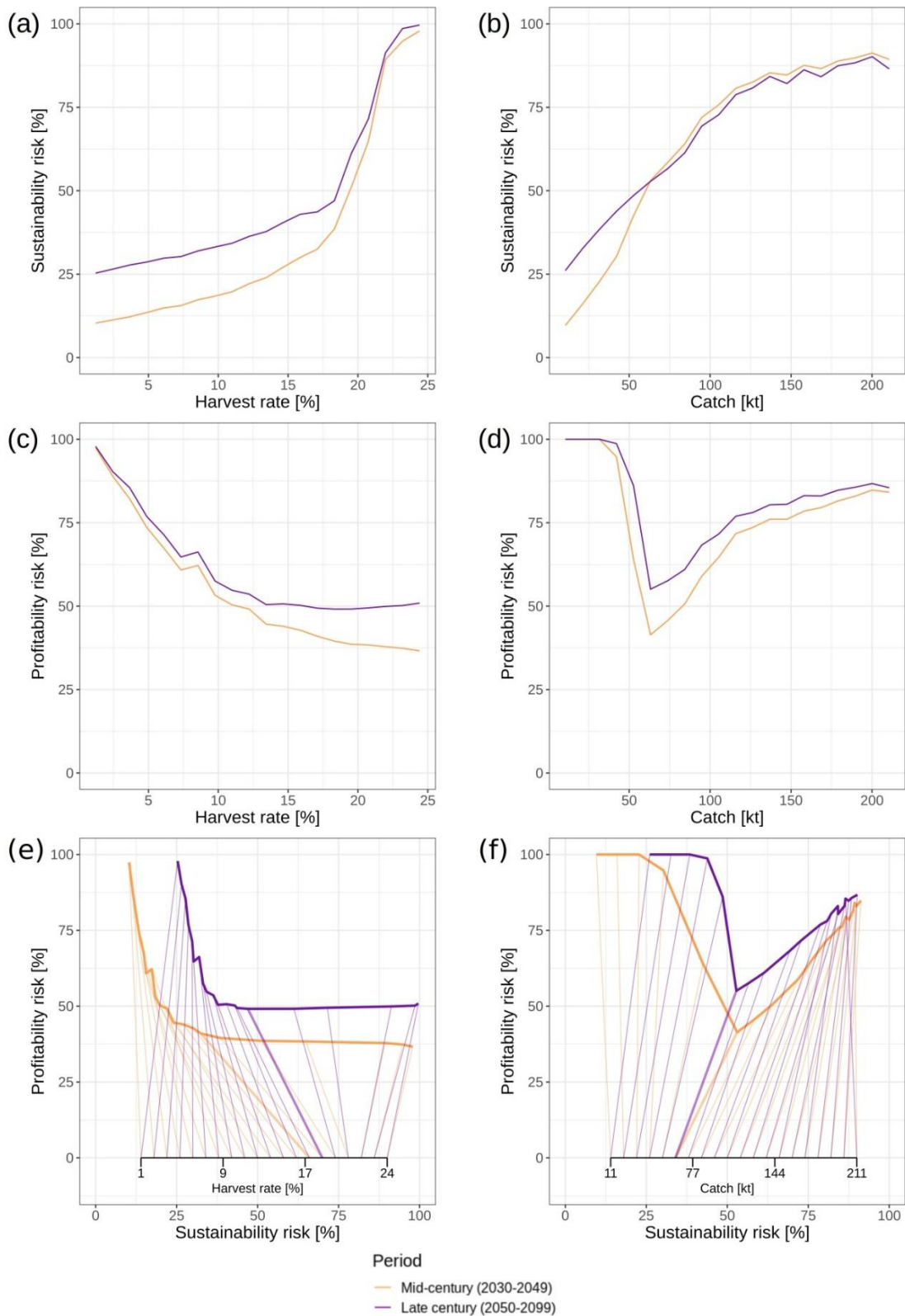


Figure CI.4: Relationship between sustainability risk and exploitation for harvest-rate (a) and fixed-catch projections (b), as well as relationship between profitability risk and exploitation (c, d), and the relationship between sustainability and profitability risks as well as exploitation intensity (inserted x-axis and connecting segments indicate exploitation level associated with a specific risk combination) (e, f). Risks were calculated over both climate scenarios. Colors represent periods within the projection time series: yellow: 2030-2049 (mid-century), blue: 2050-2099 (end-of-century). Thick segments in (e) and (f) represent exploitation rates leading to minimum summed risk and a ratio of risks nearest to 1 (see SI CI.12 for details).

## 2.5 Discussion

We conducted a novel Management-Strategy-Evaluation-(MSE)-like study for North Sea cod that unlike traditional application followed Robust Decision Making (RDM) protocols. RDM shifts emphasis from improving model predictions through increasing model complexity to improving management decisions (Lempert, 2019). RDM hence seeks to increase the understanding about the consequences of management actions under a large spectrum of possible scenarios, eventually defining a management strategy that is robust to a multitude of equally possible futures (Lempert & Popper, 2005). Our RDM projection study consequently aimed to evaluate the potential to achieve a sustainable management of North Sea cod given uncertainties in the recruitment process and the future course of climate change.

A major result of our study is that uncertainty about future recruitment under climate change has a similar impact on management success as the harvest control rule strategies we applied. Uncertainty in recruitment is a well-known challenge for biomass projections and specification of harvest levels for exploited fish stocks (Wiedenmann & Jensen, 2017; Collie et al., 2021). Our study goes beyond this general knowledge and demonstrates that density-independent productivity of the stock and the strength of the negative effect of increasing SSTs (reflected by the  $\log(\alpha)$  and  $\gamma$  parameters in a SR model, respectively) are of predominant importance for management success in our simulations of North Sea cod. The importance of  $\log(\alpha)$  points towards the long-standing discussion in fisheries science whether compensatory or depensatory (i.e. the Allee effect) processes dominate at low stock sizes (Hilborn et al., 2014). If depensation prevails, recovery of overexploited stocks is inhibited and has been shown to exist especially for cod populations (Rowe et al., 2004; Keith & Hutchings, 2012; Kuparinen et al., 2014; Neuenhoff et al., 2019) and recently for North Sea cod (Winter et al., 2019). Empirical evidence is however overall stronger for compensatory effects in fish stocks, i.e. increasing productivity at low stock sizes and hence high recovery potential (Hilborn et al., 2014). Nevertheless, our results reinforce that critically low stock sizes should be avoided to not critically endanger fish stocks and to not impede their recovery when depleted (Britten et al., 2017; Gaines et al., 2018; Sguotti et al., 2019; Möllmann et al., 2021).

Our study reinforces that climate change is challenging fisheries management because it introduces further sources of uncertainty to the decision-making process (Brander, 2007; Miller et al., 2010; Punt et al., 2014; Holsman et al., 2020; Szuwalski et al., 2023). We focused on evaluating the importance of uncertainty in recruitment, because it is likely the most im-

portant process affected by the consequences of climate change in the ocean (Britten et al. 2015) especially in North Sea cod (O'Brien et al., 2000; Beaugrand et al., 2003; Olsen et al., 2011). Nevertheless, our model remains a gross simplification of the many climate-related processes affecting not only the recruitment of cod in the North Sea, but also growth (Pilling et al., 2007) and distribution shifts (Engelhard et al., 2013). Furthermore, finding relationships between environmental variables and recruitment is difficult because these notoriously have a poor fit (Myers, 1998). The importance of uncertainty in the *gamma* parameter (reflecting the strength of the negative effect of increasing SSTs) for sustainable management in our simulations demonstrates the importance of reliably considering the effect of climate on recruitment. Moreover, uncertainty in SR model parameterization was more important than the type of emission scenario, revealing that considering the future course of climate change is less decisive than structural uncertainty in the model. Nevertheless, the future strength of climate change will still be important for North Sea cod since our projections revealed that towards the end of the century recruitment and subsequently SSB will significantly be reduced at RCP8.5 compared to RCP4.5 (SI CI.9), increasing the sustainability and profitability risks.

A further major result of our study is that none of the management strategies we applied in our simulations is fully robust to the uncertainty in model parameterization and future climate change. Specifically, no constant catch or harvest rate was able to meet sustainability targets for North Sea cod over the entire simulation period. However, a harvest-rate strategy provided a safer operation space with a threshold-like transition to less safe exploitation levels than a constant catch strategy with its less-distinctly bounded space. This result confirms the theory that while providing stable catches, a constant catch strategy may lead to excessive exploitation rates at low stock sizes, while a constant-F strategy is more responsive to fluctuations in stock size (Deroba & Bence, 2008; Restrepo & Powers, 1999). Our harvest rate strategy corresponds effectively to a constant F strategy (Free et al. 2022). However, because we were not primarily interested in finding the better management strategy, but rather exploring the effect of uncertainties on successful management, we used harvest rate, and considered  $F_{MSY}$ , in addition to  $B_P$ , as one of our management targets under both harvest control rules.

Using both a target F and a limit biomass reference point, we mimicked the MSY strategy implemented in EU fisheries management by ICES (European Union, 2013; ICES, 2012). We however disregarded the threshold F rule implemented which is likely the most resilient management approach to uncertainties and climate change effects (Kritzer et al., 2019; Mildemberger et al., 2021; Free et al., 2022), but was not useful to implement in our study, as some

unfavourable scenarios might have enforced a permanent down-scaling of  $F$  and thus reduced the validity of results attributed to certain harvesting levels (especially where sustainability was achieved with the permanently reduced  $F$ ). Stress-testing the EU MSY strategy under climate change scenarios would hence be a valuable study in general. Our approach additionally required constant reference levels over the entire simulation period, disregarding the adaptation of management targets and limits (i.e.  $F_{MSY}$  and  $B_P$ , respectively) in the ICES benchmark process. Such a process accounts for productivity changes in the stock, and failing to account for such time-varying processes can result in biased biomass and  $F$ -based reference points (Thorson et al., 2015; Szuwalski & Hollowed 2016). However, non-stationary MSY-based reference points may introduce more uncertainty in management strategy evaluations and should only be based on sound mechanistic understanding of the environmental influence (Punt et al., 2014, Zhang et al., 2021) and can even result in unintended management outcomes (Szuwalski et al., 2023).

Given that our simulations for North Sea cod revealed no management strategy that is fully robust to uncertainty in model parameterization and future climate change, we conducted a risk and trade-off analysis, exploring the trade-off between the risk of not achieving sustainability targets and the risk of the fishery of not operating in a profitable way. Such a risk assessment can be valuable decision support tool for fisheries managers that usually must consider both ecological and economic (and hence social) objectives. For North Sea cod our results indicate that even the best trade-offs of sustainability and profitability would require low catches or harvest rates compared to historical levels, reflecting the presently low productivity of the stock. Our profitability reference level was set quite arbitrary to a mean over years 2000 to 2018, and hence further sensitivity studies would be required for an extended use. Our representation of the economy in our modelling approach is furthermore quite simplistic since North Sea cod is usually caught in a mixed fishery (ICES, 2021b) that would affect the profitability of the respective fleets (Hamon et al., 2007). We are nevertheless convinced that this first approximation of profitability holds for our single-species approach.

An additional constraint to direct practical implementation, our approach deviates from typical MSE procedures i.a. by not simulating observation- and implementation errors, and not simulating future stock assessments and reference-point re-estimations (as outlined in e.g. Punt et al., 2016), as we adopted a more theoretical approach focusing on the impact of deep uncertainties on long-term policy success. We suggest our approach as a pre-analysis to classical MSE (i.e., a form of sensitivity analysis concerning recruitment uncertainties). Extended

studies could furthermore aim at an integration into the existing / more applied MSE model frameworks.

In conclusion, we here provided the first study that considered principles of decision-making under deep uncertainties (DMDU) in a fisheries management framework. Our study contributes a novel aspect to MSE approaches in fisheries by taking the principle to consider multiple operating models with multiple assumptions about the impact of climate change (Punt et al. 2016, Jacobsen et al. 2022) to its extremes, thereby accounting for uncertainty in stock productivity in a more holistic way. We furthermore show how robust decision-making (RDM) approaches can support a management system to consider and to cope with deep uncertainties by considering risks and trade-offs between multiple goals. Arguably, our single-species approach is simplistic compared to state-of-the-art multispecies or food web modeling approaches (Holsman et al., 2020; Craig and Link, 2023), but allowed us to follow the RDM philosophy of shifting emphasis from improving model predictions to improving management decisions (Lempert, 2019). We consider our approach as an addition to the toolbox of MSE methods that is required to develop ecosystem-based fisheries management approaches that are instrumental in developing a sustainable exploitation of our world fisheries resources.

## **2.6. Data availability**

All data and code will be made available on [https://github.com/imf-uham/DMDU\\_North\\_Sea](https://github.com/imf-uham/DMDU_North_Sea) and on zenodo.org upon publication of the study in a scientific journal and are available from the author on request.

## **2.7 Conflict of interest**

The authors declare no conflicts of interest.

## **2.8 Acknowledgements**

The authors wish to thank Nicole Funk (Universität Hamburg) for designing the icons used in fig. CI.1.

JC received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 820989 (project COMFORT, Our common future ocean in the Earth system – quantifying coupled cycles of carbon, oxygen, and nutrients for determin-

ing and achieving safe operating spaces with respect to tipping points). The work reflects only the authors' view; the European Commission and their executive agency are not responsible for any use that may be made or the information the work contains.

SF received funding from the German Federal Ministry of Education and Research (BMBF) through the project SpaCeParti (Coastal Fishery, Biodiversity, Spatial Use and Climate Change: A Participative Approach to navigate the Western Baltic Sea into a Sustainable Future, grant no. 03F0914A-F)

RV was partly funded through the GenClim project, under the 2019-2020 BiodivERsA joint call for research proposals, under the BiodivClim ERA-Net COFUND programme, and with the funding organisations Deutsche Forschungsgemeinschaft (DFG, German Research Foundation), Department of Science and Innovation (DSI - South Africa), Funda para a Ciia e a Tecnologia, I.P. (FCT - Portugal), and Innovation Fund Denmark (IFD - Denmark). Funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) 451396406.

CS was funded by the EU Horizon RESET (Resilience Estimation to SET management goals in marine ecosystems) project (101065994) under the HORIZON-MSCA-2021-PF.

### 3. Chapter II: Safe Operating Space reveals climate-adaptation thresholds for sustainable management of Atlantic cod (*Gadus morhua* L.)

Jan Conradt<sup>1\*</sup>, Steffen Funk<sup>1</sup>, Thorsten Blenckner<sup>2</sup>, Christian Möllmann<sup>1</sup>

<sup>1</sup>Institute of Marine Ecosystem and Fishery Science, Universität Hamburg, Germany

<sup>2</sup>Stockholm Resilience Center, Stockholm University, Stockholm, Sweden

\*Principal author

#### 3.1 Abstract

Climate change increasingly challenges traditional fisheries management with classical concepts such as maximum sustainable yield (MSY) appearing less suitable in light of reduced stock productivity and shifting species distributions. Moreover, severe uncertainty on the mechanisms of climate impacts on key processes of stock dynamics do exist. Fisheries management hence requires an assessment framework for long-term strategies under continuing climate change. Here we present an environment-based safe operating space (SOS) approach for guiding climate-ready fisheries management. We apply our approach to 19 stocks of Atlantic cod (*Gadus morhua* L.), historically one of the most important living marine resources globally. We explicitly consider deep uncertainties on stock productivity in our simulations and base our SOS design on a risk assessment framework for biological vulnerability of these stocks. We show that the majority of Atlantic cod stocks exhibits a SOS clearly defined by interacting effects of fishing and temperature with either an upper- or a lower temperature boundary. Existence and extent of the safe space varied regionally with many western Atlantic coastal stocks exhibiting no discernable SOS. Safe spaces of mid-latitude eastern Atlantic stocks were limited by upper catch- and temperature boundaries and interacting harvesting- and temperature effects. We also found the potential to harvest minimum historical levels of catch to strongly depend on stock size, which indicates that rebuilding and maintaining stocks at healthy levels is crucial for climate-proof harvesting. We propose our SOS approach as a tool for long-term strategic planning in climate-ready fisheries management, and suggest a regular updating of the analysis as knowledge about climate response of the stocks improves.

**Key words:** Safe operating space, climate-ready fisheries management, deep uncertainty, population modelling, Atlantic cod



### 3.2 Introduction

Fisheries management is increasingly facing challenges to implementing sustainable harvesting (e.g. Pitcher & Cheung, 2013) as climate change alters the environmental and ecological foundations determining biological productivity (Lotze et al., 2019; Tittensor et al., 2021; Boyce et al., 2022). Many fish stocks respond in unforeseen ways to management actions and goals such as rebuilding of stock biomass is often not achieved to the extent or within the time frame envisioned (Sguotti et al., 2019, Winter et al., 2020; Blöcker et al., 2023a). Current management plans are often based around the principle of maximizing long-term yield (maximum sustainable yield, MSY) (Tsikliras & Froese, 2019), the underlying assumption of which is that biological characteristics of the target stock such as offspring production and survival and individual growth remain constant. Application of the MSY principle theoretically ensures that stock size remains on a level with high chance of reproductive success and would provide fishers with stable yields to base their livelihoods on. However, biological consistency is no longer a given since productivity has seen severe, sometimes abrupt declines in several commercially important stocks whose habitat becomes increasingly less suitable in response to a multitude of fishing- and climate effects (e.g. Köster et al., 2005; Pershing et al., 2015; Free et al., 2019; Sguotti et al., 2019). At high latitudes, on the other hand, the same species can show unprecedented high levels of production as the environment becomes increasingly habitable and rich in food (Haug et al., 2017; Kjesbu et al., 2014). At the same time, many fish stocks worldwide are considered over-fished and thus do not bear the conditions for MSY-based management but instead require rebuilding efforts, a challenge itself under environmental change (Cheung et al., 2022). As a result, the ability of traditional management practice to generate stable yields and healthy stocks under future climate change is doubtful in many cases (e.g. Holsman et al., 2020; Lindegren et al., 2010; Gaines et al., 2018).

Fisheries management, especially in Europe, employs a rather short-term approach to future planning. Stock assessments are conducted each or every few years and short-term projections are conducted to determine acceptable catch levels that have a high likelihood of achieving management goals (either maintaining a stock at or rebuilding it to save biological levels that are able to generate MSY) (ICES, 2021a; Restrepo et al., 1998; DFO, 2006; NAFO, 2021). Regular re-evaluation of stock perception during do-called “benchmark assessments” ensures an adaptation of management strategies and goals to changes in stock productivity (ICES, 2013). While being a valuable approach to short-term tactical management, the current management scheme does lack the ability to consider broader, long-term effects of environmental

change on stock productivity. Apart from broad-scale projections that project a loss of marine biomass under future climate change (Lotze et al., 2019; Tittensor, 2021), the quantitative limits to and potentials for maintaining specific fisheries at current or historical levels are still largely unexplored.

The constraints and opportunities that climate change poses to environmental management are increasingly quantified via the “safe operating space” (SOS) concept. The SOS concept originates from the framework of “planetary boundaries” that estimates tipping points of anthropogenic impact on the environment that would likely lead to irreversible changes to Earth system functioning (Rockström et al., 2009; Steffen et al., 2015). Within the SOS context, the “planetary boundaries” are replaced by limits to specific forms of utilization of natural resources, and the objective becomes keeping a local system of interest within a desirable state (Scheffer et al., 2015). An important component of the SOS framework is the consideration of uncontrollable (natural) driver variables that are often related to climate change. The SOS concept is particularly suitable for addressing management challenges in (eco-) systems affected by non-linear responses, i.e. tipping points, where the SOS boundary represents conditions leading to irreversible state shifts (Selkoe et al., 2015). Given that such safe spaces are often based on modelled data, their boundaries are usually extended by a “zone of (model) uncertainty”.

The SOS concept has seen practical application in a variety of ecological contexts, including e.g. wetland use for water extraction and nutrient disposal (Green et al., 2015). In management of lake fisheries it is frequently utilized to determine how the extent of safe policies is altered in response to uncontrollable environmental change (Hansen et al., 2019; Ofir et al., 2022). An extension of the concept is the “safe-and-just operating space” that integrates a social foundation (comprised of e.g. need for employment and energy) as a lower boundary of the SOS (Raworth 2012; Dearing et al., 2014). The SOS concept has been successful in developing both a theoretical understanding for stressor interactions and management requirements on an ecosystem level (Selkoe et al., 2015; Scheffer et al., 2015) and applied guidance frameworks for very localized, smaller-scale management systems (e.g. Hansen et al., 2019). However, large-scale management of fisheries still relies on traditionally established mechanisms that tend to respond to environmental drivers only through short-term adaptation measures. Yet strong evidence for climate sensitivity of fish populations especially with regard to offspring survival (Drinkwater, 2005) combined with projected increases of global temperatures to unprecedented levels (Riahi et al., 2017) strongly suggest that fished stocks will not behave

in a status-quo manner where reactive adaptation to shifting stock productivity can ensure healthy stock status. Rather, fish stocks can be expected to react in highly non-linear manners to management under climate-change effects, where management may result in hysteretic responses (Sguotti et al., 2019; Blöcker et al., 2023a). Planning long-term management goals for fisheries under climate change would therefore likely benefit from a more holistic picture of the boundaries to sustainable harvesting imposed by climate change.

Numerical modeling offers an opportunity of investigating the response of fish stocks to combined effects of fishing and climate change, and thus to determine conditions for sustainable harvesting and achieving acceptable catch levels (e.g. Clark et al., 2003; Lindegren et al., 2009; Voss et al., 2019). A practical implementation within fisheries management is e.g. the concept of Management Strategy Evaluation (MSE), where various candidate harvesting policies are tested for their sustainability under various assumptions about population processes (Punt et al., 2014). Fundamental uncertainty about a key process in population dynamics determining stock productivity, namely recruitment of juvenile fish is, however, widely recognized as an impediment for long-term stock forecasts of acceptable precision (Subbey et al., 2014; Howell et al., 2013). Recruitment strength shows strong evidence for climate dependence (Drinkwater, 2005), but any clear relationship or even climate thresholds are clouded by limited and debated knowledge about pre-recruit life history (e.g. Cardinale et al., 2008; Howell et al., 2013). Recruitment is thus an example of a “deep uncertainty”, a term from the decision-making literature that describes key system components whose uncertainties are (nearly) impossible to quantify (Marchau et al., 2019).

Here we present an environment-based safe operating space (SOS) approach for guiding climate-ready fisheries management. We apply our approach to 19 stocks of Atlantic cod (*Gadus morhua* L.), historically one of the most important living marine resources globally (Rose, 2018c). Cod shows clear and strong signs of climate sensitivity, is over-fished in many regions of the North Atlantic and often experienced non-linear productivity shifts (Drinkwater, 2005; Rose, 2018d; Sguotti et al., 2019). Following a robust approach to decision-making under deep uncertainty (Lempert, 2019), we here conceived a risk-based SOS that trades in the typical tipping-point-related boundary for an empirical risk threshold derived from integrating over a multitude of potential climate-dependent recruitment processes. Our study revealed strong variability in the existence and extent of SOS between major fishing areas: The western Atlantic stocks frequently exhibiting only a marginal or no discernable SOS at all, i.e. a lack of potential for sustainable management independent of warming, while the mid-

latitude eastern-Atlantic stocks showed a clear trade-off between warming and fishing pressure, and higher-latitude stocks were mostly driven by fishing only. We also found catch potential to strongly depend on stock size, indicating that rebuilding and maintaining stocks at healthy levels is a necessary condition for climate-proof harvesting.

### 3.3 Methods

We developed a three-step approach for generating and analyzing safe operating spaces (SOS) for Atlantic cod stocks. First, we fitted environmental stock-recruitment (SR) models forced by sea-surface temperature (SST) for each of the stocks for which quantitative age-structured data were available (19 in total covering the western and eastern Atlantic coasts and the northern waters;  $> 60^{\circ}\text{N}$ ; fig. CII.1; see SI CII.7, SI CII.8, SI CII.10). Second, we incorporated these SR models into stock-specific age-structured single-species population models and simulated their dynamics under fixed levels of SST, catch and initial stock biomass until equilibrium conditions were reached. Third, from a set of model simulations conducted with various parameterizations of the SR model accounting for uncertainty in the SR relationship, we calculated the risk of not achieving sustainable stock size for every combination of catch and SST increase. Sustainable stock size was defined as any level of spawning stock biomass (SSB) larger than a threshold precautionary reference point ( $B_{\text{PA}}$  or  $\text{MSY } B_{\text{trigger}}$  in ICES assessments [ICES, 2021a], “upper stock reference” in DFO assessments [DFO, 2006], in this study referred to as  $B_p$ ). A SSB level below this reference point typically indicates increased danger of reproductive failure (ICES, 2021a). Fourth, we set a threshold risk as the SOS boundary and analyzed the relationship between risk level and SOS size, varying target risk between zero and 100 %. Finally we determined the boundary catch- and SST levels resulting in 50 % risk, as well as the biomass required for allowing minimum historical catch under future warming and maintaining sustainability (fig. CII.2).

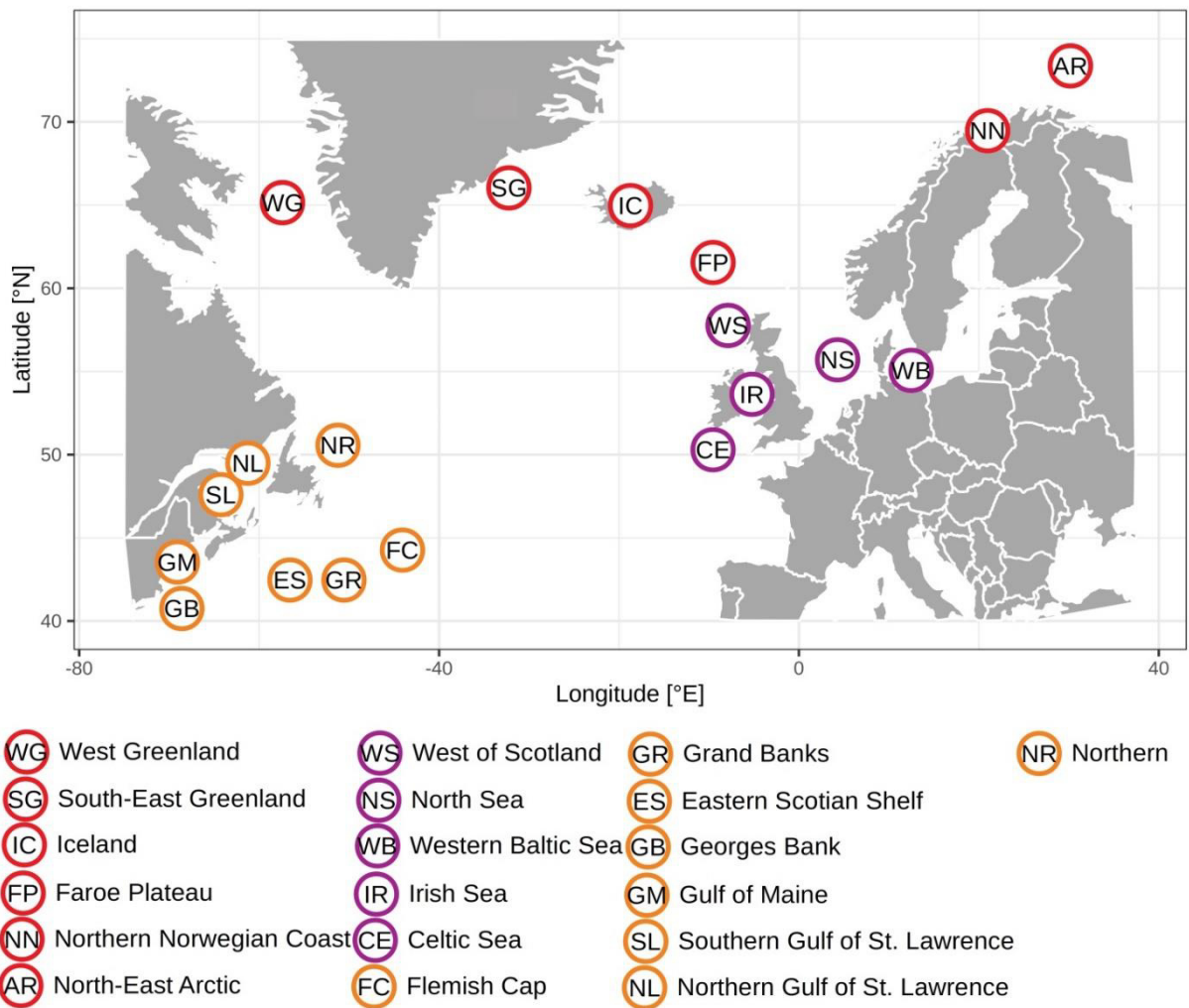


Figure CII.1. Location of the cod stocks. Colors denote a broad geographical classification into western Atlantic stocks (orange), mid-latitude eastern Atlantic stocks (purple) and high-latitude stocks (red)

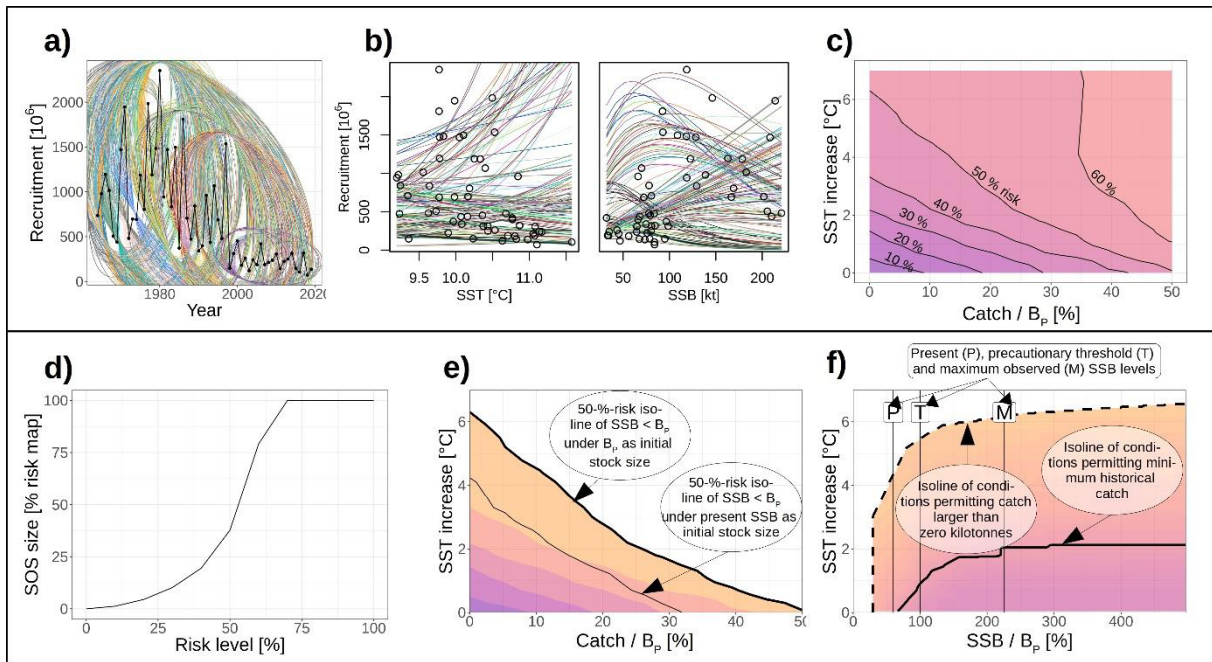


Figure CII.2. Modeling approach for estimating the SOS of Atlantic cod. SR functions are fitted over a large range of segments of the stock time series (“moving-window” approach) (a), resulting in a large variety of SR relationships with varying magnitude and direction of SST effect and varying effect of SSB on recruitment (b). Incorporation of these SR relationships into a population model and projecting under a range of levels of catch and SST increase results in a risk mapping of  $B_p$  exceeding SSB (c). The SOS is defined by the risk isoline for a selected risk level, and the relationship between SOS size and risk level is analyzed (d). The final risk level for further analyses is set to a value associated with strong dynamics in SOS size in most stocks (i.e., 50 %), and the resulting SOS is analyzed for effects of harvesting and warming (e). Projecting with different initial levels of SSB leads to a shift in the extent of the SOS, and threshold SST increase enabling distinct catch levels changes with the level of initial SSB (f)

### 3.3.1 Design of the population model

An age-structured population model (Allen, 1975) as used in the official stock assessments for Atlantic cod was used to simulate stock dynamics individually for each stock (SI CII.1, SI CII.5). This model projects the dynamics of cohorts of equally-aged fish through time (at steps of one year), which underlie instantaneous natural- and fishing mortality (F), reducing their numbers. The stock is replenished annually with juvenile fish recruiting into the fishery (recruits; the recruitment age class varies between stocks). Recruitment strength depends on the level of SSB and environmental forcing (see below); SSB is affected by fishing as average individual weight and maturity rate vary between age classes. F was derived from catch (SI CII.1, SI CII.5); age-specific maturity, individual weight and natural mortality were held constant in the projection (SI CII.1, SI CII.7) The population model was identical in basic design among all stocks, but was modified in some cases to account for specific assumptions about mortality fractions before spawning according to assessment model specifications.

### 3.3.2 Stock-recruitment modelling and uncertainty (fig. CII.2a,b)

We used the environmental modification of the Ricker equation (Ricker, 1954; Ricker, 1975) to model the functional relationship between SSB, environmental forcing and recruitment (eq. CII.1) individually for each stock (SI CII.2-4). The Ricker function assumes a positive effect of SSB on recruitment strength as well as an exponential negative effect of SSB that becomes most pronounced at large stock size and represents density-related processes like cannibalism (Steingrund et al., 2009). Environmental forcing was allowed to be either positive or negative, depending on statistical fit; we selected SST as driver variable, which is commonly regarded as a suitable proxy for a variety of environmental effects (e.g. Serpetti et al., 2017).

$$R_t = N_{t,1} = \alpha SSB_{t-l_s} e^{-\beta SSB_{t-l_s} + \gamma E_{t-l_e} + \delta}$$

Equation CII.1: Environmental Ricker (1975) stock-recruitment-model equation. R = recruitment, N = population number, SSB = spawning-stock biomass, E = environmental variable,  $l_s$  = SSB-recruitment lag,  $l_e$  = lag between environmental effect and recruitment

SR relationships are notoriously uncertain (Subbey et al., 2014) due to them being a very simplistic representation of a complex but only partially explored set of biological and physical processes (e.g. Houde, 1987; Lomartire et al., 2021; Nilssen et al., 1994). Existence and direction of environmental effects in particular are uncertain and may appear and disappear over time as recruitment time series are extended or analyzed in subsets (Myers, 1998; Free et al., 2022; Szuwalski et al., 2019). Further, SR relationships may change over time as a result of changing depensation effects (Tirronen et al., 2022) or climate-related but mechanistically difficult-to-describe regime shifts in stock productivity (Sguotti et al., 2019, Vert-pre et al., 2013). Ignoring such regime shifts can lead to erroneous assumptions about stock recovery potential (Caddy & Seijo, 2005). We accounted for SR uncertainty by fitting SR models on fractions of the stock time-series of various lengths (minimum 10 years and discarding models that had a poorer fit than a model fitted on the full time series of data) (SI CII.3), an approach similar to the analytical fitting of time-varying environmentally-sensitive SR relationships for forage-fish by Szuwalski et al. (2019). Thus we traded in generalizability of the partial SR fit for robustness against strong uncertainty about spuriousness in SR relationships (Myers, 1998) and potential productivity regimes. We fitted models assuming both a SST-recruitment time lag equaling the SSB-recruitment time lag and a time lag extended by an additional year (simulating a SST effect on spawner habitat selection and –condition, indications of which

were found in distribution- and condition observations on Western Baltic cod [Funk, 2020; Funk et al., 2021; Receveur et al., 2022] and likely resulting changed egg / larvae quality).

### **3.3.3 Simulation strategy**

Our goal was to determine a SOS for harvesting cod under future warming and hence we simulated stock dynamics under a range of fixed levels of catch and SST increase relative to the observed maximum SST. Catch levels ranged from zero kt to 50 % of the  $B_P$  estimate of each stock.  $B_P$  ( $B_{PA}$  in ICES notation) is that level of SSB below which stock reproduction is endangered of being reduced through harvesting (ICES, 2021a). A catch equaling 50%  $B_P$  is thus unlikely to endanger a stock at healthy biomass levels (i.e.  $SSB \gg B_P$ ) and productivity, but lies within historical catch ranges for most stocks. Levels of SST increase ranged from zero °C to the maximum projected over all stock areas under the SSP5-8.5 climate scenario of the IPCC (IPCC, 2021; Riahi et al., 2017), which is appx. 7 °C based on climate-model output (see SI CII.11).

In addition to the different levels of SST increase, we tested a range of initial stock sizes. Evidence is growing that healthy stock size is a requirement for mitigating climate effects on stock productivity (e.g. Sumaila et al., 2011; Free et al., 2022), hence it may be an additional dimension required for defining the SOS for a climate-sensitive fish stock. Independent from climate effects, healthy stock size is also required for attaining acceptable catch levels, as maintaining a stock at low levels naturally limits the amount of catch that can be taken, with or without precautionary limitations. We tested a range of initial stock sizes ranging from zero to 500 %  $B_P$ , which is a slightly higher level than the maximum historical ratio observed over all stocks (see SI CII.9).

In total, for each stock, we simulated for 20 levels of catch, levels of SST increase and levels of initial SSB, and tested 40 different SR relationships, with parameterizations sampled from the parameter estimates of SR relationships fitted on the various time segments of the assessment data (fig. CII.2a,b). One set of 40 parameterizations was tested for each of the two SST-recruitment lags and for each of the two variants of sequential parameter fitting (SI CII.3), yielding a total of 160 different SR parameterizations.

### **3.3.4 Risk assessment and safe operating space (fig. CII.2c-f)**

The goal of fisheries management is to maintain a target stock at a size that reduces the chance of reproductive failure and thus has a high probability of ensuring sustained harvest



(Cochrane, 2002), which equals in theory, though not necessarily in practice, a sustained maximum yield (Tsikliras et al., 2019; Rindorf et al., 2017). We accordingly evaluated combinations of catch and SST increase by comparing simulated SSB with the stock-specific precautionary reference point  $B_P$ , which separates healthy stock size from levels that increase risk of reproductive failure (ICES, 2021a). As we simulated stock dynamics under very large uncertainty about stock productivity inherent to the SR relationship (see SI CII.4), we did not use resulting average SSB directly, but rather calculated the risk of SSB dropping below  $B_P$  over all SR relationships and all iterations of the simulation (SI CII.6) (fig. CII.2c).

We then defined the SOS to be bordered by a specified risk level, i.e. all combinations of drivers resulting in a given risk or less would be part of the SOS; all others would lie outside the SOS. From a conservation point-of-view, risk should naturally be as low as possible, but natural systems like living marine resources are of interest to multiple stakeholders. A potentially very small SOS stemming from the adoption of a low risk level, with a very small maximum catch, would largely disregard the socio-economic importance of cod fishing and the associated hardship implied in the consideration of very low allowable catches. Hence, drawing from the concept of the “safe-and-just operating space” (Raworth 2012; Dearing et al., 2014), we initially investigated the effect of risk level on the magnitude of the SOS, with magnitude defined as the relative number of projection setups (combinations of catch level and level of SST increase) yielding risk equal to or less than a given threshold (fig. CII.2d). We conducted this analysis both for simulations with initial SSB equaling  $B_P$  and such with initial SSB equaling maximum initial SSB tested (500 %  $B_P$ ). We analyzed the trade-off between risk level and size of the SOS and investigated variation therein among major geographical stock areas.

Based on our risk-SOS-size analysis, we then set those driver conditions resulting in 50 % risk as the border of our SOS for the remainder of our analyses. We do not consider 50% risk as a level that could be used to mark a policy as completely “safe”, but is used here to separate policies that are more likely from those that are less likely to yield sustainable results. Furthermore, SOS size was considerably variable between stocks at 50-% risk level (see *Results - Relationship between risk level and size of the Safe Operating Space*), indicating a good foundation for further comparing SOS properties. We analyzed the SOS and investigated the relationship between catch and SST (fig. CII.2e) for simulations conducted with an initial SSB equaling  $B_P$ , as most stocks of Atlantic cod are currently over-fished and the reference

level is the nearest “good level” of stock size. For comparison, we also analyzed the SOS for simulations conducted with initial SSB equaling present stock size.

In addition, for each stock, we investigated the potential for achieving historical minimum catch or any level of catch larger than zero kt within the SOS, i.e. at a risk of unsustainable stock size  $\leq 50\%$ , and the constraints that SST increase and initial stock size put to this (fig. CII.2f). To this end, we determined the combinations of SST increase, initial SSB and catch that yielded  $\leq 50\%$  risk of stock SSB decreasing below  $B_p$ , and from this subset extracted and visualized the combinations of SST increase and initial SSB that corresponded to minimum historical catch, as well as to minimum catch larger than zero kt.

### **3.3.5 Data sources**

We used official stock assessment data (for references see SI CII.10) to initialize and parameterize our population models, as well as to fit our SR models.  $B_p$  reference points were also derived from those data where available, and were estimated from limit ( $B_{lim}$ ) reference points using ICES estimation method (ICES, 2021d) for stocks without an official  $B_p$  reference point.

NOAA SST reconstructions (ERSST V5; Huang et al., 2017) were used to fit the SR models. SST projections for climate scenarios SSP1-2.6 and SSP5-8.5 from a variety of Earth System Models were used to establish the range of expected levels of SST increase tested in our simulations (see SI CII.11 for more details).

### **3.3.6 Software**

Model projections were conducted in Python (van Rossum, 1995). Fitting of the SR functions, as well as analysis and visualization of the results, were conducted in R (R Core Team, 2020) using i.a. the “minpack.lm” (Elzhov et al., 2016) and “tidyverse” (Wickham et al., 2019) packages. Model runs were conducted on the “Levante” high-performance computer of Deutsches Klimarechenzentrum (DKRZ) (Hamburg, Germany).

## **3.4. Results**

### **3.4.1 Relationship between risk level and size of the Safe Operating Space**

We found the size of the safe operating space to be positively related to the risk level chosen to define its border (fig. CII.3). The SOS was undefined for a risk level of zero % for all stocks. For the majority of western Atlantic stocks, a discernable SOS only emerged at risk

levels of appx. 70 % (with Flemish-Cap- and Northern cod as clear exceptions [fig. CII.3 FC, NR]). In contrast, the SOS had a considerable size at markedly lower risk levels ( $\leq 25$  %) for most eastern-Atlantic stocks and especially those residing at higher latitudes, e.g. West-of-Greenland cod and North-East-Arctic cod (the SOS had a considerable size even at risk levels  $\ll 10$  % for these two stocks) (fig. CII.3 WG, AR). The West-of-Scotland and Irish-Sea stocks, showed a pattern closer to that of the western Atlantic ones, however (fig. CII.3 WS, IR). When projecting with a higher initial stock size, SOS size was generally somewhat higher but showed a similar relationship to risk level as observed for simulations conducted with initial SSB equaling  $B_P$ .

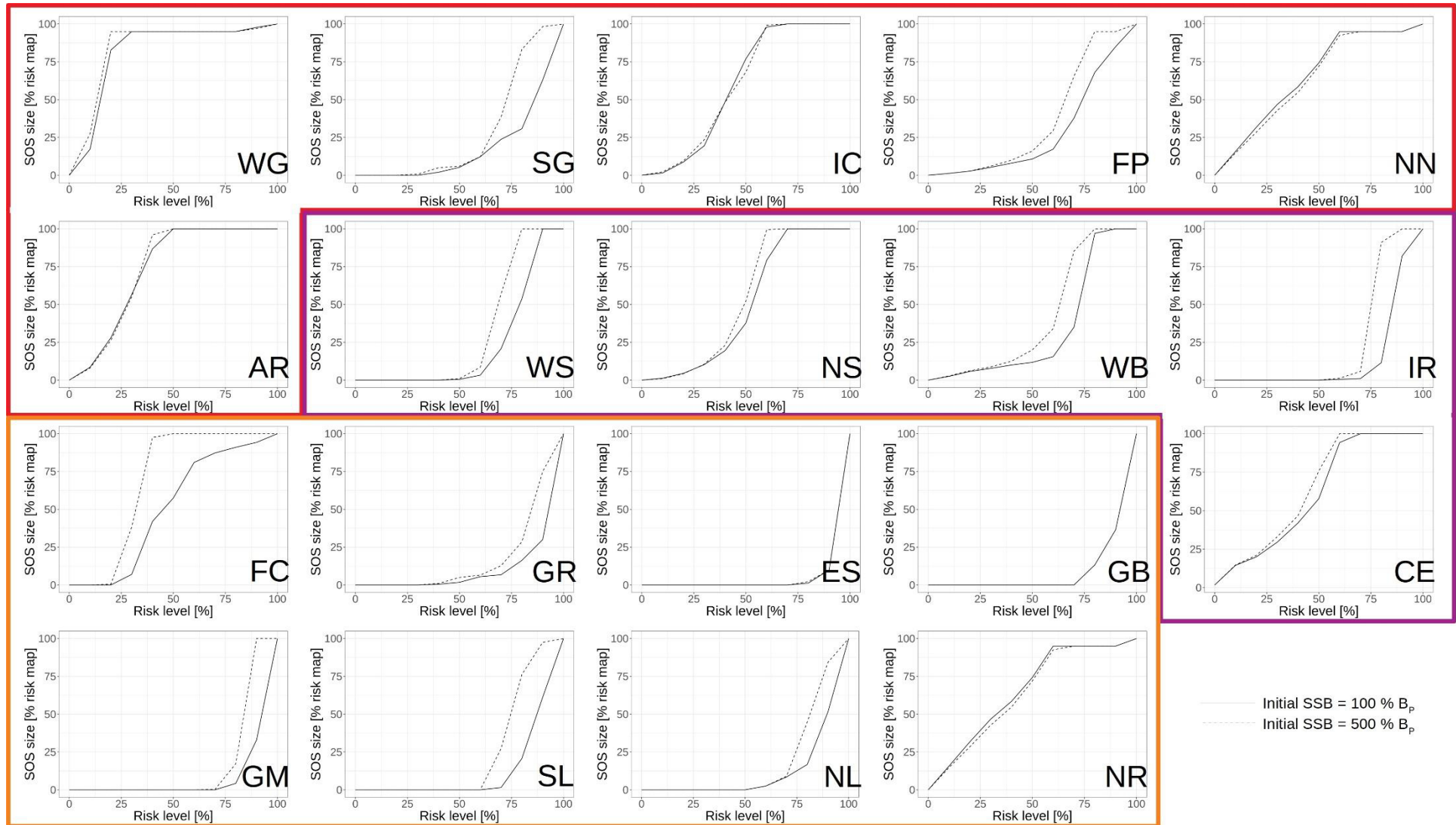


Figure CII.3. Relationship between SOS size and risk level of 19 stocks of Atlantic cod. Solid line indicates relationship for projections conducted with initial SSB equaling  $B_p$ , dashed line indicates relationship for projections with initial SSB equaling five-fold  $B_p$ . Colors denote broad geographical classification; for stock abbreviations see fig. CII.1

### 3.4.2 Characteristics of the safe operating space

Given the high variability of SOS size between stocks at 50 % risk, we selected that level as border of the SOS for the remaining analyses. We found the safe operating spaces generated for the 19 Atlantic cod stocks to exhibit three general patterns in existence, extent and direction with respect to SST increase (fig. CII.4). First, for a number of stocks no or hardly any SOS could be detected when assuming an initial SSB equaling  $B_p$ . This means that (almost) all combinations of catch and SST increase yielded a risk higher than 50 % of generating unsustainable stock size. These stocks were located almost exclusively in the West Atlantic (West-of-Scotland- and Irish cod being exceptions located in mid-latitude eastern-Atlantic areas [fig. CII.4 WS, IR]), and are generally characterized by a long history of poor stock condition and over-fishing (SI CII.9).

Second, a number of stocks mostly located on the European shelf and mostly at mid-latitudes ( $< 60^\circ\text{N}$ ) exhibited a recognizable SOS with a clear trade-off between SST increase and catch: Lower levels of SST increase supported higher levels of catch, and vice-versa, at 50 % risk of sustainable management; this trade-off typically covered the entire range of catch levels tested (fig. CII.4). The extent of the SOS in terms of maximum catch and SST varied, however, with some stocks like North-Sea and Celtic cod supporting almost the full range of SST increase tested (up to close to  $7^\circ\text{C}$ ; at marginal catch levels) and / or the full range of catch levels tested (up to 50 %  $B_p$ ) or beyond (fig. CII.4 NS, CE). For other stocks, e.g. Western Baltic cod and Faroe Plateau cod, their respective SOS supported notably lower levels of SST increase and catch (often less than half of the range tested) even at marginal levels of the respective other driver (fig. CII.4 WB, FP). The stocks belonging to this category generally show a relatively gradual historical decrease of SSB from safe to unsafe levels over time (SI CII.9).

Finally, a number of stocks displayed an SOS without any or with a high SST bound (higher than the range tested) or a lower rather than upper SST bound at 50 % risk of unsustainable management. A negative trade-off between catch and SST increase was still visible in most stocks, but was mostly limited to catch levels in the upper half of the range tested. Most stocks showed a relatively large number of SR relationships with positive environmental effects (SI CII.4), and were located in areas of higher latitudes (e.g. Northeast-Arctic cod, South-East Greenland cod [fig. CII.4 AR, SG]) and / or in off-shore waters (Flemish Cap cod [fig. CII.4 FC]). Most of these stocks also showed a relatively large SOS extent with respect to catch. An extreme case, Northeast-Arctic cod displayed no threshold in either catch or SST

increase in the ranges tested (fig. CII.4 AR). Of those stocks less limited by SST or positively affected by SST, most have very healthy stock sizes ( $SSB \gg B_P$ ) (fig. CII.5); the sole exception is Northern cod, which is in poor state but shows signs of recovery (SI CII.9); notably its SOS had a lower SST boundary (fig. CII.4 NR).

The extent of the SOS was notably smaller for some stocks (e.g. Celtic cod and North Sea cod) with respect to both catch and SST increase when assuming current stock size rather than a stock size corresponding to  $B_P$ , which in these cases typically exceeds current stock size (SI CII.9).

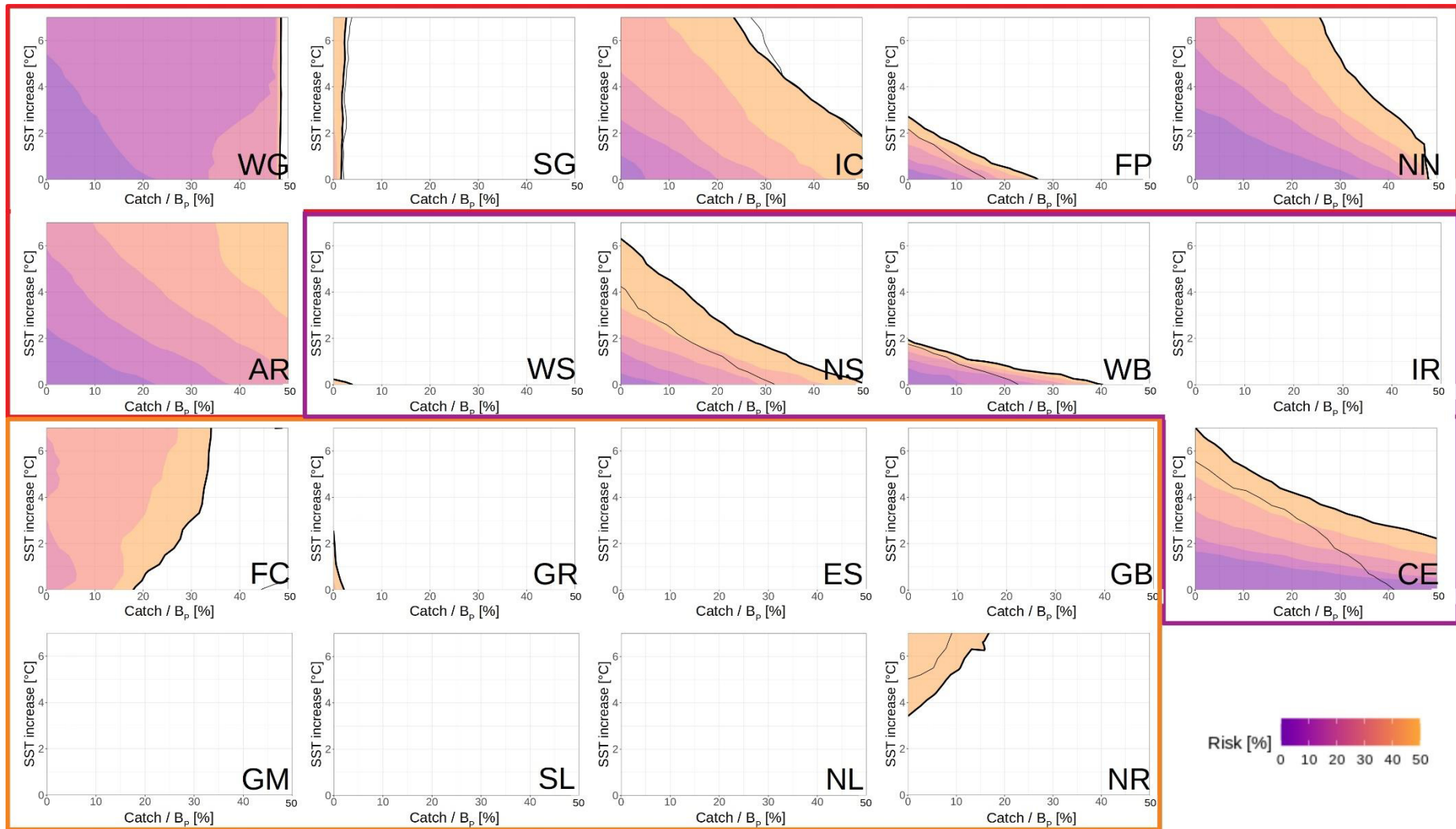


Figure CII.4. SOSs of 19 stocks of Atlantic cod under habitat warming and harvesting. Each panel shows the risk of SSB being equal to or smaller than  $B_p$  under combinations of catch (shown as %  $B_p$ ) and SST increase. Color shows risk. Thick black line is the SOS boundary, i.e. the 50%-risk isoline, under initial stock size equaling  $B_p$ . Thin black line is the SOS boundary under initial stock size equaling current SSB. Frame colors denote broad geographical classification; for stock abbreviations see fig. CII.1

### 3.4.3 Catch potential within the safe operating space

Catch potential that kept stock size at a 50 % chance of remaining above  $B_P$  depended strongly on both the level of SST increase and initial stock size for most stocks (fig. CII.5). Catches generally only fell within the SOS under increasing levels of SST increase when stock size increased, as well. However, the relationship between SST increase and stock size followed a saturation curve in most cases, thus safe catch was only possible up to a threshold level of SST increase. Likewise, safe harvest was not possible below a certain stock size in most stocks.

The threshold in SST increase for taking any level of catch under  $\leq 50$  % risk of unsustainable exploitation varied from the maximum tested, 7 °C, for e.g. Northern Norwegian coastal cod (fig. CII.5 NN), to a minimum of appx. 1.8 °C for Western Baltic cod (fig. CII.5 WB), for stock sizes well above  $B_P$ . SOSs of Northern- and South-East Greenland cod displayed lower thresholds of appx. 3.5 °C and 2 °C, respectively, above which harvesting was safe (fig. CII.5 NR, SG). Threshold stock size was relatively consistent among stocks at appx. 25 to 33 %  $B_P$ .

When aiming for catches no less than the historical minimum, both the threshold levels of SST increase and of stock size tended to be markedly lower and higher, respectively. For example, for Faroe Plateau, North Sea and Western Baltic cod (fig. CII.5 FP, NS, WB), threshold stock size related to attainment of minimum historical catch was closer to  $B_P$  compared to that related to attainment of any catch level larger than zero kt. For Celtic cod in contrast, the threshold stock sizes were similar to each-other (fig. CII.5 CE) (it should be noted that minimum historical catches vary strongly between stocks). Threshold SST increase ranged between approx. one and two thirds of the overall threshold for any level of safe catch.

Stocks not limited by SST increase when aiming for minimum historical catch include North-east Arctic, Northern Norwegian, Flemish Cap and Western Greenland stocks (fig. CII.5 AR, NN, FC, WG). For Iceland cod, minimum historical catch fell outside the range covered in the simulations ( $> 50$  %  $B_P$ ) (fig. CII.5 IC).

Notably, the SOSs of South-East Greenland- and northern Norwegian cod displayed an optimum level of initial SSB markedly lower than maximum initial SSB tested with respect to the threshold level of SST increase (fig. CII.5 SG, NN).



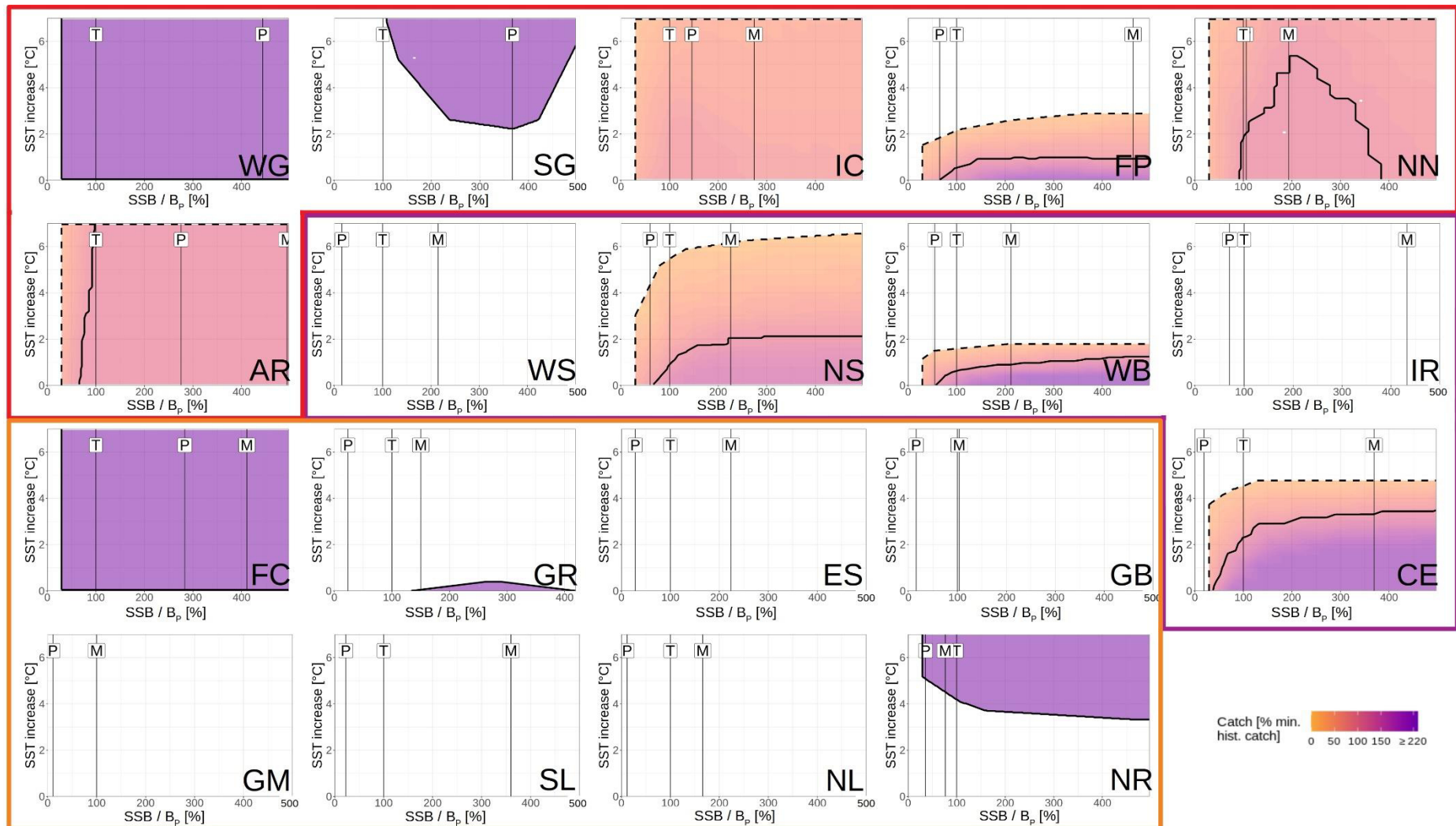


Figure CII.5. Catch potential within the SOS under different levels of stock size. Each panel shows the maximum extent of the SOS in terms of SST increase and maximum “safe” catch (i.e. catch yielding  $\leq 50\%$  risk), under a range of initial stock sizes (given as the ratio of initial SSB to  $B_p$ ). Color denotes catch level (in relation to minimum historical catch). Solid line shows maximum SST increase within the SOS that allows minimum historical catch, under different levels of stock size. Dashed line is the same for any level of catch  $> 0$  kt. Vertical lines show present SSB (P),  $B_p$  (T) and maximum observed SSB (M). Frame colors denote broad geographical classification; for stock abbreviations see fig. CII.1. For SG cod, note that compared to fig. CII.4, a lower SST-increase boundary exists, as catches of 0 kt or only marginally higher were excluded

In summary, larger SOSs both with respect to tolerable SST increase and to potential future catch under moderate warming were primarily associated with stocks that had a comparatively high level of stock size in recent decades (fig. CII.6). The large majority of these stocks is located on the European shelf and in the Greenland area (exceptions to the rule are Flemish Cap and West of Scotland cod) and unlike most of the western Atlantic stocks did not show collapse-like historical dynamics (SI CII.9). Several European stocks, most of them among the stocks with largest recent stock size and located in northerly waters, showed neither a threshold in tolerable SST increase nor limitations to future catch potential under lower levels of SST increase in the ranges tested (fig. CII.6). A trade-off between catch and SST increase was, however, visible in most of these stocks, i.e. the catch threshold for sustainable harvesting was reduced to levels below the maximum tested under increasing SST (fig. CII.4).

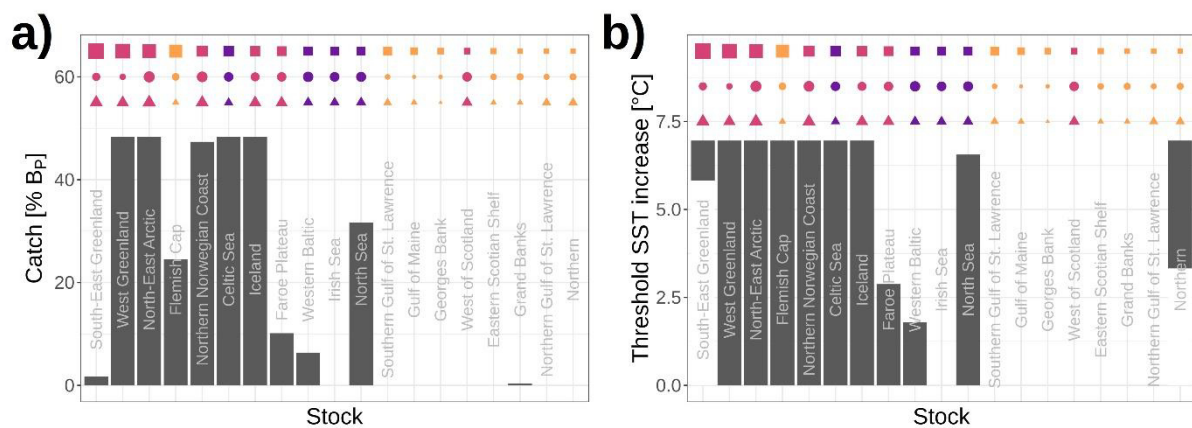


Figure CII.6. Variability of SOS properties over stock locations. Maximum catch (as % B<sub>P</sub>) at 1.5 °C SST increase for a stock with initial size equaling B<sub>P</sub> (a) and maximum safe SST increase at initial stock size equaling 5 \* B<sub>P</sub> (b). Square size indicates relative median SSB over the last 20 assessment years, dot size indicates relative longitude, triangle size indicates relative latitude, for stocks on the European shelf (purple), American shelf (yellow) and around Greenland (red). Note that a SST increase of 7 °C was the upper limited tested and is not necessarily a threshold. For Northern cod, a lower threshold of SST increase is shown

### 3.5 Discussion

In our study we operationalized the concept of “safe operating space” (SOS) for Atlantic cod fisheries for investigating the long-term viability of harvesting policies under future levels of ocean warming. The SOS concept is commonly used in applied management to identify thresholds of sustainable use of natural resources under the influence of uncontrollable driver variables (Scheffer et al., 2015; Green et al., 2017; Hansen et al., 2019). In particular, we here aimed at identifying the dependency on and relationship to future temperature increase of safe-catch thresholds, and also explored the requirement of “good stock” status to cope with climate effects on productivity.

Our results clearly indicate that future climate change will put a limit to the ability of Atlantic cod stocks to maintain a stock size that allows sustainable management in many areas of the North Atlantic. Many of these stocks are located in mid-latitudes on the European shelf, where stock depletion has been a relatively recent phenomenon compared to the situation on the North-American shelf. The clear negative climate effect in these stocks is not particularly surprising given the fact that cod is a cold-water-adapted species and is known to suffer from warming in multiple direct and indirect ways in originally temperate waters, e.g. through reduced physiological condition in both embryos and spawning adults (Dahlke et al., 2020; Receveur et al., 2022) and reduced hatching habitat due to warming-induced oxygen depletion and food limitations (Köster et al., 2005). The SST effect on northerly cod stocks ( $> 60^{\circ}\text{N}$ ) was negative to indistinct, but never clearly completely positive. The future effect on these stocks, which presently inhabit waters limiting productivity (Chabot & Claireaux, 2019) is particularly uncertain. Physiology-related studies predict an increase in available habitat and food as a consequence of sea-ice retreat (Stenevik & Sundby, 2007); on the other hand early life stage mortality may increase in response to further warming in the Barents Sea (Koenigstein et al., 2017). Potential for future sustainable management in these stocks appears to depend on uncertainty more so than in mid-latitude stocks; a current benefit potentially mitigating climate effects is their relatively good biomass status (SI CII.9) (Grafton et al., 2005). The atypically small SOS of South-East Greenland cod, (compared to those of other northerly stocks) likely results from a particularly weak SR relationship dominated by erratic extreme recruitment events (SI CII.4) possibly related to stock mixing and uncertainty about stock identity (ICES, 2022a).

The fact that a SOS only became discernable at very high risk levels for almost all cod stocks on the eastern North-American shelf, where stocks have been depleted for several decades, some since the beginning of the assessment time series (SI CII.9), points to the importance of quick management success in terms of stock recovery for the future viability of cod fisheries in stocks where severe depletion has not yet occurred (i.e. mostly in stocks on the European shelf). The clear positive relationship between SOS extent, and thus catch potential, and stock biomass adds to the importance of short-term rebuilding of stock biomass to multiples of the threshold level  $B_P$  in stocks that are not yet (fully) depleted. Management theory suggests that such “reserves” can be valuable buffers against environmental fluctuation (Grafton et al., 2005; Bell et al., 2023) and climate change (Sumaila et al., 2011; Free et al., 2022). Low stock sizes are a particular threat to fisheries management under climate change due to the atypical responses of stock dynamics to management and environmental variation observed in such

regimes: Phenomena like depensation and truncated age structures often associated with depleted stock size are known to limit recovery in general and to increase sensitivity to climate variation (Perälä et al., 2022; Winter et al., 2019; Hsieh et al., 2006). A prime example is the Northern cod, where fishing moratoria implemented after the stock collapse in 1992 did not have the expected effect of a quick rebuilding, and where biomass levels to this date are markedly below  $B_p$ ; an outcome likely resulting from both low stock size and habitat cooling (Dutil et al., 2003; Taggart et al., 1994) (our SOS indicates that habitat warming of 4 °C or more might be a theoretical necessity for achieving sustainable management [figs. CII.4,5]). The more linear relationship between SOS size and risk level (fig. CII.3) also points to a greater degree of manageability in better-conditioned stocks, further supporting the value of maintaining high levels of stock size.

The clearly defined lower-than-maximum optimum of initial SSB for resilience to warming that was detected in two stocks points to negative effects of too high population density (compensatory effects) (e.g. Rose et al., 2001). Its occurrence suggests that building of stock reserves should not be done to excessive extents; a precaution that is currently of little relevance to the many depleted stocks for which rebuilding would be clearly beneficial, however.

European fish stocks have frequently shown signs of non-linear, regime-shift-like stock dynamics (Blöcker et al., 2023a) and hysteretic reaction to management action (Sguotti et al., 2019) in response to combined effects of fishing and climate change. These dynamics typically occurred in over-fished stocks, giving further support for the importance of maintaining stocks at levels well above  $B_p$  in order to make them climate-resilient. Adequate management action can be difficult to come by in face of non-linear stock dynamics, but is ultimately key to achieve these aims and avoid declines (Möllmann et al., 2021). Of particular importance is to account for (potential) environmental effects in recruitment dynamics (Clark et al., 2003), even when the validity of environment-recruitment relationships is debated (e.g. Howell et al., 2013; Kell et al., 2005) or when assessment updates lead to the break-down of previously existing significant relationships (Myers, 1998). Evidence suggests that univariate environment-recruitment relationships may change sign and effect strength as other habitat properties change as well, as observed for SST-recruitment relationships in response to bottom temperature (Drinkwater, 2005). The diversity of our SST-recruitment functions fitted to time-series segments of variable length (SI CII.4) support the notion that environmental effects on recruitment are not temporally constant but still likely to exist. Fixation on a single perception of the stock appears to increase the risk for unintentional management failure and stock decline, as happened with Northern cod, where recruitment over-fishing was largely ruled out

before the 1992 collapse (Walters & Maguire, 1996), and even when accounting for environmental effects, as in Pacific sardine (Free et al., 2022). Accounting for (large-scale) uncertainty in stock perception, like here by implementing robust-decision-making methodology (Lempert, 2019) or by integrating over an ensemble of models (Szuwalski & Hollowed, 2016), thus appears to be a necessity for successful management; the clear dependence of SOS size on risk level indicates that recruitment uncertainty does have a profound effect on management success and should not be disregarded.

Ultimately, maintaining fishing activity on present levels while managing stocks sustainably appears to have little chance for mid- and low-latitude stocks under expected future levels of warming, at least in the long term. Mitigation actions for the short- and mid-term include more flexible harvest control rules that adapt to changing productivity situations (Kritzer et al., 2019; Free et al., 2022), though care must be taken in their design to avoid unintentional outcomes related to uncertainty and strategies based on narrow perception of stock-environment interactions (Szuwalski & Punt, 2013). Also, constraints to (short-term) harvesting increases following productivity increases appear warranted in light of the concept of desirable environmental “buffer” capacities (Bell et al., 2023; Free et al., 2022). Szuwalski et al. (2023) suggest a paradigm shift away from yield maximization towards aiming for stock stability in management under climate change. The limitations that warming puts on achieving even minimum historical catch and the importance on stock size in enabling catch under warming found in our study support the notion of a conservation-oriented management paradigm that aims for maintaining large stock biomass and also allows flexibility in reacting towards stock decrease (see also Caddy & Seijo, 2005). While much of present-day management follows maximum-sustainable-yield policies (e.g. European Union, 2013; U.S. Department of Commerce, 2007), first steps towards more flexible management have been taken e.g. through the establishment of the  $F_{ECO}$  reference point in Irish Sea cod, a variation on the target harvesting level  $F_{MSY}$  that is adjusted depending on environmental indices (Bentley et al., 2021; ICES, 2022b). Long-term climate effects may make more fundamental re-organizations of the fishing sector necessary in several regions to achieve a “safe-and-just operating space” (Raworth, 2012), however. These can include shifting target species (as in the shift from cod to lobster in the Gulf of Maine [Le Bris et al., 2018; Hamilton et al., 2004]) or diversifying livelihood (Roscher et al., 2022).

Our study is, to our knowledge, the first to implement the SOS concept on a large-scale fisheries-management scenario. We expand the existing frameworks that are most often imple-

mented to define resource-use- and environmental thresholds for very concrete management questions based on data-analysis methods (e.g. Ramírez et al., 2021; Carpenter et al., 2017) by addressing a long-term management issue and accordingly using modeling techniques and introducing consideration of larger degrees of uncertainty. The SOS concept adds to classical MSE setups (Punt et al., 2016) the testing of a broader range of policies and environmental scenarios, as well as, in our case, a broader range of uncertainty.<sup>1</sup> This approach allows for a larger degree of process understanding and detection of dominant patterns (over the various uncertain scenarios) than a selection of discrete “most likely scenarios” could, even though some scenarios might appear extreme from today’s perspective. The concepts of “planetary boundaries” and “safe operating space” have been criticized for emanating a “top-down” perspective to political guidance (reviewed in Biermann & Kim, 2020), a short-coming that also exists in current fisheries management (Schwermer et al., 2021a). We advocate our SOS design to highlight stock responses to combined harvesting and warming and to estimate likely thresholds for sustainable management in the two drivers, but concur that effective management should draw upon a multiplicity of stakeholder inputs.

We do caution not to over-interpret the results for stocks that show no clear upper SST boundaries in their SOS or instead a lower SST boundary. While one can expect positive SST effects on recruitment (SI CII.4), which are the basis for the mentioned SOS properties, to hold near the observed SST range, the dominance of negative SST-recruitment relationships especially in warmer areas suggests that effect direction will likely switch sign as habitat conditions change to novel levels (*sensu* Drinkwater, 2005). Impacted by this might also be the recovery potential for Northern cod suggested by our SOS to be enabled only at higher degrees of warming (figs. CII.4,5). Also, we advise to consider assessment confidence when drawing conclusions for policy-making from our SOSs; for example, confidence in the perception of Western Baltic cod is currently relatively low (ICES, 2023b), hence there is potential for the respective SOS to be too optimistic. Further, the assessment data for most of the western-Atlantic stocks almost exclusively contain post-collapse data, which are known to be affected by depensatory effects (Neuenhoff et al., 2019). We were thus unable to fit SR relationships corresponding to higher-productive earlier regimes, and the SOSs for these stocks might be comparatively conservative. Despite the constraints that SR uncertainty obviously still poses for the estimation of productivity ranges in specific cases, we are convinced that our SOS

---

<sup>1</sup> development of a SOS-based MSE would entail the simulation of the entire management cycle, i.a. the additional simulation of stock monitoring, -assessment and management implementation and associated errors when aiming for very concrete management advice (Punt et al., 2016)

concept is robust enough for an overall assessment of future manageability of Atlantic cod under warming given currently available knowledge.

In conclusion, our SOS-based analysis revealed a high variability of SST- and harvesting effects on the future viability of Atlantic cod fisheries. We showed that management needs to consider climate effects, even if they are obscured by temporally changing or “fuzzy” relationships, if sustainability is to be achieved. Sustainable management will, however, most likely not be possible under strong warming expected for some stocks and under the extreme degree of depletion limiting productivity in others. Maintaining or achieving a stock size well above  $B_p$  appears to be the safest bet against negative environmental effects (Free et al., 2022; Lauck et al., 1998), and to be a prerequisite for sustainable catch on (minimum) historical levels under climate change. While our SOS concept certainly leaves room for extension, by e.g. considering mixed-fisheries- or food-web aspects, we believe that as presented here, it is a handy, comprehensive and robust tool for performing quantitative assessments of future harvesting potential of climate-sensitive fish stocks.

### **3.6 Data availability**

All data and code will be made available on [https://github.com/imf-uham/SOS\\_Cod](https://github.com/imf-uham/SOS_Cod) upon publication of the study in a scientific journal and are available from the author on request.

### **3.7 Conflict of interest**

The authors declare no conflict of interest.

### **3.8 Acknowledgements**

We would like to thank Diana González-Troncoso (Instituto Español de Oceanografía), Charles Perretti (Northeast Fisheries Science Center), Paul Regular (Fisheries and Oceans Canada), Pia Schuchert (afbi Agri-Food & Biosciences Institute) and Gary Shepherd (Northeast Fisheries Science Center) for making available additional assessment data to us, and for generously providing insights on and help with the assessments of the western North-Atlantic cod stocks.

We would further like to thank Eleanore Campbell (Stockholm Resilience Center) for preparing the SST-projection data for our modeling work, and Hanna Robitschko (Universität Hamburg) for helping to extract data from the stock-assessment reports.

JC received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 820989 (project COMFORT, Our common future ocean in the Earth system – quantifying coupled cycles of carbon, oxygen, and nutrients for determining and achieving safe operating spaces with respect to tipping points). The work reflects only the authors' view; the European Commission and their executive agency are not responsible for any use that may be made or the information the work contains.

SF received funding from the German Federal Ministry of Education and Research (BMBF) through the project SpaCeParti (Coastal Fishery, Biodiversity, Spatial Use and Climate Change: A Participative Approach to navigate the Western Baltic Sea into a Sustainable Future, grant no. 03F0914A-F).

CM was partly funded by the marEEshift project (Marine ecological-economic systems in the Western Baltic Sea and beyond: Shifting the baseline to a regime of sustainability, grant no. 01LC1826) funded by the German Federal Ministry of Education and Research (Bundesministerium für Bildung und Forschung, BMBF).



## 4. Chapter III: Designing sustainable management strategies for Atlantic cod (*Gadus morhua* L.) under deep uncertainty via multi-objective optimization

Jan Conradt<sup>1\*</sup>, Steffen Funk<sup>1</sup>, Christian Möllmann<sup>1</sup>

<sup>1</sup>Institute of Marine Ecosystem and Fishery Science, Universität Hamburg, Hamburg, Germany

\*Principal author

### 4.1 Abstract

Management of living marine resources is increasingly affected by climate change, which introduces uncertainty about stock response to the effect of fishing. Established paradigms regarding yield maximization tend to lose validity under non-equilibrium conditions and are strongly affected by uncertainty regarding stock productivity, which limits long-term management strategies. Here we present a novel approach to designing and investigating fisheries management strategies robust to climate change: Adopting techniques from the field of decision-making under deep uncertainty, we optimize a time series of fishing mortality (F) in a simulated cod population facing both uncertainty and climate-sensitivity in the recruitment process. We optimize for both increasing the chance of achieving sustainable stock size and of making a viable catch, and test the potential of achieving a range of target catch levels, under a scenario of future warming. Our approach generates sensible harvesting trajectories that, by reducing F, enable stock biomass to remain at healthy levels in spite of temperature-driven recruitment reductions. Optimal harvesting trajectories are on a much reduced level when considering a wide range of potential stock-environment-recruitment (SER) relationships, leading to enlarged risk of missing higher levels of target catch but maintaining risk of stock depletion at a low level. Finally, we embed the optimization approach into a management simulation, aiming to mitigate the effects of a temporally changing SER relationship by optimizing F with consideration of deep uncertainty to SER every five years. Resulting stock size and catch are markedly higher compared to a classical MSY-based approach not informed by deep uncertainty. We conclude that mathematical optimization under deep uncertainty can be an important tool for guiding the development and dynamic adaptation of suitable harvesting pathways under dynamic climate development and unpredictable dynamic SER relationships.

**Key words:** Long-term management planning, deep uncertainty, climate change, Western Baltic cod, optimization

## 4.2 Introduction

Globally, fisheries face increasing uncertainty towards their manageability under climate- and other environmental change. Productivity of fish stocks increases or decreases, both on an individual and on population level (Pörtner & Peck, 2010), and their geographical distribution changes (Tittensor et al., 2021), with magnitude and direction depending on their physiological tolerances (Smalås et al., 2023) and life-history traits (Hollowed et al., 2013; Kuo et al., 2021) and simultaneous alterations of food availability (Cominassi et al., 2020), predator abundance (e.g. Swain et al., 2015) and habitat (e.g. Huserbråten et al., 2019). A general consensus is, however, that the majority of fish populations will (eventually) respond negatively to warming (Free et al., 2019). As a result, long-term ecosystem projections predict a significant loss of marine biomass in the course of the 21<sup>st</sup> century, as well as major re-distributions of living marine resources around the ocean (Lotze et al., 2019; Blanchard et al., 2012) and fisheries yield (Free et al., 2019). Even advanced, ecosystem-based management is predicted to have limited capability of climate mitigation (Holsman et al., 2020). The poor state of many fish stocks, i.e. in terms of stock biomass and truncated age structure (Barnett et al., 2017), which result from major over-fishing by industrialized nations in the latter half of the 20<sup>th</sup> century (e.g. Myers et al., 1996), exacerbates the risk from climate change due to their reduced productivity (Ohlberger et al., 2022) and increased sensitivity against averse environmental conditions (e.g. Taggart et al., 1994; Hsieh et al., 2006).

Fisheries management and scientific advice, while increasingly needed to mitigate these crises (*sensu* Galappaththi et al., 2021; *sensu* Holsman et al., 2020), is challenged by rapid environmental change, as well. This manifests in fish stocks reacting in unforeseen ways to management action, often not achieving the population growth expected from harvest control measures such as catch limitations (e.g. Hutchings & Rangeley, 2011; Hutchings, 2000) due to climate change exacerbating the consequences of over-fishing, e.g. Allee effects (Sguotti et al., 2019; Winter et al., 2019). Management plans, e.g. intended for rebuilding an over-fished stock, as well as scientific understanding of population dynamics, get confounded as a consequence, eliciting uncertainty about future harvesting potential (Britten et al., 2017). A prime phenomenon in unforeseen population response is the occurrence of non-linearities and productivity regimes (Ottersen et al., 2013), characterized by marked differences in recruitment production (Blöcker et al., 2023a) and stock response to fishing (Sguotti et al., 2019). Such non-linear stock behavior might be caused by i.a. compensatory mechanisms in depleted stocks (e.g. Perälä et al., 2022), such as increased vulnerability to predation (e.g.

Swain & Sinclair, 2000) and environmental forcing (Lilly et al., 2013), and reduced physiological condition (Receveur et al., 2022), but general causes are often not finally resolved and capability to predict regime shifts is limited (Szuwalski & Punt, 2013; King et al., 2015).

With status-quo fishing becoming increasingly unlikely under climate change (e.g. Brander, 2007; Holsman, 2020), an emerging concept in fisheries management is the adoption of long-term management plans, guided by so-called Management Strategy Evaluation (MSE) (Smith, 1994). MSE tests alternative harvest-control rules (HCRs), such as a fixed harvest rate, for its long-term viability against various scenarios of population dynamics (Punt et al., 2016). MSE then seeks to identify HCRs that generate an acceptable trade-off between different (e.g. conservation- and economical) objectives informed by stakeholders (Holland, 2010). So far, the incorporation of environmental change into MSE has met with limited success, with the major constraint being the limited predictability of regime shifts and difficulty in characterizing within-regime stock behavior (King et al., 2015; Szuwalski & Punt, 2013). Regular updates of MSE-based plans with developing perception of stock response to environmental drivers, and / or the adoption of strategies robust to uncertainty, i.e. to a variability of stock assumptions, have been proposed as means to mitigate predictive limitations (Skern-Mauritzen et al., 2016). A frequently-formulated challenge still is defining the principles by which to select (or weight) such alternative stock models (e.g. Punt et al., 2016; Sainsbury et al., 2000; Butterworth & Punt, 1999).

The appropriate selection and communication of uncertainties are common challenges in environmental management, including fisheries management (e.g. Ho & Budescu, 2019; Payne et al., 2016; Holland, 2010). A relatively novel perception is the importance of assessing the consequences of management action given uncertainties, compared to improving comprehensive system understanding and skill of model predictions and deriving management advice thereof, as fatality of decision consequences under a less-probable but critical state may weigh stronger than predicting such a state erroneously (*sensu* Pielke et al.; 2000; Rademeyer et al., 2007). Modern decision-making approaches propose that when significantly improving model skill is unlikely to be achieved with available knowledge, resources and time, (timely) selection of management strategies should be informed by robustness and / or capacity for adaptation to uncertainty (Lempert et al., 2004; Lempert & Popper, 2005). This approach has been proposed in particular for the management of ecosystems faced with novel environmental conditions related to e.g. climate change in the

future (Schindler & Hilborn, 2015). The conceptual guidelines of Decision-Making under Deep Uncertainty (DMDU) suggest considering a very broad range of possible system states when selection according to probabilistic means proves difficult (Marchau et al., 2019). A common approach, termed Robust Decision-Making (RDM), is to stress-test a set of candidate strategies against these states, in order to determine such strategies whose performance does not deteriorate, or does so to the lowest extent, in any state (Lempert, 2019).

An exemplary species with an uncertain future is Atlantic cod (*Gadus morhua* L.), which has high commercial importance (as well as socio-cultural value) that experienced significant over-fishing and is currently in poor condition throughout much of its distributional range (Rose, 2018a; Rose, 2018b). The Western Baltic cod stock is particularly affected by climate change and uncertainty: It displays clear signs of climate sensitivity in the recruitment process (Planque & Frédou, 1999), as well as productivity regimes, and now resides in a stable state or low productivity (Sguotti et al., 2019; Möllmann et al., 2021). The Western Baltic cod stock is historically of primary importance to the fisheries in the Baltic area, as one of only three roundfish species of major commercial interest in the area (ICES, 2022c). It is subject to recent rebuilding failures, forcing major catch reductions and evoking threats to local fishers (Möllmann et al., 2021; German Federal Ministry of Food and Agriculture, 2022). The stock also features a weak stock-environment-recruitment relationship (see fig. 3.7 in ICES [2021]), indicating that early life history and its dependence on environmental pressures is complex and / or highly variable. Devising robust management strategies for this stock is thus of major relevance to the local fishery and if successful could be considered a benchmark for stocks in better condition and / or with more resilient fisheries.

The need for robust strategies for ecosystem management, and fisheries management in particular, is generally recognized (Schindler & Hilborn, 2015), given the difficulty in predicting recruitment and thus precisely projecting stock dynamics (Subbey et al., 2014; Haltuch et al., 2019; Payne et al., 2016; Szuwalski & Hollowed, 2016), and especially stock response to climate change (Myers, 1998). However, a framework for devising management strategies that can account for deep uncertainty is so far missing. A particular difficulty in adapting the RDM approach for the exploration of fisheries management strategies is the dynamic nature of what constitutes a “robust” policy under environmental change – HCRs based around a constant harvest rate are beneficial because they adapt the catch to stock biomass (Walters & Parma, 1996), but are at the same time limited in skill because the

optimal rate may change with increased environmental pressure (Szuwalski & Hollowed, 2016). Steps towards accounting for uncertain stock response to a dynamic environment include relating harvesting intensity to stock biomass (Kritzer et al., 2019) or regular checks for and, if applicable, incorporation into management planning, of environmental effects on a target stock (Skern-Mauritzen et al., 2016). These approaches are reacting rather than forward-looking, however. The design of strategies that consider the long-term effects of harvesting under combined deep uncertainty and dynamic environmental change is thus a remaining challenge.

We here introduce a novel procedure for adding to the design of robust and adaptive management pathways intended to keep a fishery sustainable under climate change and uncertainty about the recruitment regime. We use mathematical optimization with constraints to generate a trajectory of fishing mortality ( $F$ ) that maintains a fish stock at sustainable levels of biomass under a scenario of ocean warming and simultaneously attempts to attain a specified level of target catch, but not at the expense of the former objective. Following the RDM approach, we incorporate a multitude of temperature-sensitive stock-recruitment functions fitted to various segments of the historical stock time series in order to account for the poorly-defined and potentially variable (regime-based) recruitment process. A progression from both classical MSE- and RDM protocols, we here replace the testing of different management *strategies* with the testing of different management *targets*, relying instead on the “intelligent optimization” to devise the most robust strategy for each target, and report the risk of not achieving sustainable stock size and target catch as our robustness metric. We then test our approach by repeating the optimization under uncertainty every five years in a scenario with a single but temporally changing underlying stock-recruitment relationship, with the switches being random and unpredictable. We stress that our approach is intended to test potential additions to MSE in a comparatively simpler model framework, which allows for their more rapid evaluation before incorporation in the full MSE framework.

### **4.3 Methods**

Our optimization approach consists of the following key steps: A recurrent neural network (RNN) makes a prediction of  $F$  in steps of one year. The  $F$  is incorporated into an age-based population model that predicts age-specific stock size, spawning biomass (SSB) and catch. Recruitment to the population is predicted from SSB and projected sea-surface-temperature (SST) data. The procedure is repeated for every year in a time series from 2022 until 2100,

and over different assumptions about the stock-recruitment relationship, as inferred from parameterizations drawn from partial fits of the SR function over time-series segments. The cumulative divergence between SSB and the precautionary reference level (termed  $B_{PA}$  by the assessment agency International Council for the Exploration of the Sea [ICES], here referred to as  $B_p$ ), as well as between catch and a target catch level, is used to update the RNN's parameters, in order to improve the  $F$  prediction and reduce the divergence of predictions to the specific objectives. A risk computation aggregating results obtained under different assumptions about the SR relationship completes the analysis (fig. CIII.1).

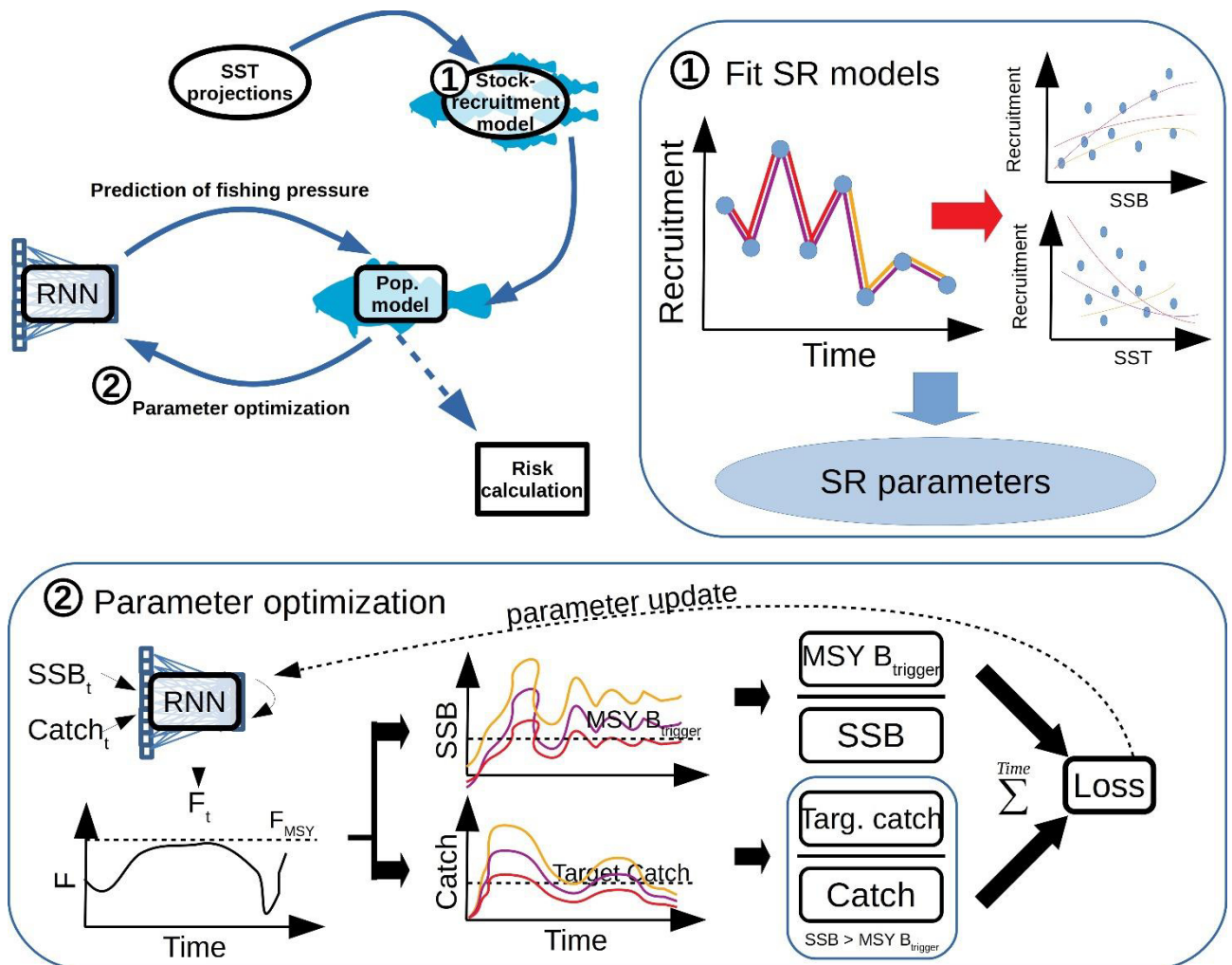


Figure CIII.1: Design of the modeling and optimization procedure: A population model incorporates a climate-sensitive stock-recruitment model, which is forced with temperature (SST) model data corresponding to a climate scenario. Fishing pressure is predicted by the recurrent neural network (RNN), and is incorporated in the population model to predict population survival numbers and catch. The ratio of the precautionary reference SSB level ( $B_p$ ) to projected SSB, and the ratio of target catch to projected catch, is used to update the RNN parameters (via gradient descent) and thus improve the time series of fishing pressure. Multiple SR parameterizations based on partial fits of the SR function on segments of the recruitment time series were incorporated to account for SR uncertainty, and parameter updates were conducted by averaging over the projections for parameterizations. Risk analyses were conducted to evaluate the performance of the optimized fishing trajectory with respect to sustainability- and catch objectives.

### **4.3.1 Population model**

The population model is a classical age-based model (Allen, 1975) that closely matches the population model used in fish stock assessments (see SI CIII.1, SI CIII.4). Cohorts of fish are projected through time and age classes in annual steps, their numbers are reduced by age-specific natural- and fishing mortality (F) (age-specificity in the latter corresponds to variable selection of size classes). The population spawns annually, with SSB depending on population size and age-specific weight and maturity rates. As processes describing the highly stochastic early-life-stage period are not well explored and not described mechanistically in the model, the recruitment of juvenile fish to the stock is instead predicted from a statistical relationship with SSB and SST; the latter represents an environmental pressure on the early life-stages. Recruitment is the only source of stock replenishment, as all other processes lead to reduction of stock numbers. Catch is calculated from cohorts by multiplying the ratio of fishing- to total mortality with the number of non-surviving fish.

We initialized the population model with assessment estimates of stock numbers and SSB from the 2021 assessment of Western Baltic cod (ICES, 2021e) (SI CIII.11) and projected the stock until the year 2100, forcing recruitment with projected SST data from a collection of physical ocean models of the western Baltic Sea (Saraiva et al., 2018; Meier et al., 2019) for the IPCC emission scenario RCP8.5 (Moss et al., 2010). Age-specific natural mortality, maturity and individual weight were kept constant at 2021 values (SI CIII.11). For reference, we also projected the stock with SST kept constant to the 2020 value, which represents static environmental conditions.

### **4.3.2 Stock-recruitment model**

The relationship between SSB, environmental drivers and recruitment is highly stochastic but follows the basic assumptions I) that recruitment increases asymptotically with increasing SSB up to a level informed by ecological limitation and II) that recruitment decreases with increasing SST in a negative exponential relationship. These mechanisms are formulated in the Beverton-Holt stock-recruitment (SR) equation (Hilborn & Walters, 1992) (SI CIII.2).

We initially fitted a SR model to data covering the period 2006-2020 (with respect to SSB), which reflects the current relatively distinct regime of reduced stock productivity of our model population, the Western Baltic cod stock (Möllmann et al., 2021). SSB- and recruitment data were taken from the 2021 stock assessment (ICES, 2021e), and SST data were taken from the reconstructions produced by the Baltic Sea Ice Ocean model (Lehmann

& Hinrichsen, 2000; Lehmann et al., 2002; Lehmann et al., 2014) (quarter-3 SST, average over the entire western Baltic Sea). We utilized this SR relationship for an initial optimization analysis aimed at understanding the population- and catch dynamics resulting from the optimized F trajectories.

Within model projections, we limited recruitment predictions to the maximum historically observed recruitment (appx. 222 million fish [ICES, 2021e]), in order to avoid unnaturally high recruitment predictions.

### **4.3.3 Incorporation of RDM techniques**

To explore the potential for optimizing F for robustness against uncertainty about the recruitment process, we fitted SR models on several periods of different length (vectors of consecutive data; minimum length 10 years) of the historical stock data (period 1985-2020) (SI CIII.2). The approach resembles somewhat the analytical fitting of time-varying environmentally-sensitive SR models for forage fish by Szuwalski et al. (2019), but is used here to generate possible future SR scenarios. We then sampled the resulting value range of each of three SR-model parameters at a constant interval to obtain a set of 90 SR models (SI CIII.2) that differ widely in predicted recruitment strength for equal levels of SSB and SST (fig. SI CIII.8 / 1). The approach allowed accounting for the high level of SR stochasticity, which can manifest in difficult-to-predict productivity regimes (e.g. Szuwalski & Punt, 2013), and also for the observed spuriousness of environment-recruitment relationships (Myers, 1998).

### **4.3.4 Design of the neural network**

We utilized a simple form of a recurrent neural network (RNN) for making optimal decisions on F (SI CIII.3), as neural-network-based optimization- / machine-learning approaches have shown promising results in simulated environmental management, including fisheries management (e.g. Strnad et al., 2019; Lapeyrolie et al., 2022) and RNNs are a powerful tool for such approaches (Kapturowski et al., 2019). (For validation, we compared RNN-based optimization with optimization of a simpler logistic model and with direct optimization of fishing mortalities, and obtained markedly lower catch risk in the first approach [SI CIII.10]). RNNs are a type of neural network frequently utilized in processing of time-series data, e.g. natural language (e.g. Goodfellow et al., 2016). Core to the RNN is a so-called long-short-term-memory (LSTM) cell that processes state-dependent input data (e.g. spoken words) to make a numeric prediction or decision. Parameterized connections between equal cell



components at different time steps form the network structure of a simple RNN (Hochreiter & Schmidhuber, 1997).

We incorporated a RNN with a single LSTM cell (RNNs for tasks involving complex data usually contain multiple cells) for “predicting” (or deciding)  $F$  at each time step of the population projection, with SSB and catch as input data.  $F$  was calculated by multiplying the RNN output, ranging between 0 and 1, with a maximum  $F$  set to  $F_{MSY}$  (0.26).  $F$  predictions made from state information from all 50 SR models was averaged to yield the final  $F$  “decision”. The decided  $F$  was then incorporated into the population model at a given time step to predict cohort reduction, SSB and catch. The results of letting the applying the RNN to the population model over the whole projection time series were trajectories of  $F$  decisions and resulting SSB, catch and recruitment.

#### **4.3.5 Design of the optimization procedure**

We updated the parameters of the RNN iteratively via gradient descent on the loss function yielded by the population model. In order to allow for maximum flexibility in terms of attaining year-specific optimum  $F$  values, we treated the RNN parameters as random, i.e. optimized a discrete set of parameters for each projection year. We calculated total loss as the added ratios of  $B_P$  to projected SSB and target catch to projected catch, summed over all projection time steps and averaged over all 50 SR models (SI CIII.6). Our target was to increase both SSB and catch, i.e. to optimize both for sustainability and for achieving / exceeding a target catch. (An increase of SSB or catch leads to a decrease of the respective ratios and thus of the loss).

We added a constraint that the SSB ratio should only be computed when SSB was equal to or lower than  $B_P$  and that the catch ratio should only be computed when catch was below the target catch level and when SSB was higher than  $B_P$  (SI CIII.6), in order to enable a balanced optimization sensitive to stock status, with sustainability taking precedence over achieving target catch.

Optimization was performed using the “Adam” algorithm (Kingma & Ba, 2014), which is a state-of-the-art optimizer for neural networks (see SI CIII.5 for hyper-parameter settings). As we were not interested in the mathematically exact optimal solution, but in discovering sensible harvesting trajectories in a sensible amount of computing time, we performed heuristic optimization (Wang & Chen, 2013) by running parameter updates for 10,000

iterations, and validating for loss stabilization as an indicator of approximate convergence on optimal parameterization (SI CIII.8).

#### **4.3.6 Target catch levels**

For the initial exploratory optimization runs conducted with a single SR relationship, we set the target catch level to the maximum historical catch in the assessment time series (appx. 53 kt [ICES, 2021e]), in a purely functional capacity to avoid  $F$  being reduced to zero to maximize SSB. In order to evaluate the catch potential of Western Baltic cod under SR uncertainty and future climate change, we optimized for a range of target catch levels from 0.5 to 16 kt, i.e. appx. one eighth to four times recent catch (2021; appx. 4 kt) in those runs conducted with variable SR-model parameterization.

#### **4.3.7 Risk analysis**

We evaluated the performance of the optimized  $F$  trajectories by aggregating the projected SSB- and catch time series and calculating two risks, namely the risk of SSB being below  $B_P$  (termed “sustainability risk”) and the risk of catch being below target catch (termed “catch risk”), for each level of target catch and each year. Risk was defined as the number of occurrences of undesirable events divided by the total number of SR parameterizations (SI CIII.7).

#### **4.3.8 Optimization scenarios**

In order to obtain insight into the basic properties of the optimization procedure under equilibrium stock conditions, we initially conducted an optimization for a single SR relationship (see above) and keeping SST at constant (2020) level. Next, we expanded on this set-up by incorporating a trajectory of SST as projected under the RCP8.5 scenario, in order to investigate the temperature sensitivity of the optimization and the climate-adaptiveness of the predicted management pathways. Finally, we incorporated the full set of SR relationships fitted on various time segments of the full stock-assessment time series in order to obtain optimal management-pathways adapted to SR uncertainty and climate change.

#### **4.3.9 Testing under dynamic SR scenario**

To assess the performance of optimization approach in a management scenario (fig. CIII.2a), we generated a sequence of random SR relationships sampled from the 90 different parameterizations generated above, with the SR relationship changing every five years (fig. SI

CIII.8 / 2). This sequence represents the simulated “ground truth” that is unknown to the manager. Starting from the first projection year, we optimized the trajectory of  $F$  every five years for the remaining years, over all 90 SR parameterizations (as above). We then applied the optimized  $F$  for five years, with recruitment generated by the corresponding SR relationship from the ground-truth sequence, thus obtaining the actual population- and catch trajectories for that time frame. We then repeated the procedure for the following five-year periods, until the projection year 2100.

We compared this approach with the classical  $F_{MSY}$  approach incorporating the ICES advice rule (ICES, 2021a) (fig. CIII.2b), on the same ground-truth sequence of SR relationships. According to the ICES advice rule, the stock is fished with  $F_{MSY}$ , and  $F$  is linearly reduced by multiplication with the ratio of  $SSB$  to  $B_P$  once the former drops below the latter to reduce the risk of reproductive failure. Once  $SSB$  is below the limit reference point ( $B_{lim}$ ),  $F$  is set to zero due to imminent danger of reproductive failure.

We repeated both procedures for five randomly generated sequences of SR relationships, and optimized for a target-catch level of 4 kt. The number of optimization iterations was here limited to 1000 for every five-year period due to the constraint of total computation time.

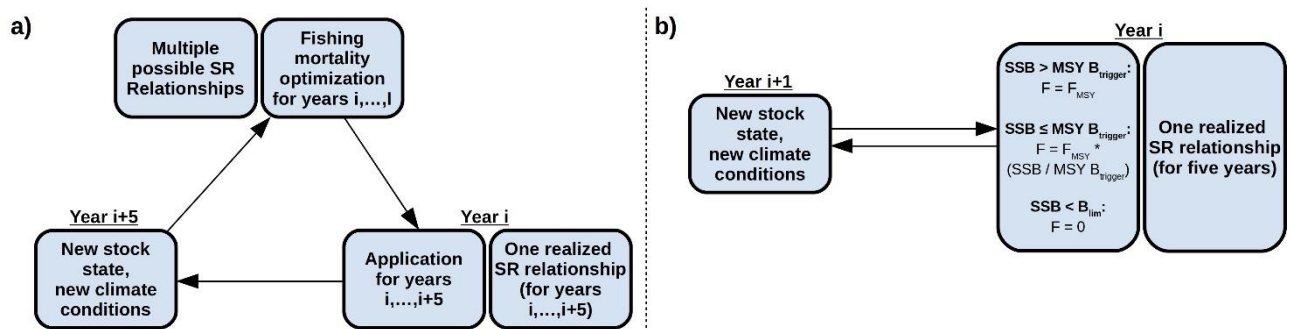


Figure CIII.2: Procedure of testing the optimization approach in a dynamic SR scenario. (a) Optimization approach: fishing mortality ( $F$ ) is optimized every five years for the remaining time period while considering the full range of SR uncertainty. It is applied to a stock whose actual SR relationship changes randomly every five years. The optimization is then repeated, and the optimized  $F$  applied on the next period of five years, etc. (b) Application of the  $F_{MSY}$  / ICES advice rule approach (ICES, 2021a) on the same underlying system.  $F$  is set to  $F_{MSY}$  or reduced to a lower level or set to zero depending on  $SSB$

#### 4.3.10 Software

The population model was written in C++ (Stroustrup, 1996) for access with Template Model Builder (Kristensen et al., 2016) through the R programming language (R Core Team, 2020). Feeding of the model with input data, as well as optimization, was conducted in R. Fitting of

the SR models was done with the “nlsLM” optimizer available from the “minpack.lm” R package (Elzhov et al., 2016). Risk analysis and visualization were performed using the “tidyverse” (Wickham et al., 2019) R package.

#### 4.4 Results

Our results clearly demonstrate the capability of our rule-constrained optimization procedure to generate sensible management pathways under steady environmental conditions and without stochasticity to the functional relationship between SSB, SST and recruitment:  $F$  was maintained at zero for two years followed by an almost instant increase to  $F_{MSY}$  (fig. CIII.3a), following a strong exponential increase of SSB within these first two years (fig. CIII.3c). Consequently, catch increased similarly quickly (fig. CIII.3d), while recruitment increased only slightly from the initial level (fig. CIII.3b), an indication of the low productivity regime reflected by our SR relationship. SSB exceeded  $B_P$  (c. 23 kt) approximately 5 years into the projection and attained a stable level of appx. 37 kt by the early 2030s; catch reached its stable maximum of about double current levels (appx. 7.8 kt vs appx. 4 kt in 2021) at a similar time.

Management- and stock pathways were notably altered under the RCP8.5 warming scenario: An initial increase in  $F$ , SSB and catch was likewise observed, but the maxima of SSB and catch noted above were never reached (fig. CIII.3). SSB peaked early at appx. 30 kt and was then maintained at and occasionally slightly above  $B_P$  (fig. CIII.3c). Conversely, recruitment,  $F$  and catch all showed two phases of strong decrease throughout the projection trajectory: Recruitment was almost halved from an early high level in the mid-2020s to a relatively stable level of on average 10 million fish (though with temporal variability of appx.  $\pm$  5 million fish) by the late 2020s, which was maintained until 2060 (fig. CIII.3b).  $F$  and catch followed suite, with the former decreasing from  $F_{MSY}$  to, on average, 0.2 (fig. CIII.3a) and the latter decreasing by appx. 2 kt to on average 4.5 kt, by the mid-2030s (fig. CIII.3d). A second major recruitment decrease occurred around 2060, with again an almost-halving to on average 5-6 million fish (fig. CIII.3b).  $F$  and catch were consequently sharply halved by the mid-2060s, and did not stabilize but further decreased, albeit gradually, as did recruitment. At the end of the projection, catch was only appx. 10 % of the early maximum, while SSB was still stable at  $B_P$ .

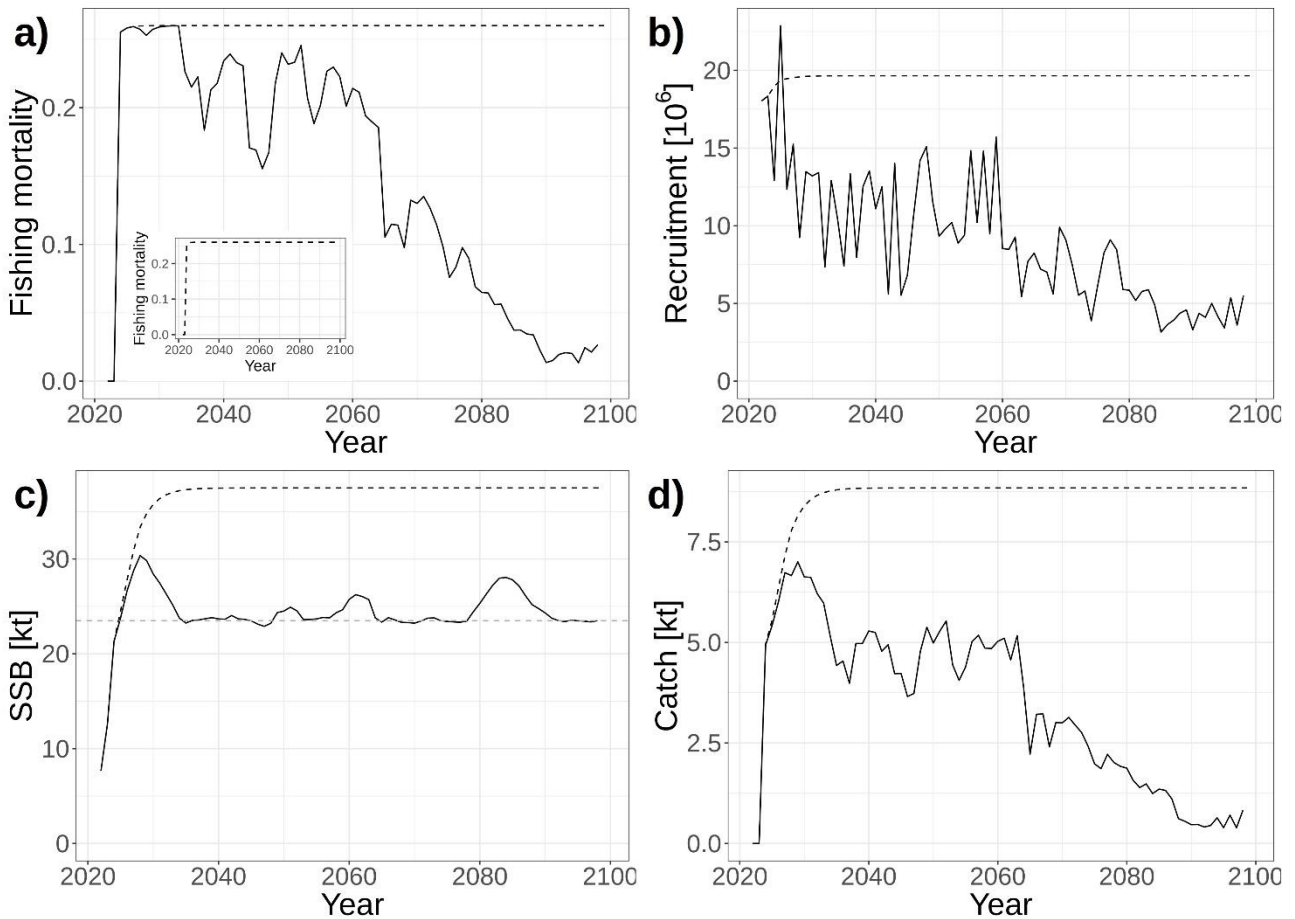


Figure CIII.3: Trajectories of optimized  $F$  (a) and resulting recruitment (b), SSB (c) and catch (d) under a single SR relationship, for a constant-(2020)-SST scenario (black dashed line) and the RCP8.5 warming scenario (solid line). Faint dashed line in (c) represents  $B_p$ . For the corresponding SST trajectory, see SI CIII.12

A comparison of the harvesting- and stock trajectories from the start and the termination of optimization revealed a notable effect of optimization on trends:  $F$  in particular was markedly higher from the 2060s until the end of the projection in the non-optimized trajectory, by more than 0.05 units compared to the final trajectory by the late 2090s (fig. CIII.4a). Catch was also slightly higher during that period (twice the level of the final trajectory, but only appx. 0.7 kt in difference at the end of the projection) (fig. CIII.4d), and notably SSB dropped below  $B_p$  in the mid-2060s and showed a further decreasing trend (fig. CIII.4c), indicating an improvement of stock health through optimized harvesting. In contrast, the recruitment trajectory was almost equal between start and termination of the optimization (fig. CIII.4b), indicating that SSB and catch were largely driven by harvesting and not recruitment, and that recruitment was almost exclusively driven by SST rather than SSB.

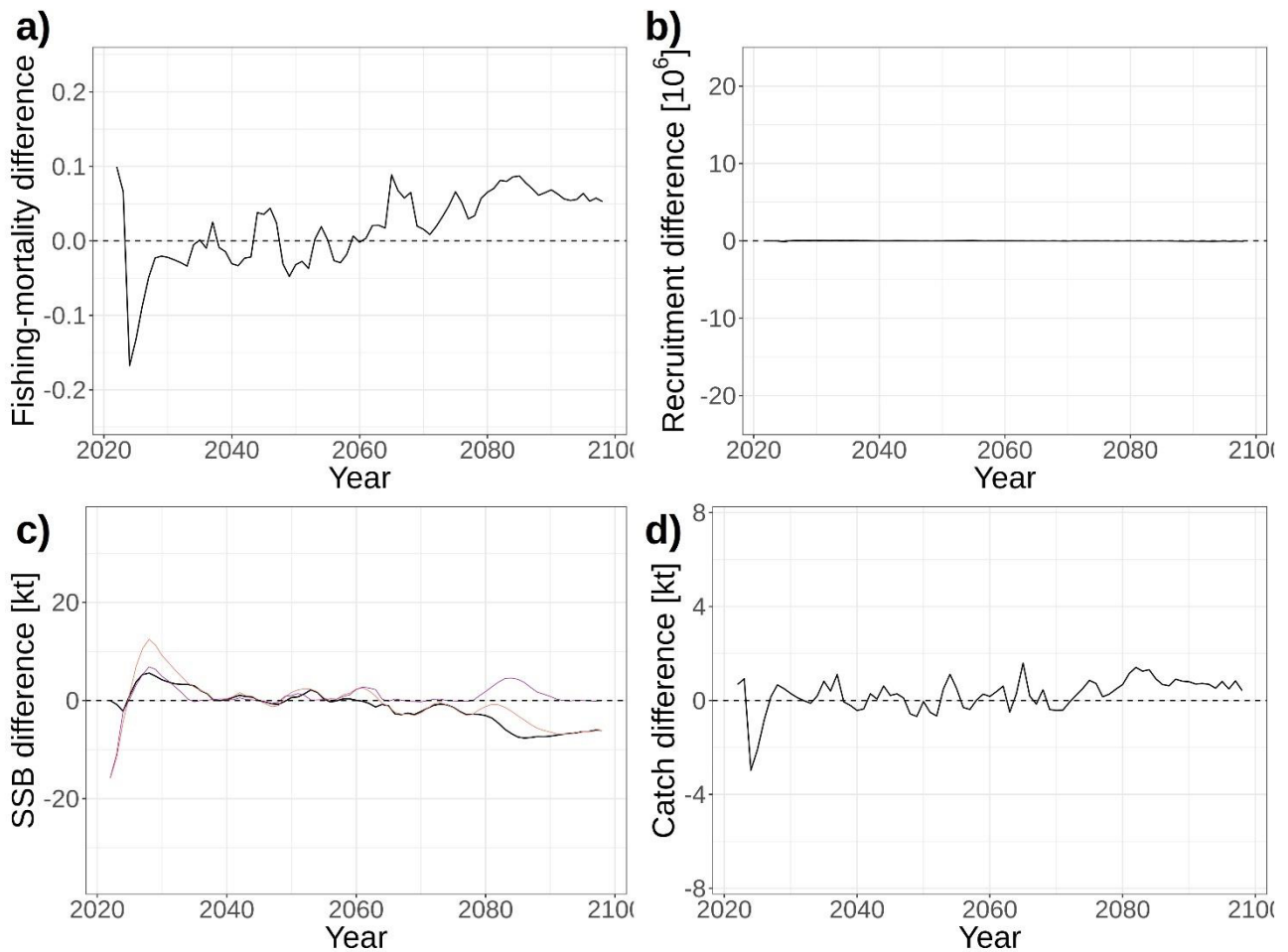


Figure CIII.4: Trajectories of the difference in F (a), recruitment (b), SSB (c) and catch (d) between the first and the terminal optimization iterations. Scales chosen according to the temporal variability of the original variables (see fig. CIII.3). Panel (c) also displays the difference of SSB to  $B_p$ , for the first (orange) and for the final optimization iteration (purple)

Optimization under uncertainty about the SR relationship and for different levels of target catch led to overall similar trends in F compared to the trend generated without consideration of SR uncertainty. These are characterized by a short moratorium phase in the beginning and a drop around the 2060s (fig. CIII.5). However, the decrease in F after the initial peak in the late 2020s was of much larger magnitude (approximately halving F), indicating an early impact of SR uncertainty on stock productivity and thus on harvesting optimization. Furthermore, the magnitude of F was overall limited to a markedly lower range, with F rarely exceeding 0.1 (less than 50 %  $F_{MSY}$ ) after the mid-2030s, and an average F of appx. 0.05 or less, depending on target-catch level: For the lowest levels of target catch, 0.5 and 1 kt, F remained on an average level of appx.  $\leq 0.025$  or roughly 1/10th of  $F_{MSY}$  (fig. CIII.5a,b).

The study of average trajectories of model output is of little utility when considering deep uncertainties (Marchau et al., 2019); hence we rather investigate trajectories of sustainability- and catch risk derived from logical comparison of SSB and catch with management targets:

Sustainability risk was reduced to levels close to zero at the mid-2020s after an initial phase of very high risk (fig. CIII.5c,d), reflecting the rebuilding of SSB to levels above  $B_P$  observed above. The very low level of risk after mid-2020s indicates that rebuilding success and maintenance of healthy stock size was largely independent of SR uncertainty, given the reduction of  $F$ . However, risk increased gradually after 2060 to a level of appx. 20 % by the end of the century, indicating a failure of management efforts to maintain SSB above the precautionary level in a considerable amount of scenarios.

Contrary to the large similarity between sustainability-risk trajectories, catch risk varied strongly between target-catch levels, with risk being at minimum appx. 10 % (averaged over temporal variability) and close to 50 % in late decades for target catch of 4 kt and higher, and at maximum appx. 25 % and close to zero % in earlier decades for lower catch levels of 1 kt and lower (fig. CIII.5e,f). This indicates that catch did not reach the target levels of 4 kt or more in many SR scenarios despite catch increase being one of the two optimization targets, and that achieving  $SSB > B_P$  and target catch simultaneously is not possible in many scenarios. Apart from the larger variability and higher overall magnitude (fig. CIII.5d,f), catch risk followed trajectories similar in dynamics to those of sustainability risk, with an initial phase of very high risk (i.e. the rebuilding phase associated with  $F$  set to zero and corresponding lack of any catch observed above) followed by a phase of relatively low risk and a steady risk increase after 2060, with the phase of initial risk reduction being higher for target catch levels of 4 kt and more.

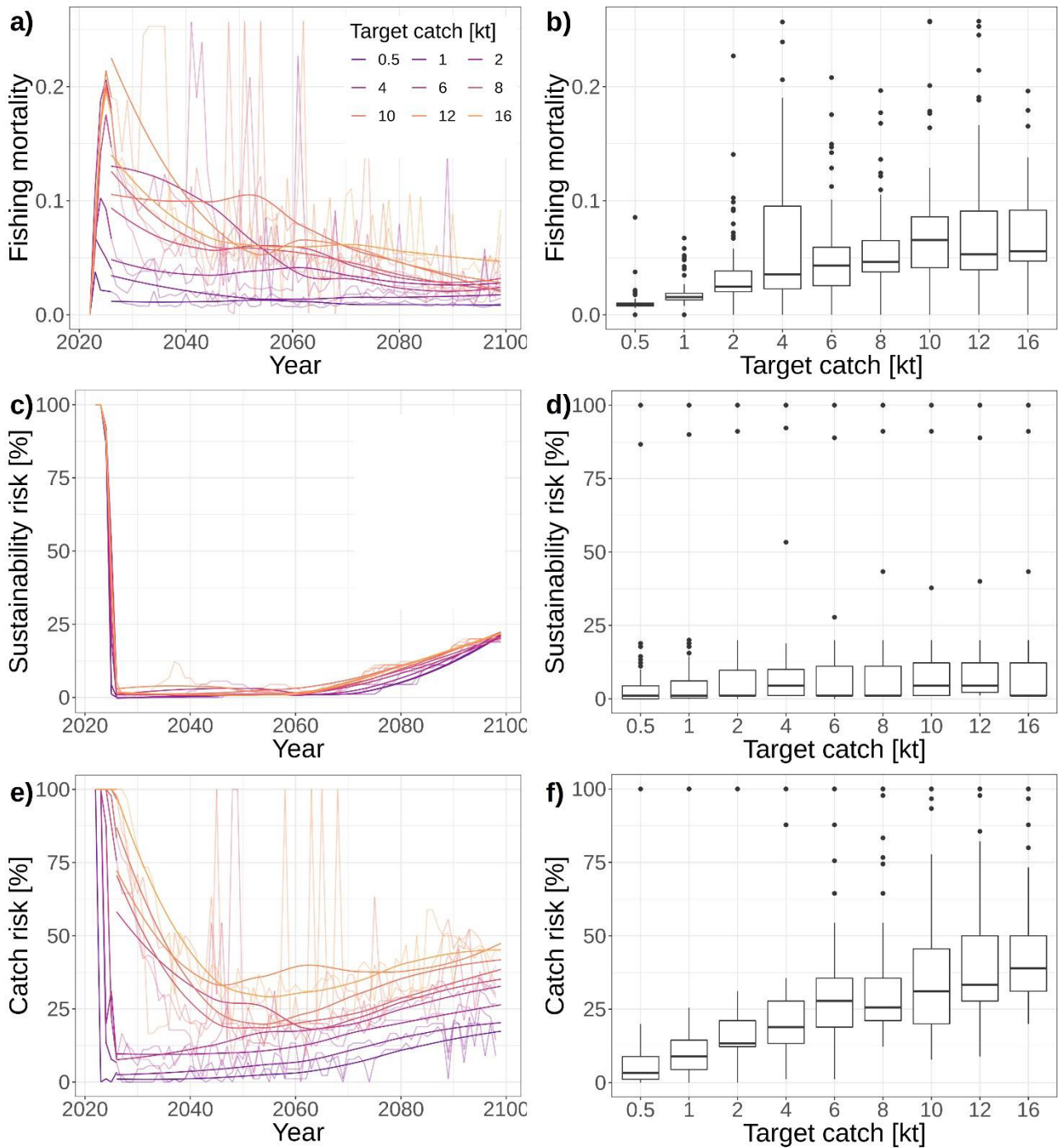


Figure CIII.5: Temporal trajectories and ranges of optimized  $F$  (a,b) and corresponding trajectories of sustainability risk (c,d) and catch risk (e,f) under deep SR uncertainty, for various levels of target catch. Solid lines show smoothed trends (starting from 2026), transparent lines show actual dynamics

Optimization both decreased risks and improved the trade-off between sustainability- and catch risks towards sustainability: The former clearly decreased over optimization iterations (reaching a stable low level after appx. 50 iterations) and the latter increased from a minimum associated with relatively high sustainability risk to a stable level of higher risk (for higher target-catch levels) (fig. CIII.6a). Optimization for target catch still showed an effect by reducing catch risk from intermittent higher levels. The process of optimizing  $F$  was



characterized by a large reduction of magnitude and by a change of trajectory characteristics between early, intermediate, and late optimization iterations (fig. CIII.6b). In particular, the early zero-fishing moratorium was fully established by the 150<sup>th</sup> iteration, and a differentiation between higher F in earlier and lower F in later decades was present by the 10000<sup>th</sup> iteration but not yet by the 150<sup>th</sup>.

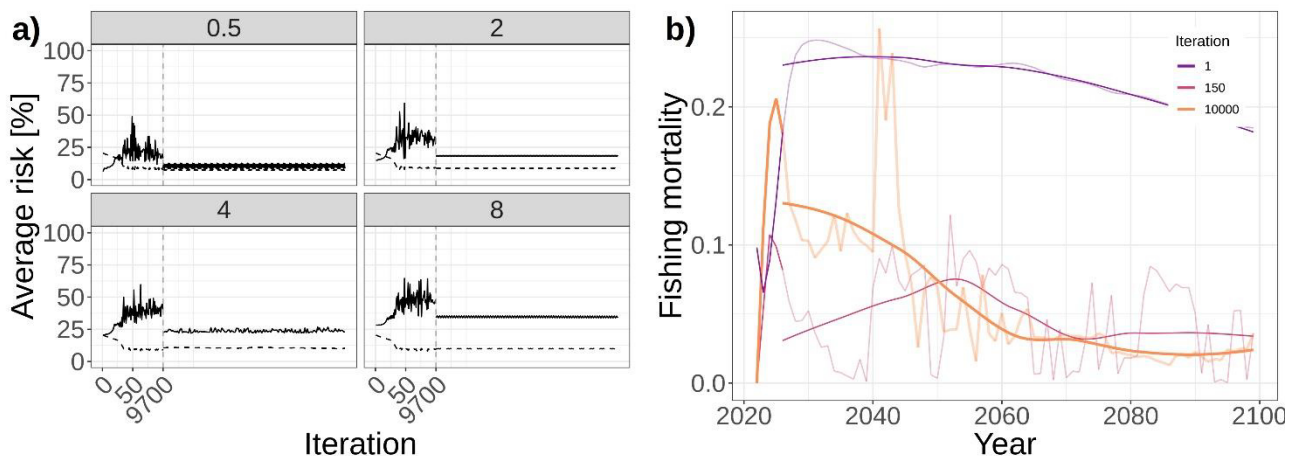


Figure CIII.6: Trajectories of average risk over iterations of optimization for four levels of target catch (a) and trajectories of F at three different iterations of optimization for target catch level 4 kt (b). Iterations 1-100 and 9700-10000 are shown in (a). Solid line in (a) represents catch risk, dashed line represents sustainability risk. Solid lines in (b) shows smoothed trends, transparent lines show actual trends. For optimization trajectories for the remaining catch levels, and for the risk trajectories corresponding to the selected F trajectories, see SI CIII.9

Incorporating the optimization over uncertainty into a management scenario with temporally changing SR relationship, where optimization was conducted every five years in the simulation, clearly led to higher stock size and catches compared to the  $F_{MSY}$ -based approach where uncertainty about future stock productivity is not used to set the level of F applied (fig. CIII.7)<sup>2</sup>. Optimized fishing-mortality trajectories were highly dynamic but did feature discernible periods of higher and lower fishing pressure (fig. CIII.7a). The sequence of these periods varied strongly between the five random sequences of SR relationships tested, indicating that the sequence of SR relationships had a strong effect on stock dynamics and on the optimization. Overall, fishing pressure was lower than in the  $F_{MSY}$ - / advice-rule approach. Notably, F, SSB and catch tended to decrease in later decades in four of the five random replicates (with exact timing varying between replicates), parallel to the stronger increases in warming (SI CIII.12), a timing similar to the observed increase in risks observed in the above analysis.

<sup>2</sup> Note that these catches are also higher than those obtained from the single-SR scenario (fig. CIII.3d), as the SR relationship used there covered only a low-productive period of the stock-assessment time series, whereas those used here, in the multi-SR scenario, cover high- and low-productive periods (see also *Material & Methods / Stock-recruitment model*)

SSB trajectories were also variable between the random SR sequences but were similar in dynamics between the optimization-based and the advice-rule-based approaches (fig. CIII.7b). The latter were of markedly lower magnitude and came close to dropping  $B_P$  especially towards the end of the time series, which was at no time, except the early rebuilding phase, the case for SSB resulting from optimized harvesting. SSB was clearly and constantly larger in the optimization-based approach (fig. CIII.7d). Catch was occasionally lower in the optimization-based approach compared to the advice-rule-based approach, and also occasionally dropped slightly below target-catch level (set to 4 kt) (fig. CIII.7c). Summed over the entire trajectory, the optimization-based approach did result in a relatively clear net gain in catch compared to the advice-rule-based approach, however (fig. CIII.7e).

Sustainability- and catch risks were not negatively affected by the sequential optimization approach, as they remained relatively constant (or decreased slightly) for the future years among the different optimization instances (fig. SI CIII.13 / 1).

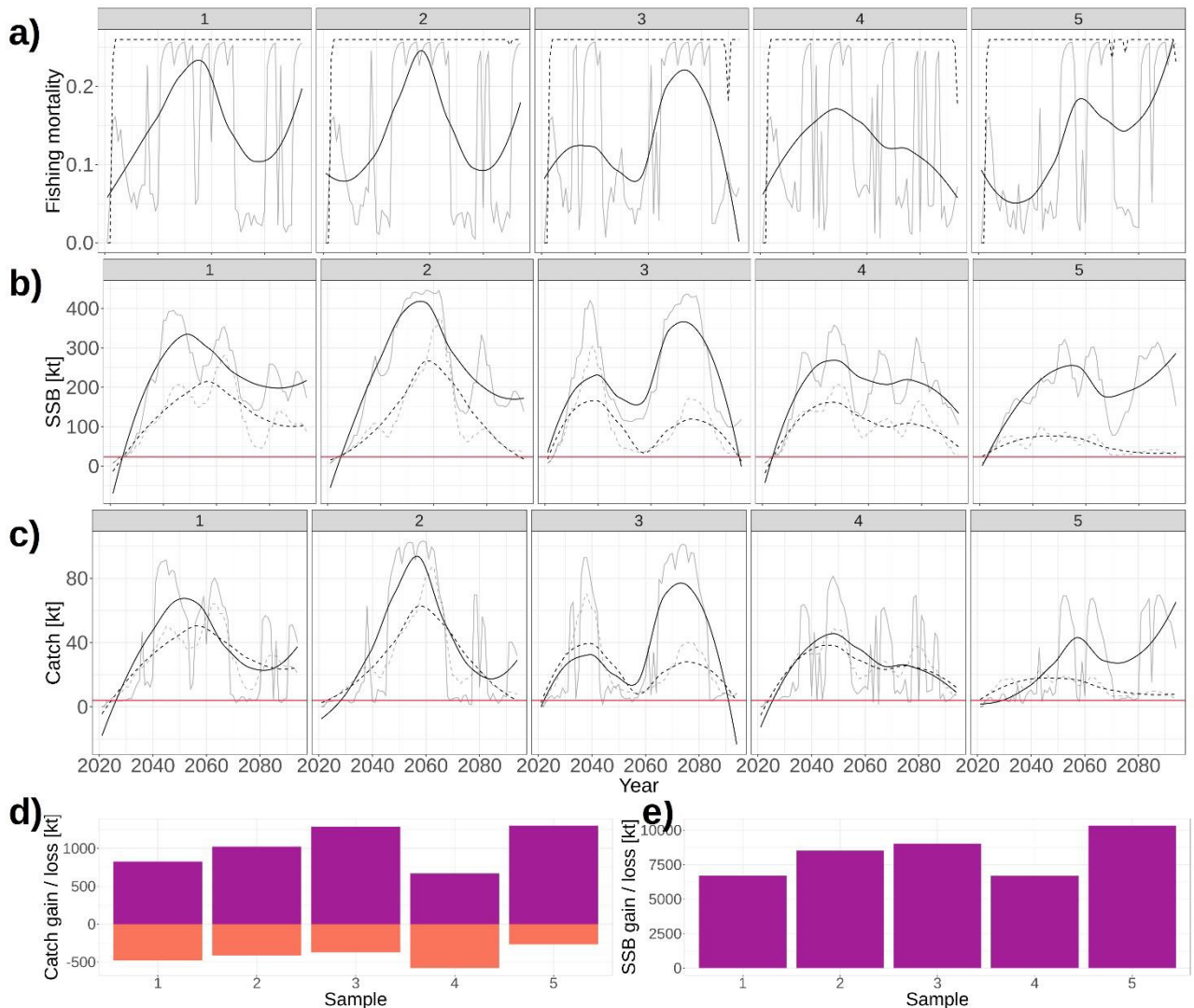


Figure CIII.7: Testing the optimization approach in a management scenario. **(a)** Trajectories of optimized  $F$  (solid grey line and smoothed trajectory in solid black line) and  $F$  resulting from application of the ICES advice rule (dashed line). **(b)** Resulting SSB trajectories. **(c)** Resulting catch trajectories. **(d)** Gains (purple) and losses (orange) in catch from the optimization approach compared to the advice-rule approach, summed over time. **(e)** Gains in SSB from the optimization approach. Panels #1-#5 shows results for five different random sequences of SR relationships. See also SI CIII.14 for a validation of the effect of the smoothed  $F$  on SSB and catch

## 4.5 Discussion

Our work clearly demonstrates the opportunities that intelligent application of mathematical optimization on a population model can offer for environmentally-informed MSE. The combination of sustainability- and simple economic objectives (attaining target catch) together with a simple rule ignoring economic objectives when stock size is critical has yielded sensible harvesting trajectories that maintain SSB at desirable level or maintain risk of attaining unhealthy stock size at marginal levels (when considering deep SR uncertainty) but also aim for generating high catch levels. The resulting harvesting strategies are thus the product not of pure maximization of yield (the key method behind the concept of maximum-sustainable yield [Tsikliras & Froese, 2019]), but of an optimization for catch strictly

constrained by the condition of maintaining healthy stock size in the long term. The optimization principle thus respects the precautionary approach outlined in EU fisheries legislation (European Union, 2013). Harvesting optimization as implemented in the field of resource economics typically aims for (proven) optimal resource use using very complex mathematical procedures (e.g. Braack et al., 2018), but is not usually employed in designing fisheries management strategies or research thereon. Memarzadeh et al. (2019) still showed the utility of such approaches in improving harvesting decisions for stock rebuilding under stock-assessment uncertainty. The strong performance and sensible harvesting trajectories achieved for both uncertainty-free and deeply-uncertain scenarios show that harvesting-optimization approaches can also be used very effectively for investigating adaptive fisheries management strategies, even with a comparatively simple heuristic framework as used by us.

The strongly altered stock- and harvest trajectories resulting from optimization under climate change show that maintaining the cod stock above precautionary biomass levels would require massive efforts in form of catch reductions, with stock rebuilding allowing only a marked increase of catch above present (2021) levels for a few years until the early 2030s, and with massive reductions necessary by the mid-2060s. Interestingly, these effort reductions were sufficient to maintain SSB at the precautionary level, indicating that temperature-driven recruitment reductions alone were not sufficiently severe to reduce SSB below precautionary levels, but that instead fishing would still determine stock healthiness. However, the fact that consideration of uncertainty in the SR relationship led to much reduced fishing levels and an inability to completely prevent stock decline indicates that maintaining management control would require i) perfect knowledge about the recruitment process and ii) a SR relationship with sufficient productive capacity to counteract climate effects. Both requirements are highly unlikely to be met with certainty (*sensu* Szuwalski & Punt, 2013). Premature confidence in understanding of the recruitment process, especially with respect to the effect of environmental drivers (Free et al., 2022), and ignorance of shifts in productivity (Möllmann et al., 2021) have led to management failure and stock decline in the recent past, highlighting the importance of acknowledging uncertainties in designing management plans.

The behavior of our optimization algorithm that massively reduced fishing effort when multiple SR relationships were considered indeed shows that SR uncertainty is not trivial and should not be ignored in fisheries management. By integrating a large range of possible SR relationships (which are shaped by ecosystem drivers), the approach essentially prepares for natural variability not entirely unlike the ecosystem-based management (EBM) approach

(Pikitch et al., 2004), which has a high potential for effectively generating sustainable management pathways when accounting for dynamics of ecosystem drivers (Lindegren et al., 2009). EBM is often linked to ecosystem monitoring and the availability of precise information to alter management action in response to early-warning indicators (e.g. Selkoe et al., 2015). Such information may be difficult to come by, however, especially when monitoring capabilities are limited and high-quality monitoring data are required (Carstensen, 2014). EBM may also prove ineffective when indicator quality is uncertain, as can very well be the case when trying to predict recruitment (Myers et al., 1998). Thus, although consideration of ecosystem drivers is important for fisheries management, under limited knowledge a simple prediction-based approach is likely insufficient for making robust management decisions. Rather than relying on development of descriptive models that might ultimately fail in critical situations (e.g. Basson, 1999), ecosystem-related management may fare better by testing potential harvesting strategies for robustness and flexibility against a wide variety of possible dynamics (Schindler & Hilborn, 2015), as more generally described in the RDM approach (Lempert, 2019). The reported difficulty in selecting “plausible” scenarios in MSE (Punt, 2017) appears therefore most easily resolved by not discarding any scenario in the first place.

The optimization behavior resembles the “bet-hedging” strategy of keeping reserve stock biomass to account for variability and uncertainty in stock productivity (Lauck et al., 1998) and environmental variation (Grafton et al., 2005). This strategy does come at the price of foregone yield when the SR relationship favors high recruitment output (e.g. through reduced climate sensitivity or increased positive response to SSB), as evident from the overall higher and stronger fluctuating catch risk for relatively small levels of target catch. However, larger buffers (as generated from applying our optimized harvesting trajectory under a highly-productive SR scenario) are generally regarded as preferable to limited buffers due their increased capacity at limiting over-fishing (Wiedenmann et al., 2017), and robust strategies are preferred to optimal ones to reduce the probability of very undesirable management outcomes (Holland et al., 2010). Improvements in uncertainty-sensitive management may be obtained by regularly repeating MSE- or risk analyses with extended data for (and possibly improved knowledge about) the stock (Skern-Mauritzen et al., 2016; Roux, et al., 2022). Collie et al. (2021), optimizing for catch, found that accounting for stock size and productivity at any given point in time could generate high-performance harvesting outcomes compared to static HCRs. Our incorporation of the optimization approach into a simulated management procedure, with optimization performed every five years, supports the value of regularly re-

defining harvesting strategies, as, compared to one-time optimization under deep uncertainty, the approach resulted in both healthy stock size *and* considerable catches ( $\gg$  target catch) without compromising sustainability risk in subsequent years. Its strong performance under temporally shifting recruitment regimes indicates the added value of considering the *long-term* consequences of harvesting under full consideration of uncertainty about future productivity (by temporally lowering  $F$  which likely leads to build-up of reserve stock biomass) when designing dynamic HCRs. Still,  $F$ , SSB and catches did show a decreasing trend in later decades (after  $\sim 2060$ ), suggesting that high levels of warming will reduce management potential even when deep uncertainty is accounted for in the optimization of harvest intensity.

Climate change forced a dynamic trajectory of  $F$  in our optimization approach. Dynamic alteration of fishing effort is not considered in traditional harvest-control rules like “constant- $F$ ” or “constant-catch”, which were designed to work under stock productivity in equilibrium (Cadima, 2003). However, these are considered less suitable under environmental change when optimal  $F$  might change in response (Szuwalski & Hollowed, 2016). Under such conditions, more dynamic approaches like “threshold- $F$ ” or biomass-based  $F$  rules, where  $F$  is automatically reduced when stock size decreases below specified limits or follows a more continuous adaptation with stock size, respectively, are regarded to be potentially more suitable (Free et al., 2022; Kritzer et al., 2019). HCRs utilizing environmental information to adapt  $F$  were also found to be superior to classical approaches under severe environmental impact (Brunel et al., 2010). Our approach extends dynamic adaptation of  $F$  to a maximum by allowing it to vary from year to year largely independent of a mechanistic rule while considering long-term effects under a large range of recruitment assumptions. The fact that catch risk increased gradually with increasing target catch indicates that  $F$  was adapted sensibly, i.e. with consideration of both maintaining SSB above precautionary levels but also of preventing unnecessarily foregone yield. Our optimization procedure thus appears to achieve climate-adaptive management strategies that are at least as sensible as rule-based approaches. The more deterministic way of adapting  $F$  under deep uncertainty adds to the existing adaptive HCRs by removing the need for precise predictions of SSB for generating sustainable management plans. Regular estimation of stock size apparently leads to better yield, but is not required for attaining low risk of sustainable harvesting, as long-term harvesting impacts under uncertainty are accounted for.

The approach presented is intended as a first exploration of the potential of optimization for management-strategy design. We deliberately limited the model set-up to a single population model as opposed to the dual-model (“operating-model-assessment-model”) system typically implemented in MSE – our primary aim was to investigate the impact of larger-scale uncertainties rather than that of assessment errors typically addressed in MSE (e.g. Punt et al., 2016). Still, the distinction between simulating with a fixed sequence of SR models and optimizing for a large set of possible SR models does present a simple case of distinguishing between biological ground truth and manager’s knowledge. Furthermore, we omitted a simulation of benchmark assessments that can lead to changes in the precautionary reference point and thus constitute an adaptation to reduced stock productivity itself (Travers-Trolet et al., 2020). The nature of decreasing threshold  $F$  under climate change has albeit been criticized as a short-term / reactionary adaptation (Travers-Trolet et al., 2020); optimization based on fixed reference points thus appears to be preferable from a multi-stake-holder point-of-view. Finally, we limited the uncertainties considered to the uncertainties in the SR relationship. While likely the largest source of uncertainty, future studies might consider testing for uncertainty in other biological parameters with impact on stock dynamics, e.g. natural mortality and individual weight, as well.

In conclusion, we here presented a novel approach to management-strategy design based on the combination of mathematical optimization for both conservation- and catch objectives and robust decision-making that we believe to be of value for integration into policy guidance. Its strong performance shows that consideration of i) the dynamic development of environmental drivers like SST and ii) deep uncertainty in stock productivity combined with the technique of mathematical optimization leads to the generation of sensible harvesting pathways with reduced risk of future overfishing. The regular implementation of the procedure in combination with updated stock-size estimates revealed that this novel precautionary approach, which more strongly emphasizes the long-term consequences of fishing under uncertainty, can lead to larger (safer) stocks and higher catches than the classical MSY-based approach, which focuses mostly on short-term stock development. A requirement for the practical implementation is, however, a high degree of policy flexibility especially with regard to inter-annual quota variability. We believe that the approach can be of utility to real management planning in a dynamic and deeply uncertain future for the fisheries sector.

#### **4.6 Data availability**

All data and code will be made available on [https://github.com/imf-uham/Optimization\\_WBC](https://github.com/imf-uham/Optimization_WBC) upon publication of the study in a scientific journal and are available from the author on request.

#### **4.7 Conflict of interest**

The authors declare no conflict of interest.

#### **4.8 Acknowledgments**

The authors thank Guilherme Pinto (German Centre for Integrative Biodiversity Research [iDiv] Halle-Jena-Leipzig) for preparing the SST historical reconstructions and projections.

JC received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 820989 (project COMFORT, Our common future ocean in the Earth system – quantifying coupled cycles of carbon, oxygen, and nutrients for determining and achieving safe operating spaces with respect to tipping points). The work reflects only the authors' view; the European Commission and their executive agency are not responsible for any use that may be made or the information the work contains.

SF received funding from the German Ministry for Education and Research (BMBF) under the project SpaCeParti (Grant No. 03F0914A).



## 5. General Discussion

The present dissertation aims at determining the potential for, constraints to and possible ways of managing Atlantic cod (*Gadus morhua* L.) under future climate change towards the aim of achieving sustainable harvesting. The analysis of future stock dynamics and development of future management strategies calls for the use of long-term model projections, the precision of which is, however, severely limited by deep uncertainty about key processes determining stock productivity. Robust-Decision-Making (RDM-) analyses methods were used to investigate the impact of deep uncertainty in the stock-environment-recruitment- (SR-) relationship and in future climate development on the ability to identify robust harvesting strategies (Chapter I). A risk-based “Safe Operating Space” (SOS) was then developed to explore the interactive effects of harvesting and warming on sustainability, as well as the effect of stock size on climate resilience (Chapter II). Finally a conservation-oriented optimization procedure was developed to uncover sustainable future management pathways and adaptation strategies under climate change and deep and dynamic uncertainty (Chapter III).

### 5.1 Summary of the results

The work presented yielded four major findings on the manageability of Atlantic cod under future climate change:

- I) Uncertainty about key processes in stock productivity, namely recruitment, has a major impact on the potential for sustainable harvesting of cod, independent of future warming, and can prohibit the identification of a safe fixed management strategy.
- II) The response of cod to fishing and future warming strongly varies between major geographical areas of its distribution, and appears to be related both to exploitation history / current stock status, and to the geographical latitude of a stock’s habitat area.
- III) Maintaining stock biomass well above the precautionary limit appears to be essential for achieving higher chances at climate resilience in many stocks, but is not sufficient to prevent high risk of stock decline at more severe levels of warming.
- IV) Accounting for long-term uncertainty in the recruitment process and adopting flexibility in setting harvesting policies can lead to a more effective management in terms of increasing stock biomass and catches under dynamically changing stock productivity.

## **5.2 Impacts of Deep Uncertainty on future manageability of cod**

The results of the present study clearly show that uncertainty about future stock productivity puts limits to mid- to long-term (i.e. multi-decade) management plans that aim for achieving sustainable harvesting under a certain level of catch or harvest rate, i.e. fixed-policy plans. Statistical analyses show that deep uncertainty about stock productivity is a prevailing issue in harvested systems affected by climate change: Difficult-to-predict regime shifts, i.e. major shifts in stock productivity, are common in harvested fish stocks and can result in both a mid-to-long-term decrease or an increase in productivity (Szuwalski & Punt, 2013; Sguotti et al., 2019; Blöcker et al., 2023a). While analyses of model simulations showed that regime shifts can be a result of (cumulative) unfavorable environmental effects combined with poor stock status (Collie et al., 2004), inferring that they might be predictable to some extent in specific cases, the overall perception from empirical- and model studies is that regime shifts in marine ecosystems cannot (yet) be reliably anticipated (e.g. Möllmann et al., 2015; Szuwalski & Punt, 2013). Howell et al. (2013) showed that dynamically changing environmentally-sensitive SR relationships, which reflect different productivity regimes, can lead to deep uncertainty in projections of stock size when accordingly considering alternative SR hypotheses within the model used for projections. Applying the scenario-exploration method of Robust Decision-Making (RDM) to population projections conducted with a multitude of random hypothetical stock-environment-recruitment- (SR-) relationships confirms this observation, as equal catch policies were found to lead to highly sustainable or very unsustainable outcomes under different SR relationships (Chapter I). The results further showed that no policy was prone to deep uncertainty in terms of achieving sustainability, thus demonstrating that inflexible / fixed-policy management is of low utility in environments characterized by regime shifts. Adaptive management strategies that can alter fishing pressure in response to regime shifts have been developed in theory (King et al., 2015; Szuwalski & Punt, 2013). These approaches are limited, however, by the poor ability to predict regime shifts, which hinders a practical implementation (Szuwalski & Punt, 2013). An alternative approach is to aim for strategy robustness (Howell et al., 2013) and design a “bet-hedging” strategy, where management aims to maintain stock size at higher levels than those that would be considered “biologically safe” under equilibrium conditions, e.g. by means of marine reserve areas, in order to prepare for the event of potentially reduced / over-estimated productivity (Lauck et al., 1998; Grafton & Kompas, 2005; Free et al., 2022). The differing optimization behaviors observed under “completely certain” and deeply uncertain conditions, where  $F$  was set to mostly much lower levels in the latter compared to the former case (Chapter III), demonstrate the

practicality of this notion: Low  $F$  would lead to stock growth to high levels under favorable productivity conditions, but might be only barely sufficient to ensure biologically safe stock levels under low stock productivity, hence low  $F$  was preferred as a precaution against low-productivity scenarios.

This “buffering strategy” can, however, come at the price of foregone yield (or economic gain), especially when the buffer is relatively large e.g. in response to data limitations (Free et al., 2022; Wiedenmann et al., 2013). The present study shows as well that deep uncertainty about stock productivity puts severe constraints to yield: achieving even the relatively low recent profit levels of North Sea cod had a relatively high risk of failure ( $> 50\%$  under most levels of harvesting tested and especially under levels leading to lowest risk of unsustainable fishing) (Chapter I). Similarly, conservation- and yield-targeted optimization of harvesting on western-Baltic cod under uncertainty led to  $> 25\%$  risk of missing even historically moderate catch levels (6-16 kt) (Chapter III). Missing out on potential yield due to a lack of knowledge about stock productivity is likely to be detrimental to fisheries under risk of decline due to pressure from i.a. long-term over-exploitation and climate change (e.g. the western-Baltic small-scale fisheries [Möllmann et al., 2021; Döring et al., 2020]). Adaptive management strategies might enable a degree of mitigation, as they are generally considered to enable higher long-term yields in addition to improved conservation performance compared to inflexible approaches like catch caps (Wiedenmann et al., 2017; Kritzer et al., 2019). This becomes visible in the reduced economic risk of constant-harvest-rate strategies (where catch is adapted to stock size) compared to the constant-catch strategies found in this study for North Sea cod (Chapter I). Even so, optimum removal rates may change under changing productivity (Szuwalski & Hollowed, 2016), calling for even higher degrees of flexibility, e.g. threshold- $F$  rules, where the amount of harvest relative to stock size is decreased once stock size drops below a reference level (e.g. Kritzer et al., 2019; Free et al., 2022). Other proposed forms of adaptation include a constant monitoring for e.g. the emergence of potent environmental indicators to be used in stock assessment and harvesting advice (Skern-Mauritzen et al., 2016) or for unusual signals in stock- and ecosystem indicators to supplement assessments for generating precautionary advice (e.g. catch reductions) (Dorn & Zador, 2020), as well as maintaining a high assessment frequency (Wiedenmann et al., 2017) to enable quick reactions to emerging productivity reductions. The present study clearly demonstrates the value of combining stock monitoring with full policy flexibility for achieving sustainable stock size and relatively high yields: The comparatively high catches resulting from step-wise harvesting optimization on an “unfolding” but unpredictable simulated pathway of shifting productivity

levels (Chapter III), as well as the general dependency of catch potential on stock size (Chapter II), show that a situation-specific adaptation of buffering effort indeed improves management under deeply-uncertain dynamic productivity development.

A common challenge in fisheries management is not only the selection of the right strategy but also the timely recognition of its (proneness to) eventual failure and the development of awareness for the consequences of failure. For example, the collapse of the Northern cod fishery and ensuing economic decline of the Newfoundland populace (Walters & Maguire, 1996; Lear & Parsons, 1993) as well as the surprising sudden inability to correctly predict Pacific sardine (*Sardinops sagax*) dynamics via sea-surface-temperature- (SST-) (Free et al., 2022) may be attributed to over-reliance on established management rules and hesitant management response by policy-makers (Taylor, 1995; *sensu* Brown et al., 2012). RDM-based approaches can help provide a better overview of the (long-term) consequences of management strategies in uncertain settings. RDM was designed in particular to detect potentially detrimental consequences of policy implementation under unfavorable conditions (Lempert & Popper, 2005; Lempert et al., 2013), to avoid misguided policy choice (Pielke et al., 2000). In the present work, RDM enabled the recognition that any management strategy can fail to achieve sustainable harvesting under unfavorable relationships between spawning-stock biomass (SSB), environmental factors and recruitment in North Sea cod, with higher harvesting levels increasing risk of failure (Chapter I), and that this is also true for the other cod stocks analyzed (Chapter II). These observations suggest that blind-sighted adoption of fixed long-term management policies without preparing adaptation strategies is unwarranted when aiming for responsible management. RDM further led to the identification of thresholds in SST increase and stock size that, when passed, lead to high risk of unsustainable management (Chapter II), thus showing that awareness of critical stock- and environment-related conditions is important for successful strategy selection and plans for eventual strategy substitution. The improvement of stock- and catch dynamics obtained from the combination of RDM with long-term optimization over those obtained from the implementation of the “static” advice rule (Chapter III) also suggests that an awareness of the long-term consequences of policies under un-/favorable conditions (here leading to automatic temporal reduction of harvesting intensity) will lead to improved pathways of harvesting policies under dynamically changing stock productivity.

In summary, the existence of deep uncertainty in future stock productivity found in the present work indicates that a change of paradigms in management-strategy design and –planning is necessary. The existence of deep uncertainty and the detrimental impact it can have on as-

sumption-based management strategies need to be taken into account and inform the design of more robust (“buffered”) strategies. In the absence of reliable methods for predicting productivity change, the best trade-off between robustness (with respect to achievement of sustainable stock size) and increasing catch lies in combining awareness of potential policy performance with precautionary buffering of harvesting effort and frequent monitoring of stock size and environmental conditions to adjust the buffering effort (i.e. increase harvest when stock size has developed favorably).

### **5.3 Future climate response of Atlantic cod and management adaptation**

Despite the prevalence of deep endogenous uncertainty in the recruitment process (i.e., in the dependence of recruitment strength on SSB and SST), the present work identified distinct modes of response of cod to future climate change (Chapter II): Stocks on the eastern-Atlantic shelf and at mid latitudes ( $< 60^{\circ}\text{N}$ ) displayed similarly strong negative impacts of both warming and harvesting, with the SOS for sustainable management defined as a “corner” under the trade-off line of the two drivers. This suggests that future warming is highly likely to exacerbate existing pressure from warming in these stocks, which reside comparatively close to their upper thermal tolerance level (e.g. Righton et al., 2010; Drinkwater, 2005). One implication for their management, independent of the actual scenario(s) of recruitment response to drivers that will establish in the future, is that time may eventually “run out” for viable and sustainable harvesting of many stocks due to an eventual crossing of threshold SST under unfavorable warming scenarios (see figs. CII / 4, SI CII.11 / 1). Catch potential and its climate robustness were clearly related to stock size in the present results (Chapter II), indicating that quick rebuilding (of over-harvested stocks, which includes all of the eastern-Atlantic mid-latitude stocks) is likely the most fruitful plan for harvesting the stocks as the cumulative future catch will be highest. This is in order to make optimum use of available potential productivity while it is not diminished by warming. The usefulness of rebuilding plans for achieving sustainable fishing has been shown empirically (Melnychuk et al., 2021), and was also implemented by the optimization algorithm introduced in the present work (notably, the rebuilding moratorium was “learned” objectively and not prescribed) (Chapter III). (Re-) building stocks to levels markedly above the precautionary reference level is recommended as an additional “insurance” against unexpected productivity losses (Free et al., 2022) and could thus mitigate the effect of shifts between productivity regimes on the risk of overfishing. The present results further support this notion, as stocks with persistent poor historical biomass status (clearly

lower than threshold reference level  $B_{p}$ ) had markedly lower catch potential under warming (smaller SOS) than stocks with relatively good historical condition (Chapter II).

Under the perspective of deep uncertainty, there is a risk that rebuilding will still not be sufficient to ensure sustainable management in the future even under moderate levels of future warming: North Sea cod exhibited scenarios of persistent low (i.e. non-precautionary) future stock size even when being subjected to marginal fishing levels only and despite starting from a rebuilt level in the simulation (Chapter I). The same holds for all 18 other cod stocks considered, and most western-Atlantic stocks only displayed such scenarios (Chapter II). This lack of manageability was found to be a result of unfavorable response of recruitment strength to SSB and SST in the presented model (see figs. CI.3, SI CI.5 / 1, SI CII.4 / 1-2), and more generally is attributable to shifts to regimes of low productivity in stock dynamics, where recruitment apparently lacks a response to stock-rebuilding action and thus ultimately thwarts the rebuilding effort (Blöcker et al., 2023a). Statistical analyses indicate that such shifts are likely robust against attempted reversal by management (Sguotti et al., 2019; Möllmann et al., 2021), which implies that a historically collapsed stock should be more prone to exist in a lower-productive regime also in the future than a currently better-conditioned one. One process suspected to hinder stock rebuilding and thus fix a low-productivity regime is depensatory (Allee-) effects (Winter et al., 2019), which can be an effect of increased predation from marine mammals (Neuenhoff et al., 2019). The present study indeed revealed a clear relationship between recent (last two decades of assessment time series) stock status and potential for future sustainable management, with most of the heavily-depleted western-Atlantic stocks having low / non-existent potential (Chapter II) (predation effects have been noted for some but not all of these stocks [Swain et al., 2019; DFO, 2019]). The main implication for management is thus to aim for rapidly rebuilding depleted stocks to biologically safe levels where possible (i.e. in many of the mid-latitude eastern-Atlantic stocks), to reduce the risk of them becoming unmanageable as well (e.g. due to Allee effects), and to set up a tight monitoring scheme for enabling early warning of altered natural (e.g. food-web) conditions (Pinsky & Mantua, 2015).

The third distinct mode of stock response to SST and harvesting is a less distinct climate response or comparatively reduced climate limitation coupled with a relatively large safe harvesting range. The present study detected this pattern almost exclusively in high-latitude stocks ( $> 60^{\circ}\text{N}$ ) (Chapter II). The SR relationships fitted for these stocks indicated that the stocks are not necessarily unresponsive to SST, but that the response may more likely be

highly variable in magnitude and direction (see figs. SI CII .4 1-2). The northerly cod stocks are indeed predicted to respond to future climate change in very variable ways through a variety of mechanisms. On one hand, warming of Arctic waters to more physiologically acceptable levels for cod and sea-ice retreat are expected to increase cod condition (Holt & Jørgensen, 2014) and to open additional feeding grounds (Kjesbu et al., 2014), respectively, creating the basis for higher stock productivity. On the other hand, stronger warming, in combination with ocean acidification, may reduce survival of early life stages and thus recruitment (though this might be mitigated by poleward movement of the stock) (Dahlke et al., 2018). Possible novel food web conditions resulting from potential spreading of cod to the north (e.g. interactions with polar cod [*Boreogadus saida*]), which could result in increased feeding opportunities or increased competition (Renaud et al., 2012), add to the multitude of potential climate effects (e.g. Kortsch et al., 2015). In summary, the current healthy status of most high-latitude stocks combined with the potential of environmental conditions becoming both more and less suitable for cod (i.e. for different life stages or for different eco-physiological aspects) forms the basis for a wider range of possible futures than exist for stocks for which warming is clearly mostly detrimental or which have low potential for recovery. The observed “reduced climate limitation” may thus be somewhat misleading, as it integrates over both very favorable and very unfavorable climate effects. Given the relatively good current condition of most higher-latitude stocks, it appears likely that management will have the potential to react effectively to emerging climate threats and perform a “bet-hedging” stock enhancement as a climate precaution (Lauck et al., 1998), however. Effective conservation measures would certainly require a broad-scale monitoring program aside from stock assessments to enable the fast recognition of novel and potentially detrimental ecological conditions and of the direction of emerging climate effects (Pinsky & Mantua, 2015; Nicol et al., 2012; Skern-Mauritzen et al., 2016), and to enable the subsequent implementation of adaptive management action.

In summary, it can be expected that most cod stocks featuring capacity for sustainable management will react either negatively, or in a multi-directional variety of ways, to warming, with the latter way being more likely in northerly stocks (Chapter II). With respect to climate change, management control will likely be strong in northerly stocks at least when positive and negative climate effects remain balanced, but will be limited by a SST threshold and interacting harvesting- and warming effects in southerly stocks. Under unfavorable productivity regimes (i.e. unfavorable SR relationships), management control will, however, be reduced to more limited warming ranges or will not exist at all. The risk of shifts to such regimes can allegedly be reduced by effective management (Sguotti et al., 2019; Möllmann et al., 2021).

Climate effect may be largely positive for some of the western-Atlantic and Greenland stocks (Chapter II), some of which currently reside at relatively low habitat SSTs that may contribute to reduced productivity (Rätz & Lloret, 2003). However, given that cod exhibits lower and upper SST limits in (early-) life-history processes (Jordaan & Kling, 2003), such a uni-directional response (which is informed by the limited range of data available) should be regarded with high caution. It seems more likely that these stocks will eventually display a mixture of responses to warming and possibly eventually a negative response, the signal of which is not yet clearly visible in the data but can be qualitatively inferred from the temperature response of eastern-Atlantic stocks. Altogether, management will most likely achieve the best chance at successful climate adaptation when keeping stock reserves, i.e. extra levels of stock biomass that would instead be caught under complete predictability (e.g. Free et al., 2022), to account for uncertainty in recruitment-driven stock productivity and when adopting a flexible approach that adjusts harvesting to stock status and to long-term risk of (partially climate-driven) stock decrease (Kritzer et al., 2019; Mildenerger et al., 2021; Chapter III).

#### **5.4 Utility of RDM, SOS and optimization for management planning**

The present study has introduced the utilization of the multi-disciplinary concepts of robust decision-making (RDM), safe operating space (SOS) and mathematical optimization, and combinations thereof, for investigating the future potential for sustainable harvesting of Atlantic cod under climate change. In addition to their use for investigating future management effectiveness and stock responses to warming, each concept contributes to potential novel approaches aimed at improved management planning:

##### **5.4.1 Robust Decision-Making (RDM)**

RDM methodologies were designed to stress-test candidate policies under even marginally-plausible scenarios in order to uncover circumstances and characteristics of critical policy performance (Lempert et al., 2013; Lempert, 2019). For long-term fisheries management planning, RDM is unlikely to identify fully sustainable management strategies that do not equal zero fishing, but it can be used to determine generalized relative trends of policy performance, including for multiple objectives, (Chapter I) and relative impacts of interaction with natural drivers (Chapter II) by i) integrating over a particularly wide range of scenarios, e.g. assumptions about the SR relationship, and ii) extracting the management-relevant information from otherwise difficult-to-assess model output of extremely high variability. Within applied management planning, RDM could address the common problem in management-strategy evaluation (MSE) of agreeing upon a set of “plausible” scenarios or weighting sce-



narios according to plausibility (e.g. Holland, 2010; Punt, 2017) while aiming for meaningful advice on policy performance. By not excluding any scenarios on grounds of low plausibility, application of RDM (e.g. within MSE) can address the issue of severely impaired policy performance under certain (potentially rare or deemed low plausible under current knowledge) scenarios (Pielke et al., 2000; Rademeyer et al., 2007). RDM could thus help avoiding management delay / -failure arising from evidence-fixated policy assessment (Hilborn & Peterman, 1995) by highlighting detrimental near-term policy outcomes under unfavorable scenarios. This switch of perspective from aiming to improve scenario realism to assessing policy vulnerability comes at the price of obtaining only relative performance indicators (risks) (Chapter I), which would necessitate frequent updates of the RDM analysis and flexibility in policy making in applied management once expected relative policy performance (risk) gradually gives way to realized policy performance. A management policy could be chosen by investigating its risk of failure (under estimated stock status and expected climate development) and settling upon a feasible combination of acceptable risk and monitoring frequency with stakeholders. Trade-off analyses as applied in the present study could then be used for communication between multiple stakeholder groups in order to discuss risks and identify a consensus-based policy or planning strategy. Such an arguably more holistic communication of potential long-term risks, management opportunities for different objectives, and especially uncertainty, compared to traditional presentation of model projections (Brander et al., 2013), could also help counteract potential misguided advice-giving practice (Steele et al., 1992) and mitigate the occasional issue of misinterpretation of assessment findings (e.g. Taylor, 1995) and lack of trust in perceived “weak science” limiting effective management (Glenn et al., 2012).

#### **5.4.2 Safe Operating Space (SOS)**

The SOS concept (Chapter II) generates a “map” of system response to multiple stressors, which can provide planning guidance to managers in a system with dynamically changing uncontrollable drivers. A faithful alignment of management to the SOS boundaries should make it possible to maintain natural systems in a desirable state (Scheffer et al., 2015). Even under deep uncertainty, where it is difficult to determine distinct driver thresholds (a key component of the original “planetary-boundaries” SOS concept introduced by Rockström et al. [2009]), relative driver-response dynamics and distinct driver interactions (e.g. trade-offs) can be identified, and can be utilized for guiding management that seeks to remain within certain risk boundaries. The SOS then enables a “looking up” of possible management actions and associated risks given a certain system state defined by SST and stock size, an improve-

ment in utility over scenario-based projections that cover only a limited number of system states. This trait could become particularly useful when long-term projections about temperature development change e.g. due to the development of novel climate scenarios (as shown in e.g. Soares et al., 2022; Tittensor et al., 2021) or when the prospect for climate-mitigation measures, and thus the relative likelihood of climate scenarios, change (e.g. IPCC, 2023). The SOS concept will likely have the greatest utility for approximating mid-to-long-term harvesting potential given a certain stock status (as inferred from stock assessment) and an expected climate development, and could therefore also be useful for policy-makers looking into the overall development potential of a local fisheries sector. A hypothetical simplified usage protocol could take the form of

- i) looking up stock-size estimates (from stock assessment) and expected SST development,
- ii) determining harvest potential within acceptable risk levels,
- iii) weighing stakeholder interests against risk,
- iv) formulating a harvesting policy,
- v) taking according measures, e.g. limiting allowable catch as a modification of assessment-based advice,
- vi) re-conducting the analysis in the following year with the new stock-size estimate and
- vii) eventually updating the SOS itself with new SSB- and recruitment estimates.

Such a longer-term planning approach that addresses the limitations that climate change, poor stock status and potentially limited productivity pose to sustainable harvest may theoretically have been useful to avoid collapse-like stock declines or generate effective stock rebuilding in fisheries where such factors were not considered (e.g. Western-Baltic cod [Möllmann et al., 2021], North-Sea fisheries [Sguotti et al., 2019] and Irish-Sea cod [Bentley et al., 2020]).

### **5.4.3 Optimization**

Optimization in fisheries management has traditionally aimed for maximizing gain from the resource without much consideration of (deep) uncertainties; the prime example is the maximum-sustainable-yield (MSY) concept (as shown e.g. in Holma et al., 2019). The approach introduced in the present study (Chapter III) differs strongly as it explicitly considers deep recruitment uncertainty and dynamic future climate development instead of assuming perfect knowledge and equilibrium system conditions (a common point of criticism of the MSY principle [e.g. Larkin, 1977; Steele et al., 2011]). Its utility lies in it generating an empirically

optimized rather than rule-based harvesting pathway that integrates stock-rebuilding needs, productivity limitations through climate change and intrinsic deep uncertainty about stock productivity, and in accounting for both conservation- and yield-related objectives. Management could utilize the approach to uncover possible adaptation pathways and detect points in time potentially requiring massive harvest reductions (under unfavorable climate scenarios) to develop precautionary long-term pathways for adapting the fishery sector (McIlgorm et al., 2010). More importantly, as shown in the present study, a useful utilization of the optimization approach could be a repeated implementation that keeps track of the actual future development of stock size (where the optimization algorithm is run every  $k$  years<sup>3</sup>, with the then-current stock size set as initial population size). Preparing for a wide range of possible future productivity states (by optimizing for robustness against all these scenarios) and taking advantage of possible favorable realized stock development can lead to satisfaction of both yield- and conservation-related objectives. Management strategies that incorporate flexibility to (unpredictable / deeply-uncertain) changes in stock size and -productivity are commonly advocated as a strategy for harvesting under non-equilibrium conditions (e.g. Schindler & Hilborn, 2015; Kritzer et al., 2019; Pethybridge et al., 2020). Wiedenmann et al. (2017) propose a combination of uncertainty buffers with high stock-assessment frequency to improve harvest potential. Uncertainty-conscious optimization as presented here adds to this by introducing the means to help map out and dynamically adapt harvesting pathways under the otherwise limiting lack of predictability of regime shifts (Szuwalsky & Punt, 2013) and under dynamic climate development (e.g. Hawkins & Sutton, 2009). Resulting harvesting plans might have relatively high inter-annual variability, a challenge for fishing-capacity management (*sensu* Smith, 1994; *sensu* Ludwig et al., 1993), which could potentially be overcome through e.g. flexible quota-sharing policies (McIlgorm et al., 2010; Harte et al., 2019).

In summary, the three concepts contribute to the development of strategies for climate-sensitive fisheries management by i) showing the importance of considering unpredictability of stock productivity for long-term management-policy-making and introducing risk-based policy-assessment methods (RDM), ii) introducing a mapping-out of stock-status- and climate-specific precautionary harvesting opportunities (SOS) and iii) providing the means for generating sensible harvesting pathways suitable for dynamic developments in climate and stock productivity (optimization).

---

<sup>3</sup>A small number, e.g. five years

## **5.5 A concept for operational management of cod under future climate change**

The above findings indicate the utility of a repeated assessment procedure informing a flexible management body. A more concrete conceptual management implementation of the approaches presented could take the following cyclical form (fig. G.1): every  $k$  years, a stock assessment is conducted to determine current stock size, as well as to extend and update the SSB- and recruitment time series. The latest climate projections for the management area are looked up, and, if existing, new SST reconstructions are also looked up. Historical SSB- and recruitment estimates and SST reconstructions are then used to fit multiple SR models (e.g. for different subsets of the assessment time series as done in Chapter II and III). A range of harvest policies of interest (e.g. target-catch levels) is identified, e.g. through stakeholder consultation.

The stock is then projected under different harvesting policies and under the different SR-model parameterizations and possibly different climate scenarios. RDM analysis (Chapter I) is conducted to generate a sound overall assessment of the future potential for sustainable harvesting, i.e. by checking for the existence of risk-free policies and determining the risks of overfishing of the current and of different candidate policies, as well as potential trade-offs between conservation- and yield- or profit-based objectives. (The trade-off analysis could be extended for testing different levels of target-yield or -profit.) SOS analysis (Chapter II) is conducted to determine the overall reaction of the stock to combined warming and harvesting, as well as to identify warming thresholds beyond which the target stock becomes largely unmanageable and which would call for a cessation of fishing. Also, the impact of building / maintaining a stock reserve on climate resilience and harvesting potential are explored. Identified warming thresholds and stocks-size targets are compared to the current estimate of stock size and to near-to-mid-term expected climate development. Short-term stock (re-) building targets are identified. Optimization analysis (Chapter III) is conducted to explore potential climate-adaptive sustainable harvesting pathways, temporal management thresholds (timing of severe climate impact on the stock) as well as the potential future benefits (for conservation- and yield-related objectives) of limiting harvesting to below classical MSY-based recommendations in the short term to account for deep uncertainty.

The results are discussed with stakeholders and policy makers, especially with regard to determining catch potential and its impact on the fisheries sector, and to formulating long-term management plans including strategies for building stock reserves and measures for the case that the target stock becomes largely unmanageable. Management plans are then adopted and

implementation started. The procedures are repeated after  $k$  years (with  $k$  being agreed upon among stakeholders, policy makers and scientists a priori) and if required or feasible, management plans are modified or drafted anew.

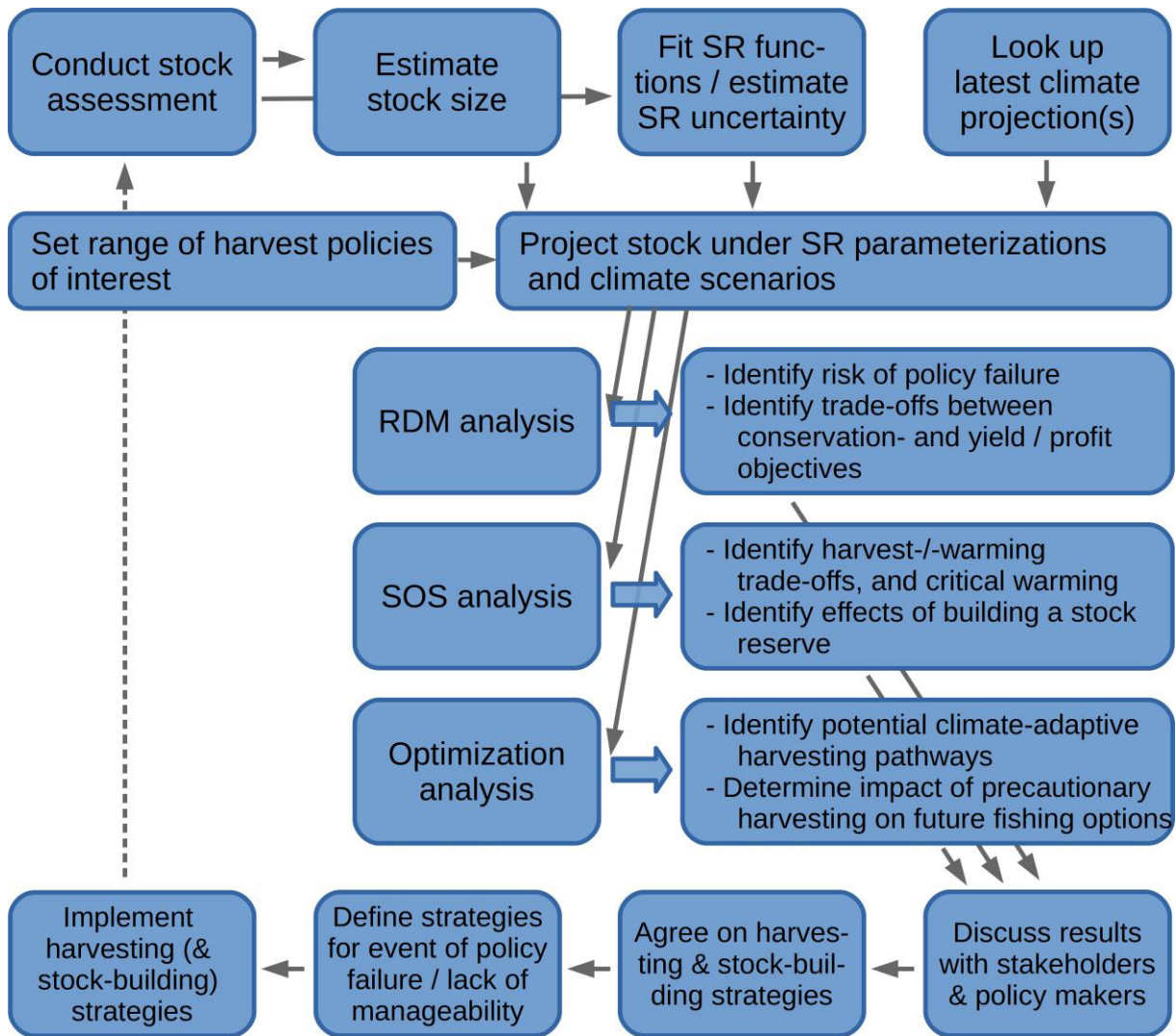


Figure G.1: Concept for a cyclical implementation of climate-sensitive management development, based on the concepts of RDM, SOS and optimization

## 5.6 Additional requirements for management implementation

The present work has uncovered the broad implications for managing the exploitation of Atlantic cod under future climate change. The applied implementation of climate-sensitive management does require, however, the additional consideration of a multitude of practical factors that themselves are subject to uncertainties. A major concern is the potential for shifting geographical distribution of cod stocks in response to warming (Brander, 2018), which has already been observed in e.g. North Sea cod (Engelhard et al., 2013). Such shifts may necessi-

tate the additional design of novel forms of trans-boundary fishing to avoid political tensions (e.g. Palacios-Abrantes et al., 2020; Gullestad et al., 2020), as they likely add to the challenges that uncertain / temporally variable stock productivity, as discussed in the present study, poses to management. Further, alterations to fish communities resulting from such shifts - or those of other species - might cause the need for novel quota-setting procedures, as different species may vary in stock status and climate sensitivity and possibly economic value (e.g. MacKenzie et al., 2007; Palacios-Abrantes et al., 2020). Apart from community shifts, management of cod might become aggravated by potentially different climate sensitivities of other species caught in mixed-species fisheries (Kühn et al., 2023). These could prompt underfishing of some species in order to account for the climate sensitivity of others, as shown in food-web-model projections (Lynam & Mackinson, 2015). Finally, the implementation of a harvest-rate- or fishing-mortality-based management strategy as proposed in some parts of the present study require a high-quality assessment of the managed stocks. Modern stock assessments (e.g. ICES, 2021f; ICES, 2022d; González-Troncoso et al., 2022) often suffer from strong retrospective bias (Mohn, 1999) where realized fishing mortality ( $F$ ) turns out to be higher than intended. This thwarts effective management, and could possibly be accounted for by lowering the intended  $F$  or harvest rate as a precautionary measure.

Performance of management measures investigated in the present study point to adaptive harvesting as being preferable for increasing the chances of a good trade-off between increasing stock size and increasing catches (or profits). It would likely be of little challenge to incorporate the presented combined RDM-/optimization approach within scientific assessment procedures (as conducted by e.g. ICES) to generate (experimental) alternative guidelines for long-term management planning and alternative target  $F$ s for the near future, the applicability of which would be subject to stakeholder discussion. Such an analysis could be conducted within benchmark stock assessments, which are typically conducted every three to five years in the ICES regions (ICES, 2023c) and could be part of a hypothetical new regular assessment- and planning workshop in the NOAA-, DFO- and NAFO management areas. Re-checks for the emergence of potential strong ecosystem drivers of recruitment, as suggested by Skern-Mauritzen et al. (2016), could be conducted simultaneously and could be directly incorporated into the RDM-based optimization via SR models fitted against variables other than SST. A concept with a sophisticated theoretical component, the hypothetical RDM-based fisheries management outlined would likely require pronounced efforts at communicating its potential for improved fisheries management to stakeholders: Policy implementation that puts little effort in knowledge coupling between interest groups has been suspected to partially

account for ineffective management-strategy implementation (Schwermer et al., 2021b). Hence, especially novel management concepts like uncertainty-conscious planning and long-term precautionary measures like “marine reserves” (Grafton & Kompas, 2005) (i.e. stock buffers) would likely require communicative skill to gain acceptance among interest groups (e.g. deReynier et al., 2010).

### **5.7 Limitations of the study**

The results obtained in this work are strongly dependent on the SR relationships incorporated in the population models and thus on the available stock-assessment outputs. The assessment time series of the western-Atlantic stocks in particular contain little-to-no data from before stock collapse and thus consist (almost) exclusively of data from low-productive regime(s), preventing the simulation of high-productivity scenarios. In general, though, and in line with the notion of increased difficulty of rebuilding marine ecosystems compared to maintaining them in good state (Hughes et al., 2005), strongly depleted stocks appear to have a higher likelihood to respond poorly to management action (i.e. to rebuild) than less- or non-depleted ones (Hutchings & Reynolds, 2004; *sensu* Winter et al., 2019). It can thus not be ruled out that the stocks concerned will eventually recover to higher-productive regimes not covered by the available data (*sensu* Rose & Rowe, 2015), but their current situation suggests that a conservative expectation of little response to management in forms of switching to higher productivity is warranted for current management guidance (e.g. Rowe & Rose, 2017). On the other hand, evidence of stocks getting recently “locked” into low-productivity regimes (Möllmann et al., 2021) suggests that the presented outlooks might in some cases be too optimistic (in the short term). Finally, the SR relationships used in this study should be understood more as scenarios rather than accurate representations of reality. Whether a recruitment pattern was generated primarily by SSB- or SST variability occasionally changed upon the addition of few data points when working with time-series subsets (Chapters II, III). With pre-recruit survival mechanisms not being well quantified (Haltuch et al., 2019), it appeared reasonable to not rule out either SSB or SST as primary driver, and to employ scenario-open RDM methodology (Lempert et al., 2019) rather than focusing efforts on finding the best statistical estimate of the “true” scenario.

The present work has the intention of illuminating possible future response of Atlantic cod to fishing and warming, and the entailing management implications, from the perspective and available knowledge of the year 2023, and for present management requirements. As uncertainty and lack of knowledge should not motivate inaction (e.g. Lemos & Rood, 2010; Roun-

sevell et al., 2021) and adaptation to changing perceptions is anyhow integral to natural-resource management, it appeared appropriate to conduct the presented analyses under the named limitations to SR modeling. It appears useful to replicate the analyses regularly to account for potential future novel knowledge on e.g. stock biology and also unexpectable stock- and ecosystem dynamics under novel climate conditions (Williams & Jackson, 2007).

The implementations of the three concepts of RDM, SOS and optimization is furthermore strongly focused on accounting for SR uncertainty and are somewhat simplified in other regards. Each approach could be expanded upon to incorporate i) further biological uncertainties, ii) environmental drivers and / or iii) processes that serve a more accurate representation of applied fisheries management. A particularly important additional biological factor that drives the productivity of a stock is natural mortality (e.g. Swain, 2011; Bryhn et al., 2022). While being historically less notorious for unpredictability than recruitment, natural mortality has been subject to major revisions of stock assessments (e.g. ICES, 2021f; Casini et al., 2016) and is considered to be temporally dynamic in some stocks (e.g. western-Baltic stock [ICES, 2021f]). Natural mortality thus has the potential to be a strong driver of future cod dynamics. Bottom-up effects, i.e. food-web reorganizations affecting food availability, can also have a notable impact on stock dynamics (e.g. Alheit et al., 2005; Lindegren et al., 2010). Further metrics potentially affected by future climate change are individual growth and size (Brander, 2010; Ipkewe et al., 2020) affecting SSB. Among environmental drivers, there are strong indications that cod may be negatively affected by ocean acidification as well and that an increase in acidification may work in conjunction with temperature increase to reduce harvesting potential (Dahlke et al., 2018; Voss et al., 2019). In the Baltic Sea, oxygen-minimum zones are an additional stressor constraining cod habitat that may evolve dynamically in the future (Köster et al., 2005; Meier et al., 2011), while cod dynamics in parts of the western Atlantic may depend on future dynamics of marine mammals (e.g. Trzcinski et al., 2006). Applied fisheries management may more accurately be modeled using classical MSE methodology, including the incorporation of assessment error (i.e., differentiating between a ground-truth of simulated population dynamics and a biased representation thereof as scientific perception) and policy-implementation error (i.e., forcing the model with biased harvest), as outlined in Punt et al. (2016).

Nevertheless, the aim of the present study is to investigate the overall management potential of Atlantic cod under future climate change. In marine systems, climate change most directly affects ocean warming (IPCC, 2023), and recruitment is a population process for which tem-



perature dependency is well established (e.g. Planque & Frédou, 1999; Clark et al., 2003; Ottersen et al., 2013) and which has arguably the strongest impact on stock productivity (Hjort, 1914; Walters & Maguire, 1996). Applied management does need to take assessment- and implementation uncertainty into account, but both are most likely markedly smaller than the recruitment uncertainties discussed here. Hence, the methodological choices made here can be considered appropriate for the stated aim. A methodological extension may be, however, a worthwhile future venture for investigating more specific management issues.

## **5.8 Conclusion**

The present study shows that management for sustainable harvesting of Atlantic cod will be possible under future climate change to a limited extent and under certain conditions pertaining to stock status and -productivity. Temperature increase will put a limit to sustainable harvesting when increasing above a stock-specific threshold, in particular in mid-latitude stocks. In northerly stocks, safe harvesting may or may not be constrained by temperature depending on the im-/balance between positive and negative climate effects. Harvesting interacts with warming effects on the risk of maintaining sustainable stock size in many stocks, thus continuing future warming will likely cause an eventual diminishment of future catch potential. Fisheries management will likely have the highest chances of achieving sustainable harvesting with relatively high yields when accounting for the potential long-term effects of fishing under deep uncertainty about stock-size- and environmental effects on stock productivity. Aiming for fast stock rebuilding in depleted stocks as well as growing a stock reserve to levels markedly above the precautionary thresholds are likely the most adequate tools to prepare for eventual unfavorable productivity conditions. Tight monitoring of stock size in combination with regular re-estimation of low-risk long-term harvesting pathways has a considerable chance of increasing both stock size and yield. Fisheries management will thus most likely be successful when adopting a high degree of policy flexibility especially in terms of setting total allowable catches and handling demands for fishing capacity. Developing emergency plans for the case of stocks becoming unmanageable with regard to attaining sustainability, which cannot fully be ruled out especially under much-increased warming, appears advisable. In summary, rebuilding stocks, building stock reserves, maintaining tight control over fishing effort and developing means for high policy flexibility are strategies that appear to have the best potential for enabling sustainable harvesting for the longest-possible duration in a changing future climate.

## 6. References

- Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V. & Wasmund, N. (2005). Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. *ICES Journal of Marine Science*, 62, 1205-1215. doi: 10.1016/j.icesjms.2005.04.024
- Allee, W. C., Park, O., Emerson, A. E., Park, T. & Schmidt, K. P. (1949). *Principles of Animal Ecology*. Saunders, London / UK, 837 pp.
- Allen, R. L. (1975). Models for fish populations: a review. *NZ Operational Research*, 4, 1-20
- Allison, E. H., Perry, A. L., Badjeck, M.-C., Adger, W. N., Brown, K., Conway, D., Halls, A. S. et al. (2009). Vulnerability of national economies to the impacts of climate change on fisheries. *Fish and Fisheries*, 10, 173-196. doi: 10.1111/j.1467-2979.2008.00310.x
- Arregui, I., Arrizabalaga, H., Kirby, D. S. & Martín-González, J. M. (2006). Stock–environment–recruitment models for North Atlantic albacore (*Thunnus alalunga*). *Fisheries Oceanography*, 15, 402-412. doi: 10.1111/j.1365-2419.2005.00399.x
- Arula, T., Laur, K., Simm, M. & Ojaveer, H. (2015). Dual impact of temperature on growth and mortality of marine fish larvae in a shallow estuarine habitat. *Estuarine, Coastal and Shelf Science*, 167, 326-335. doi: 10.1016/j.ecss.2015.10.004
- Babovic, F., Mijic, A. & Madani, K. (2018). Decision making under deep uncertainty for adapting urban drainage systems to change. *Urban Water Journal*, 15, 552-560. doi: 10.1080/1573062X.2018.1529803
- Bankes, S. (1993). Exploratory modeling for policy analysis. *Operations Research*, 41, 435-449. doi: 10.1287/opre.41.3.435
- Barnett, L. A. K., Branch, T. A., Ranasinghe, R. A. & Essington, T. E. (2017). Old-growth fishes become scarce under fishing. *Current Biology*, 27, 2843-2848.e2. doi: 10.1016/j.cub.2017.07.069
- Barrett, J., Johnstone, C., Harland, J., Van Neer, W., Eryvynck, A., Makowiecki, D., Heinrich, D. et al. (2008). Detecting the medieval cod trade: a new method and first results. *Journal of Archaeological Science*, 4, 850-861. doi: 10.1016/j.jas.2007.06.004
- Barrett, R. T., Røv, N., Loen, J. & Montevecchi, W. A. (1990). Diets of shags *Phalacrocorax aristotelis* and cormorants *P. carbo* in Norway and possible implications for gaidoid stock recruitment. *Marine Ecology Progress Series*, 66, 205-218. doi: 10.3354/meps066205
- Basson, M. (1999). The importance of environmental factors in the design of management procedures. *ICES Journal of Marine Science*, 56, 933-942. doi: 10.1006/jmsc.1999.0541
- Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S. & Reid, P. C. (2003). Plankton effect on cod recruitment in the North Sea. *Nature*, 426, 661-664. doi: 10.1038/nature02164
- Beaugrand, G. & Kirby, R. R. (2010). Climate, plankton and cod. *Global Change Biology*, 16, 1268-1280. doi: 10.1111/j.1365-2486.2009.02063.x

- Beddington, J. R. & Rettig, R. B. (1984). Approaches to the regulation of fishing effort. FAO Fisheries Technical Paper, 243, 39 pp.
- Bell, R. J., Tableau, A. & Collie, J. S. (2023). Changes in the productivity of US West Coast fish stocks. *Fisheries Research*, 264, 106712. doi: 10.1016/j.fishres.2023.106712
- Bentley, J. W., Serpetti, N., Fox, C. J., Heymans, J. J. & Reid, D. G. (2020). Retrospective analysis of the influence of environmental drivers on commercial stocks and fishing opportunities in the Irish Sea. *Fisheries Oceanography*, 29, 415-435. doi: 10.1111/fog.12486
- Bentley, J. W., Lundy, M. G., Howell, D., Beggs, S. E., Bundy, A., de Castro, F., Fox, C. J. et al. (2021). Refining fisheries advice with stock-specific ecosystem information. *Frontiers in Marine Science*, 8, 602072. doi: 10.3389/fmars.2021.602072
- Beverton, R. J. H. & Holt, S. J. (1957). On the dynamics of exploited fish populations. In: *Fishery Investigations Series II, Volume XIX*, Ministry of Agriculture, Fisheries and Food. Chapman & Hall, London / UK, 533 pp. doi: 10.1007/978-94-011-2106-4
- Biermann, F. & Kim, R. E. (2020). The boundaries of the Planetary Boundary Framework: A critical appraisal of approaches to define a “Safe Operating Space” for humanity. *Annual Review of Environment and Resources*, 45, 497-521. doi: 10.1146/annurev-environ-012320-080337
- Björnsson, B., Steinarsson, A. & Árnason, T. (2007). Growth model for Atlantic cod (*Gadus morhua*): Effects of temperature and body weight on growth rate. *Aquaculture*, 271, 216-226. doi: 10.1016/j.aquaculture.2007.06.026
- Björnsson, B., Litvak, M., Trippel, E. A. & Suquet, M. (2010). The codfishes (family: Gadidae). In: Le François, N., Jobling, M., Carter, C. & Blier, P. *Finfish aquaculture diversification*. CABI, Wallingford / UK, 290-322. doi: 10.1079/9781845934941.0290
- Blamey, L. K., Plagányi, É. A., Hutton, T., Deng, R. A., Upston, J. & Jarrett, A. (2021). Re-designing harvest strategies for sustainable fishery management in the face of extreme environmental variability. *Conservation Biology*, 36, e13864. doi: 10.1111/cobi.13864
- Blanchard, J. L., Heffernan, O. A. & Fox, C. J. (2005). North Sea (ICES Divisions IVa-c and VIIId). In: Brander, K. (ed.): *ICES Cooperative Research Report No. 274: Spawning and life history information for North Atlantic cod stocks*, ICES, Copenhagen / DK, 76-88. doi: 10.17895/ices.pub.5478
- Blanchard, J. L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J. I., Holt, J., Dulvy, N. K. & Barange, M. (2012). Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Philosophical Transactions of the Royal Society B*, 367, 2979-2989. doi: 10.1098/rstb.2012.0231
- BLE (2020). *Monatsbericht 2020. Bericht über die Fischerei und die Marktsituation für Fischereierzeugnisse in der Bundesrepublik Deutschland*. German federal office for agriculture and food (BLE), Bonn / DE, 49 pp.
- Blöcker, A. M., Gutte, H. M., Bender, R. L., Otto, S. A., Sguotti, C. & Möllmann, C. (2023a). Regime shift dynamics, tipping points and the success of fisheries management. *Scientific Reports*, 13, 289. doi: 10.1038/s41598-022-27104-y

- Blöcker, A. M., Sguotti, C. & Möllmann, C. (2023b). Discontinuous dynamics in North Sea cod *Gadus morhua* caused by ecosystem change. *Marine Ecology Progress Series*, 713, 133-149. doi: 10.3354/meps14342
- Bloemen, P. J. T. M., Hammer, F., van der Vlist, M. J., Grinwis & van Alphen, J. (2019). DMDU into practice: adaptive delta management in the Netherlands. In: Marchau, V. A. W. J., Walker, W. E., Bloemen, P. J. T. M. & Popper, S. W. (eds.): *Decision Making under Deep Uncertainty: From Theory to Practice*, Springer, Cham / CH, 321-351. doi: 10.1007/978-3-030-05252-2\_14
- Bogstad, B., Lilly, G. R., Mehl, S., Palsson, O. K. & Stefánsson, G. (1994). Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents Sea, Iceland, and eastern Newfoundland). *ICES Marine Science Symposia*, 198, 576-599
- Borg, Å., Pihl, L. & Wennhage, H. (1997). Habitat choice by juvenile cod (*Gadus morhua* L.) on sandy soft bottoms with different vegetation types. *Helgoländer Meeresuntersuchungen*, 51, 197-212. doi: 10.1007/BF02908708
- Boyd, C. E., McNevin, A. A. & Davis, R. P. (2022). The contribution of fisheries and aquaculture to the global protein supply. *Food Security*, 14, 815-827. doi: 10.1007/s12571-021-01246-9
- Boyce, D. G., Tittensor, D. P., Garilao, C., Henson, S., Kaschner, K., Kesner-Reyes, K., Pigot, A. et al. (2022). A climate risk index for marine life. *Nature Climate Change*, 12, 854-862. doi: 10.1038/s41558-022-01437-y
- Braack, M., Quaas, M. F., Tews, B. & Vexler, B. (2018). Optimization of fishing strategies in space and time as a non-convex optimal control problem. *Journal of Optimization Theory and Applications*, 178, 950-972. doi: 10.1007/s10957-018-1304-7
- Brander, K. M. (2007). Global fish production and climate change. *PNAS*, 104, 19709-19714. doi: 10.1073/pnas.070205910
- Brander, K. M. (2010). Cod *Gadus morhua* and climate change: processes, productivity and prediction. *Journal of Fish Biology*, 77, 1899-1911. doi: 10.1111/j.1095-8649.2010.02782.x
- Brander, K. (2018). Cod and climate change. In: Rose, G. A. (ed.). *Atlantic cod: a bio-ecology*. John Wiley & Sons, Hoboken, US, 337-348. doi: 10.1002/9781119460701.ch8
- Brander, K., Neuheimer, A., Andersen, K. H. & Hartvig, M. (2013). Overconfidence in model projections. *ICES Journal of Marine Science*, 70, 1065-1068. doi: 10.1093/icesjms/fst055
- Britten, G. L., Dowd, M. & Worm, B. (2015). Changing recruitment capacity in global fish stocks. *PNAS*, 113, 134-139. doi: 10.1073/pnas.150470911
- Britten, G. L., Dowd, M., Kanary, L. & Worm, B. (2017). Extended fisheries recovery timelines in a changing environment. *Nature Communications*, 8, 15325. doi: 10.1038/ncomms15325
- Brockway, A. M., Wang, L., Dunn, L. N., Callaway, D. & Jones, A. (2022). Climate-aware decision-making: lessons for electric grid infrastructure planning and operations. *Environmental Research Letters*, 17, 073002. doi: 10.1088/1748-9326/ac7815

- Brown, C. J., Fulton, E. A., Hobday, A. J., Matear, R. J., Possingham, H. P., Bulman, C., Christensen, V. et al. (2010). Effects of climate-driven primary production change on marine food webs: implications for fisheries and conservation. *Global Change Biology*, 16, 1194-1212. doi: 10.1111/j.1365-2486.2009.02046.x
- Brown, C. J., Fulton, E. A., Possingham, H. P. & Richardson, A. J. (2012). How long can fisheries management delay action in response to ecosystem and climate change? *Ecological Applications*, 22, 298-310. doi: 10.1890/11-0419.1
- Brunel, T., Piet, G. J., van Hal, R. & Röckmann, C. (2010). Performance of harvest control rules in a variable environment. *ICES Journal of Marine Science*, 67, 1051-1062. doi: 10.1093/icesjms/fsp297
- Bryhn, A. C., Bergek, S., Bergström, U., Casini, M., Dahlgren, E., Ek, C., Hjelm, J. et al. (2022). Which factors can affect the productivity and dynamics of cod stocks in the Baltic Sea, Kattegat and Skagerrak? *Ocean & Coastal Management*, 223, 106154. doi: 10.1016/j.ocecoaman.2022.106154
- Bryndum-Buchholz, A., Boyce, D. G., Tittensor, D. P., Christensen, V., Bianchi, D. & Lotze, H. K. (2020). Climate-change impacts and fisheries management challenges in the North Atlantic Ocean. *Marine Ecology Progress Series*, 648, 1-17. doi: 10.3354/meps13438
- Butterworth, D. S. & Punt, A. E. (1999). Experiences in the evaluation and implementation of management procedures. *ICES Journal of Marine Science*, 56, 985-998. doi: 10.1006/jmsc.1999.0532
- Caddy, J. F. & Seijo, J. C. (2005). This is more difficult than we thought! The responsibility of scientists, managers and stakeholders to mitigate the unsustainability of marine fisheries. *Philosophical Transactions of the Royal Society B*, 360, 59-75. doi: 10.1098/rstb.2004.1567
- Cadima, E. L. (2003). *Fish Stock Assessment Manual*. FAO Fisheries Technical Paper, 393. FAO, Rome / IT, 161 pp.
- Canada Department of the Environment (1976). Canada's 200 mile fishing limit. *Fishermen's Information / Bulletin 76-1E*, 4 pp.
- Cardinale, M., Hjelm, J. & Casini, M. (2008). Disentangling the effect of adult biomass and temperature on the recruitment dynamics of fishes. In: Kruse, G. H., Drinkwater, K., Ianelli, J. N., Link, J. S., Stram, D. L., Wespestad, V. & Woodby, D. (eds.). *Resiliency of Gadid Stocks to Fishing and Climate Change*. Alaska Sea Grant College Program, University of Alaska Fairbanks, Fairbanks, Alaska, 375 pp. doi: 10.4027/rgsfcc.2008
- Carpenter, G., Kleinjans, R., Villasante, S. & O'Leary, B. C. (2016). Landing the blame: The influence of EU Member States on quota setting. *Marine Policy*, 64, 9-15. doi: 10.1016/j.marpol.2015.11.001
- Carpenter, S. R., Brock, W. A., Folke, C., van Nes, E. H. & Scheffer, M. (2015). Allowing variance may enlarge the safe operating space for exploited ecosystems. *PNAS*, 112, 14384-14389. doi: 10.1073/pnas.1511804112
- Carpenter, S. R., Brock, W. A., Hansen, G. J. A., Hansen, J. F., Hennessy, J. M., Isermann, D. A., Pedersen, E. J., Perales, K. M., Rypel, A. L., Sass, G. G., Tunney, T. D. & van der Zanden, M. J. (2017). Defining a Safe Operating Space for inland recreational fisheries. *Fish and Fisheries*, 18, 1150-1160. doi: 10.1111/faf.12230

- Carruthers, T. R., Punt, A. E., Walters, C. J., MacCall, A., McAllister, M. K., Dick, E. J. & Cope, J. (2014). Evaluating methods for setting catch limits in data-limited fisheries. *Fisheries Research*, 153, 48-68. doi: 10.1016/j.fishres.2013.12.014
- Carstensen, J. (2014). Need for monitoring and maintaining sustainable marine ecosystem services. *Frontiers in Marine Science*, 1, 33. doi: 10.3389/fmars.2014.00033
- Casini, M., Eero, M., Carlshamre, S. & Lövgren, J. (2016). Using alternative biological information in stock assessment: condition-corrected natural mortality of Eastern Baltic cod. *ICES Journal of Marine Science*, 73, 2625-2631. doi: 10.1093/icesjms/fsw117
- Chabot, D. & Claireaux, G. (2018). *Ecophysiology*. In: Rose, G. A. (ed.): *Atlantic Cod: A Bio-Ecology*. John Wiley & Sons, Ltd., Hoboken, NJ, USA and Chichester, West Sussex, UK, 397 pp.
- Chapman W. M. (1949). *United States Policy on High Seas Fisheries*, Washington, D.C Department of State Bulletin, 67-80
- Cheney, J. (2019). The new Canadian Fisheries Act is good, but could be better. Sustainable Fisheries UW, University of Washington, <https://sustainablefisheries-uw.org/canadian-fisheries-act/>. Last access 13<sup>th</sup> August, 2023
- Cheung, W. W. L., Palacios-Abrantes, J., Frölicher, T. L., Palomares, M. L., Clarke, T., Lam, V. W. Y., Oyinlola, M. A., Pauly, D., Raygondeau, G., Sumaila, U. R., Teh, L. C. L. & Wabnitz, C. C. C. (2022). Rebuilding fish biomass for the world's marine ecoregions under climate change. *Global Change Biology*, 28, 6254-6262. doi: 10.1111/gcb.16368
- Christensen, P. & Nielsen, A.R. (1996). Norwegian fisheries 1100-1970: Main developments. In: Holm, P., Starkey, D. J. & Thór, J. T. (eds.). *The North Atlantic fisheries, 1100-1976: National perspectives on a common resource*. *Studia Atlantica*, 1. North Atlantic Fisheries History Association, Esbjerg / DK, 145-168.
- Clark, R. A., Fox, C. J., Viner, D. & Livermore, M. (2003). North Sea cod and climate change – modelling the effects of temperature on population dynamics. *Global Change Biology*, 9, 1669-1680. doi: 10.1046/j.1365-2486.2003.00685.x
- Cochrane, K. L. (2002). *A Fishery Manager's Guidebook - Management Measures and Their Application*. FAO Fisheries Technical Paper, 424. FAO, Rome / IT, 231 pp.
- Cohen, D. M., Inada, T., Iwamoto, T. & Scialabba, N. (1990). *FAO Species Catalogue, Vol. 10 Gadiform Fishes of the World*. FAO Fisheries Synopsis, 125. FAO, Rome / IT, 453 pp.
- Collie, J. S., Richardson, K. & Steele, J. H. (2004). Regime shifts: Can ecological theory illuminate the mechanisms?. *Progress in Oceanography*, 60, 281-302. doi: 10.1016/j.pocean.2004.02.013
- Collie, J., Minto, C., Worm, B. & Bell, R. (2013). Predation on prerecruits can delay rebuilding of depleted cod stocks. *Bulletin of Marine Science*, 89, 107-122. doi: 10.5343/bms.2011.1134
- Collie, J. S., Bell, R. J., Collie, S. B. & Minto, C. (2021). Harvest strategies for climate-resilient fisheries. *ICES Journal of Marine Science*, 8, 2774-2783. doi: 10.1093/icesjms/fsab152

- Cominassi, L., Moyano, M., Claireaux, G., Howald, S., Mark, F. C., Zambonino-Infante, J.-L. & Peck, M. A. (2020). Food availability modulates the combined effects of ocean acidification and warming on fish growth. *Scientific Reports*, 10, 2338. doi: 10.1038/s41598-020-58846-2
- Cook, R. M. & Trijoulet, V. (2016). The effects of grey seal predation and commercial fishing on the recovery of a depleted cod stock. *Canadian Journal of Fisheries and Aquatic Sciences*, 73, 1319-1329. doi: 10.1139/cjfas-2015-0423
- Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999). Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution*, 14, 405-410. doi: 10.1016/S0169-5347(99)01683-3
- Courtney, H. (2001). *20/20 Foresight: Crafting Strategy in an Uncertain World*, Harvard Business School Press, Boston / US, 209 pp.
- Craig, J. K. & Link, J. S. (2023). It is past time to use ecosystem models tactically to support ecosystem-based fisheries management: Case studies using Ecopath with Ecosim in an operational management context. *Fish and Fisheries*, 24, 381-406. doi: 10.1111/faf.12733
- Cushing, D. H. (1975). *Marine Ecology and Fisheries*. Cambridge University Press, Cambridge / UK, 278 pp.
- Daan, N. (1973). A quantitative analysis of the food intake of North Sea cod, *Gadus morhua*. *Netherlands Journal of Sea Research*, 6, 479-517. doi: 10.1016/0077-7579(73)90002-1
- Dahlke, F. T., Butzin, M., Nahrgang, J., Puvanendran, V., Mortensen, A., Pörtner, H.-O. & Storch, D. (2018). Northern cod species face spawning habitat losses if global warming exceeds 1.5°C. *Science Advances*, 4, eaas8821. doi: 10.1126/sciadv.aas88
- Dahlke, F. T., Wohlrab, S., Butzin, M. & Pörtner, H.-O. (2020). Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science*, 369, 65-70. doi: 10.1126/science.aaz365
- Dahlke, F. T., Puvanendran, V., Mortensen, A., Pörtner, H.-O. & Storch, D. (2022). Broodstock exposure to warming and elevated pCO<sub>2</sub> impairs gamete quality and narrows the temperature window of fertilisation in Atlantic cod. *Journal of Fish Biology*, 101, 822-833. doi: 10.1111/jfb.15140
- Da Rocha, J.-M., Cerviño, S. & Villasante, S. (2012). The Common Fisheries Policy: An enforcement problem. *Marine Policy*, 36, 1309-1314. doi: 10.1016/j.marpol.2012.02.025
- Daskalov, G. M., Grishin, A. N., Rodionov, S. & Mineva, V. (2007). Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *PNAS*, 104, 10518-10523. doi: 10.1073/pnas.0701100104
- Dearing, J. A., Wang, R., Zhang, K., Dyke, J. G., Haberl, H., Hossain, Md. S., Langdon, P. G. et al. (2014). Safe and just operating spaces for regional social-ecological systems. *Global Environmental Change*, 28, 227-238. doi: 10.1016/j.gloenvcha.2014.06.012
- Denechaud, C., Smoliński, S., Geffen, A. J., Godiksen, J. A. & Campana, S. E. (2020). A century of fish growth in relation to climate change, population dynamics and exploitation. *Global Change Biology*, 26, 5661-5678. doi: 10.1111/gcb.15298

- deReynier, Y. L., Levin, P. S. & Shoji, N. L. (2010). Bringing stakeholders, scientists, and managers together through an integrated ecosystem assessment process. *Marine Policy*, 34, 534-540. doi: 10.1016/j.marpol.2009.10.010
- Deroba, J. J. & Bence, J. R. (2008). A review of harvest policies: Understanding relative performance of control rules. *Fisheries Research*, 94, 210-223. doi: 10.1016/j.fishres.2008.01.003
- DFO (2006). A harvest strategy compliant with the precautionary approach. DFO Canadian Science Advisory Secretariat Science Advisory Report 2006/023, 7 pp.
- DFO (2019). Stock assessment of Northern cod (NAFO Divisions 2J3KL) in 2019. DFO Canadian Science Advisory Secretariat Science Advisory Report 2019/050, 20 pp.
- Dodson, J. J., Daigle, G., Hammer, C., Polte, P., Kotterba, P., Winkler, G. & Zimmermann, C. (2018). Environmental determinants of larval herring (*Clupea harengus*) abundance and distribution in the western Baltic Sea. *Limnology and Oceanography*, 317-329. doi: 10.1002/lno.11042
- Döring, R., Berkenhagen, J., Hentsch, S. & Kraus, G. (2020). Small-scale fisheries in Germany: a disappearing profession? In: Pascual-Fernández, J. J., Pita, C. & Bavinck, M. (eds.): *Small-Scale Fisheries in Europe: Status, Resilience and Governance*, Springer, Cham / CH, 483-502. doi: 10.1007/978-3-030-37371-9\_23
- Dorn, M. W. & Zador, S. G. (2020). A risk table to address concerns external to stock assessments when developing fisheries harvest recommendations. *Ecosystem Health and Sustainability*, 6, 1813634. doi: 10.1080/20964129.2020.1813634
- Drinkwater, K. F. (2005). The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES Journal of Marine Science*, 7, 1327-1337. doi: 10.1016/j.icesjms.2005.05.015
- Durant, J. M., Hjermann, D. Ø., Ottersen, G. & Stenseth, N. C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, 33, 271-283. doi: 10.3354/cr033271
- Dutil, J.-D. & Brander, K. (2003). Synergies between climate and management for Atlantic cod fisheries at high latitudes. *Fisheries Oceanography*, 12, 502-512. doi: 10.1046/j.1365-2419.2003.00243.x
- Dutil, J.-D., Gauthier, J., Lambert, Y., Fréchet, A. & Chabot, D. (2003). Cod stocks rebuilding and fish bioenergetics : low productivity hypothesis. CSAS Research Document, 2003/060, 39 pp.
- Elzhov, T. V., Mullen, K. M., Spiess, A.-N. & Bolker, B. (2016). minpack.lm: R interface to the Levenberg-Marquardt non-linear least-squares algorithm found in MINPACK, plus support for bounds. <https://CRAN.R-project.org/package=minpack.lm>. Last access 22<sup>nd</sup> June, 2023
- Emery, C. (1992). The northern cod crisis. Background papers, BP-313E. Government of Canada, Ottawa / CA, 26 pp.
- Engelhard, G. H., Righton, D. A. & Pinnegar, J. K. (2013). Climate change and fishing: a century of shifting distribution in North Sea cod. *Global Change Biology*, 20, 2473-2484. doi: 10.1111/gcb.12513



- Enghoff, I. B., MacKenzie, B. R. & Nielsen, E. E. (2007). The Danish fish fauna during the warm Atlantic period (ca. 7000–3900 bc): Forerunner of future changes? *Fisheries Research*, 87, 167-180. doi: 10.1016/j.fishres.2007.03.004
- European Union (2013). Regulation (EU) No 1380/2013 of the European Parliament and of the Council of 11 December 2013 on the Common Fisheries Policy, amending Council Regulations (EC) No 1954/2003 and (EC) No 1224/2009 and repealing Council Regulations (EC) No 2371/2002 and (EC) No 639/2004 and Council Decision 2004/585/EC. *Official Journal of the European Union*, 22-61
- FAO (1995). Precautionary approach to fisheries. Part 1: Guidelines on the precautionary approach to capture fisheries and species introductions. Elaborated by the Technical Consultation on the Precautionary Approach to Capture Fisheries (Including Species Introductions). Lysekil, Sweden, 6–13 June 1995 (A scientific meeting organized by the Government of Sweden in cooperation with FAO). FAO Fisheries Technical Paper, 350 / 1. FAO, Rome / IT, 52 pp.
- FAO (2022). The State of World Fisheries and Aquaculture 2022. Towards Blue Transformation. FAO, Rome / IT, 266 pp. doi: 10.4060/cc0461en
- Fauchald, P. (2010). Predator–prey reversal: A possible mechanism for ecosystem hysteresis in the North Sea? *Ecology*, 91, 2191-2197. doi: 10.1890/09-1500.1
- Flaaten, O. & Stollery, K. (1996). The economic costs of biological predation. *Environmental and Resource Economics*, 8, 75-95. doi: 10.1007/BF00340654
- Flávio, H., Seitz, R., Eggleston, D., Svendsen, J. C. & Støttrup, J. (2023). Hard-bottom habitats support commercially important fish species: a systematic review for the North Atlantic Ocean and Baltic Sea. *PeerJ*, 11, e14681. doi: 10.7717/peerj.14681
- Feistel, R., Weinreben, S., Wolf, H., Seitz, S., Spitzer, P., Adel, B., Nausch, G., Schneider, B. & Wright, D. G. (2010). Density and absolute salinity of the Baltic Sea 2006–2009. *Ocean Science*, 6, 3-24. doi: 10.5194/os-6-3-2010
- Folkvord, A. (1991). Growth, survival and cannibalism of cod juveniles (*Gadus morhua*): effects of feed type, starvation and fish size. *Aquaculture*, 97, 41-59. doi: 10.1016/0044-8486(91)90278-F
- Folkvord, A. (1997). Ontogeny of cannibalism in larval and juvenile fishes with special emphasis on Atlantic cod. In: Chambers, R. C. & Trippel, E. A. (eds.). *Early Life History and Recruitment in Fish Populations*. Chapman & Hall Fish and Fisheries Series, 21, 251-278, Springer, Dordrecht / NL. doi: 10.1007/978-94-009-1439-1\_9
- Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J. & Jensen, O. P. (2019). Impacts of historical warming on marine fisheries production. *Science*, 363, 979-983. doi: 10.1126/science.aau1758
- Free, C. M., Mangin, T., Wiedenmann, J., Smith, C., McVeigh, H. & Gaines, S. D. (2022). Harvest control rules used in US federal fisheries management and implications for climate resilience. *Fish and Fisheries*, 24, 248-262. doi: 10.1111/faf.12724
- Freitas, C., Olsen, E. M., Moland, E., Cianelli, L. & Knutsen, H. (2015). Behavioral responses of Atlantic cod to sea temperature changes. *Ecology and Evolution*, 5, 2070-2083. doi: 10.1002/ece3.1496

- Friedman, J. H. (2001). Greedy function approximation: A gradient boosting machine. *Annals of Statistics*, 29, 1189-1232. doi: 10.1214/aos/1013203451
- Froese, R. & Pauly, D. (eds.) (2023). FishBase. World Wide Web electronic publication. <https://fishbase.se/summary/Gadus-morhua.html>. Last access 19<sup>th</sup> September, 2023
- Frommel, A. Y., Maneja, R., Lowe, D., Malzahn, A. M., Geffen, A. J., Folkvord, A., Piatkoswki, U., Reusch, T. B. H. & Clemmesen, C. (2011). Severe tissue damage in Atlantic cod larvae under increasing ocean acidification. *Nature Climate Change*, 2, 42-46. doi: 10.1038/nclimate1324
- Funk, S., Frelat, R., Möllmann, C., Temming, A. & Krumme, U. (2020). The forgotten feeding ground: patterns in seasonal and depth-specific food intake of adult cod *Gadus morhua* in the western Baltic Sea. *Journal of Fish Biology*, 98, 707-722. doi: 10.1111/jfb.14615
- Funk, S., Frelat, R., Möllmann, C., Temming, A. & Krumme, U. (2021). The forgotten feeding ground: patterns in seasonal and depth-specific food intake of adult cod *Gadus morhua* in the western Baltic Sea. *Journal of Fish Biology*, 98, 707-722. doi: 10.1111/jfb.14615
- Gaines, S. D., Costello, C., Owashi, B., Mangin, T., Bone, J., García Molinos, J., Buden, M. et al. (2018). Improved fisheries management could offset many negative effects of climate change. *Science Advances*, 4, eaao1378. doi: 10.1126/sciadv.aao1378
- Galappaththi, E. K., Susarla, V. B., Loutet, S. T., Ichien, S. T., Hyman, A. A. & Ford, J. D. (2021). Climate change adaptation in fisheries. *Fish and Fisheries*, 23, 4-21. doi: 10.1111/faf.12595
- German Federal Ministry of Food and Agriculture (2022). BMEL-Leitbildkommission zur Zukunft der Ostseefischerei nimmt Arbeit auf. <https://www.bmel.de/SharedDocs/Pressemitteilungen/DE/2022/156-leitbildkommission-ostsee.html>. Last access 29th August, 2023
- Glenn, H., Tingley, D., Sánchez Maroño, S., Holm, D., Kell, L., Padda, G., Edvardsson, I. R. et al. (2012). Trust in the fisheries scientific community. *Marine Policy*, 36, 54-72. doi: 10.1016/j.marpol.2011.03.008
- González-Irusta, J. M. & Wright, P. (2015). Spawning grounds of Atlantic cod (*Gadus morhua*) in the North Sea. *ICES Journal of Marine Science*, 73, 304-315. doi: 10.1093/icesjms/fsv180
- González-Troncoso, D., González-Costas, F. & Garrido, I. (2022). Assessment of the cod stock in NAFO Division 3M. NAFO Scientific Council Research Document, 22/025, Serial No. N7298, 58 pp.
- Goodfellow, I., Bengio, Y. & Courville, A. (2016). *Deep Learning*. The MIT Press, Cambridge, Massachusetts / US, 800 pp.
- Gordon, H. S. (1954). The Economic Theory of a Common-Property Resource: The Fishery. *Journal of Political Economy*, 62, 124-142
- Government of Canada (2019). Fisheries Act (R.S.C. 1985, c. F-14). Published by the Minister of Justice at the following address: <http://laws-lois.justice.gc.ca>. 111 pp.
- Grafton, R. Q. (1996). Individual transferable quotas: theory and practice. *Reviews in Fish Biology and Fisheries*, 6, 5-20. doi: 10.1007/BF00058517

- Grafton, R. Q. & Kompas, T. (2005). Uncertainty and the active adaptive management of marine reserves. *Marine Policy*, 29, 471-479. doi: 10.1016/j.marpol.2004.07.006
- Grafton, R. Q., Kompas, T. & Lindenmayer, D. (2005). Marine reserves with ecological uncertainty. *Bulletin of Mathematical Biology*, 67, 957-971. doi: 10.1016/j.bulm.2004.11.006
- Green, A. J., Alcorlo, P., Peeters, E.T.H.M., Morris, E. P., Espinar, J. L., Bravo-Utrera, M. A., Bustamante, J., Díaz-Delgado, R., Koelmans, A. A., Mateo, R., Mooij, W. M., Rodríguez-Rodríguez, M., van Nes, E. H. & Scheffer, M. (2017). Creating a safe operating space for wetlands in a changing climate. *Frontiers in Ecology and the Environment*, 15, 99-107. doi: 10.1002/fee.1459
- Groves, D. G., Molina-Perez, E., Bloom, E. & Fischbach, J. R. (2019). Robust Decision Making (RDM): application to water planning and climate policy. In: Marchau, V. A. W. J., Walker, W. E., Bloemen, P. J. T. M. & Popper, S. W. (eds.): *Decision Making under Deep Uncertainty: From Theory to Practice*, Springer, Cham / CH, 135-163. doi: 10.1007/978-3-030-05252-2\_7
- Gullestad, P., Sundby, S. & Kjesbu, O. S. (2020). Management of transboundary and straddling fish stocks in the Northeast Atlantic in view of climate-induced shifts in spatial distribution. *Fish and Fisheries*, 21, 1008-1026. doi: 10.1111/faf.12485
- Gunderson, D. R. (1993). *Surveys of Fisheries Resources*. John Wiley & Sons, Hoboken / US, 256 pp.
- Haasnoot, M., Kwakkel, J. H., Walker, W. E. & ter Maat, J. (2013). Dynamic adaptive policy pathways: A method for crafting robust decisions for a deeply uncertain world. *Global Environmental Change*, 23, 485-498. doi: 10.1016/j.gloenvcha.2012.12.006
- Haasnoot, M., Warren, A. & Kwakkel, J. H. (2019). Dynamic Adaptive Policy Pathways (DAPP). In: Marchau, V. A. W. J., Walker, W. E., Bloemen, P. J. T. M. & Popper, S. W. (eds.): *Decision Making under Deep Uncertainty: From Theory to Practice*, Springer, Cham / CH, 71-92. doi: 10.1007/978-3-030-05252-2\_4
- Hadjimichael, A., Reed, P. M. & Quinn, J. D. (2020). Navigating deeply uncertain tradeoffs in harvested predator-prey systems. *Complexity*, 2020, 4170453. doi: 10.1155/2020/4170453
- Haltuch, M. A., Brooks, E. N., Brodziak, J., Devine, J. A., Johnson, K. F., Klibansky, N., Nash, R. D. M., Payne, M. R., Shertzer, K. W., Subbey, S. & Wells, B. K. (2019). Unraveling the recruitment problem: A review of environmentally-informed forecasting and management strategy evaluation. *Fisheries Research*, 217, 198-216. doi: 10.1016/j.fishres.2018.12.016
- Hamilton, L. C., Haedrich, R. L. & Duncan, C. M. (2004). Above and Below the Water: Social/Ecological Transformation in Northwest Newfoundland. *Population and Environment*, 25, 195-215. doi: 10.1023/B:POEN.0000032322.21030.c1
- Hamon, K., Ulrich, C. & Kell, L. T. (2007). Evaluation of Management Strategies for the Mixed North Sea Roundfish Fisheries with the FLR Framework. MODSIM07 - Land, Water and Environmental Management: Integrated Systems for Sustainability, Proceedings. Modelling and Simulation Society of Australia and New Zealand, Canberra / AU, 2813-2819
- Hansen, G. J. A., Winslow, L. A., Read, J. S., Treml, M., Schmalz, P. J. & Carpenter, S. R. (2019). Water clarity and temperature effects on walleye safe harvest: an empirical test of the safe operating space concept. *Ecosphere*, 10, e02737. doi: 10.1002/ecs2.2737

- Harte, M., Tiller, R., Kailis, G. & Burden, M. (2019). Countering a climate of instability: the future of relative stability under the Common Fisheries Policy. *ICES Journal of Marine Science*, 76, 1951-1958. doi: 10.1093/icesjms/fsz109
- Hastings, A. & Wysham, D. B. (2010). Regime shifts in ecological systems can occur with no warning. *Ecology Letters*, 13, 464-472. doi: 10.1111/j.1461-0248.2010.01439.x
- Haug, T., Bogstad, B., Chierici, M., Gjøsæter, H., Hallfredsson, E. H., Høines, A. S., Hoel, A. H. et al. (2017). Future harvest of living resources in the Arctic Ocean north of the Nordic and Barents Seas: A review of possibilities and constraints. *Fisheries Research*, 188, 38-57. doi: 10.1016/j.fishres.2016.12.002
- Hawkins, E. & Sutton, R. (2009). The potential to narrow uncertainty in regional climate predictions. *Bulletin of the American Meteorological Society*, 90, 1095-1108. doi: 10.1175/2009BAMS2607.1
- Heath, M. R. & Lough, R. G. (2007). A synthesis of large-scale patterns in the planktonic prey of larval and juvenile cod (*Gadus morhua*). *Fisheries Oceanography*, 16, 169-185. doi: 10.1111/j.1365-2419.2006.00423.x
- Heidbrink, I. (2011). A second industrial revolution in the distant-water fisheries? factory-freezer trawlers in the 1950s and 1960s. *International Journal of Maritime History*, 23, 179-192. doi: 10.1177/0843871411023001
- Hilborn, R., & Walters, C. J. (1992), *Quantitative Fisheries Stock Assessment. Choice, Dynamics and Uncertainty*. Chapman and Hall, London, 570 pp. doi: 10.1007/978-1-4615-3598-0
- Hilborn, R. M. & Peterman, R. M. (1995). The development of scientific advice with incomplete information in the context of the precautionary approach. In: FAO (ed.). *Precautionary approach to fisheries. Part 2: scientific papers*. Prepared for the Technical Consultation on the Precautionary Approach to Capture Fisheries (Including Species Introductions). Lysekil, Sweden, 6–13 June 1995. (A scientific meeting organized by the Government of Sweden in cooperation with FAO). *FAO Fisheries Technical Paper*, 350, Part 2. FAO, Rome / IT, 210 pp.
- Hilborn, R., Hively, D. J., Jensen, O. P. & Branch, T. A. (2014). The dynamics of fish populations at low abundance and prospects for rebuilding and recovery. *ICES Journal of Marine Science*, 71, 2141-2151. doi: 10.1093/icesjms/fsu035
- Hill, S. L., Watters, G. M., Punt, A. E., McAllister, M. K., Le Quéré, C. & Turner, J. (2007). Model uncertainty in the ecosystem approach to fisheries. *Fish and Fisheries*, 8, 315-336. doi: 10.1111/j.1467-2979.2007.00257.x
- Hinrichsen, H.-H., Lehmann, A., Peterreit, C., Nissling, A., Ustup, D., Bergström, U. & Hüseyin, K. (2016). Spawning areas of eastern Baltic cod revisited: Using hydrodynamic modelling to reveal spawning habitat suitability, egg survival probability, and connectivity patterns. *Progress in Oceanography*, 143, 13-25. doi: 10.1016/j.pocean.2016.02.004
- Hislop, J., Bergstad, O. A., Jakobsen, T., Sparholt, H., Blasdale, T., Wright, P., Kloppmann, M., Hillgruber, N. & Heessen, H. J. L. (2015). Cod fishes (*Gadidae*). In: Heessen, H. J. L., Daan N. & Ellis, J. R. (eds.). *Fish atlas of the Celtic Sea, North Sea, and Baltic Sea*. Wageningen Academic Publishers, Wageningen / NL, 186-236. doi: 10.3920/978-90-8686-878-0

- Hjort, J. (1914). Fluctuations in the great fisheries of northern Europe, viewed in the light of biological research. *Rapports et Procès-Verbaux*, XX, Copenhagen / DK, 228 pp.
- Ho, E. H. & Budescu, D. V. (2019). Climate uncertainty communication. *Nature Climate Change*, 9, 802-803. doi: 10.1038/s41558-019-0606-6
- Hochreiter, S. & Schmidhuber, J. (1997). Long short-term memory. *Neural Computation*, 9, 1735-1780. doi: 10.1162/neco.1997.9.8.1735
- Holland, D. S. (2010). Management Strategy Evaluation and management procedures: tools for rebuilding and sustaining fisheries. *OECD Food, Agriculture and Fisheries Working Papers*, 25, 67 pp. doi: 10.1787/5kmd77jhvkjf-en
- Hollowed, A. B., Barange, M., Beamish, R. J., Brander, K., Cochrane, K., Drinkwater, K., Foreman, M. G. G. et al. (2013). Projected impacts of climate change on marine fish and fisheries. *ICES Journal of Marine Science*, 70, 1023-1037. doi: 10.1093/icesjms/fst081
- Holma, M., Lindroos, M., Romakkaniemi, A. & Olinonen, S. (2019). Comparing economic and biological management objectives in the commercial Baltic salmon fisheries. *Marine Policy*, 100, 207-214. doi: 10.1016/j.marpol.2018.11.011
- Holsman, K. K., Hazen, E. L., Haynie, A., Gourguet, S., Hollowed, A., Bograd, S. J., Samhour, J. F. & Aydin, K. (2019). Towards climate resiliency in fisheries management. *ICES Journal of Marine Science*, 76, 1368-1378. doi: 10.1093/icesjms/fsz031
- Holsman, K. K., Haynie, A. C., Hollowed, A. B., Reum, J. C. P., Aydin, K., Hermann, A. J., Cheng, W., Faig, A., Ianelli, J. N., Kearney, K. A. & Punt, A. E. (2020). Ecosystem-based fisheries management forestalls climate-driven collapse. *Nature Communications*, 11, 4579. doi: 10.1038/s41467-020-18300-3
- Holt, R. E. & Jørgensen, C. (2014). Climate warming causes life-history evolution in a model for Atlantic cod (*Gadus morhua*). *Conservation Physiology*, 2, cou050. doi: 10.1093/conphys/cou050
- Holt, R. E., Bogstad, B., Durant, J. M., Dolgov, A. V. & Ottersen, G. (2019). Barents Sea cod (*Gadus morhua*) diet composition: long-term interannual, seasonal, and ontogenetic patterns. *ICES Journal of Marine Science*, 76, 1641-1652. doi: 10.1093/icesjms/fsz082
- Homans, J. S. & Homans, J. S. jr. (1858). *Cyclopedia of Commerce and Commercial Navigation*. Harper & Brothers, London / UK, 2009 pp.
- Houde, E. D. (1987). Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium*, 2, 17-29
- Howell, D., Filin, A. A., Bogstad, B. & Stiansen, J. E. (2013). Unquantifiable uncertainty in projecting stock response to climate change: Example from North East Arctic cod. *Marine Biology Research*, 9, 920-931. doi: 10.1080/17451000.2013.775452
- Hsieh, C. H., Reiss, C. S., Hunter, J. R., Beddington, J. R., May, R. M. & Sugihara, G. (2006). Fishing elevates variability in the abundance of exploited species. *Nature*, 443, 859-862. doi: 10.1038/nature05232
- Huang, B., Thorne, P. W., Banzon, V. F., Boyer, T., Chepurin, G., Lawrimore, J. H., Menne, M. J., Smith, T. M., Vose, R. S. & Zhang, H.-M. (2017). *Extended Reconstructed Sea Surface*

- Temperature, Version 5 (ERSSTv5): upgrades, validations, and intercomparisons. *Journal of Climate*, 30, 8179-8205. doi: 10.1175/JCLI-D-16-0836.1
- Hughes, T. P., Bellwood, D. R., Folke, C., Steneck, R. S. & Wilson, J. (2005). New paradigms for supporting the resilience of marine ecosystems. *Trends in Ecology & Evolution*, 20, 380-386. doi: 10.1016/j.tree.2005.03.022
  - Hunter, J. D. (2007). Matplotlib: A 2D Graphics Environment. *Computing in Science & Engineering*, 9, 90-95. doi: 10.1109/MCSE.2007.55
  - Huserbråten, M. B. O., Eriksen, E., Gjørseter, H. & Vikebø, F. (2019). Polar cod in jeopardy under the retreating Arctic sea ice. *Communications Biology*, 2, 407. doi: 10.1038/s42003-019-0649-2
  - Hutchings, J. A. (2000). Collapse and recovery of marine fishes. *Nature*, 406, 882-885. doi: 10.1038/35022565
  - Hutchings, J. A. & Reynolds, J. D. (2004). Marine fish population collapses: Consequences for recovery and extinction risk. *BioScience*, 54, 297-309. doi: 10.1641/0006-3568(2004)054[0297:MFPCCF]2.0.CO;2
  - Hutchings, J. A. & Rangeley, R. W. (2011). Correlates of recovery for Canadian Atlantic cod (*Gadus morhua*). *Canadian Journal of Zoology*, 89, 386-400. doi: 10.1139/z11-022
  - Huxley, T. H. (1883). Inaugural Meeting of the Fishery Congress: Address by Professor Huxley. William Clowes and Sons, London / UK, 22 pp.
  - ICES (2012). General context of ICES advice. ICES Advice: Recurrent Advice. Report. ICES, Copenhagen / DK, 18 pp. doi: 10.17895/ices.advice.18667652.v1
  - ICES (2013). Benchmarks at ICES. ICES website, 7 pp. <https://www.ices.dk/community/documents/advice/introduction%20to%20benchmarks%20at%20ices.pdf>. Last access: 13<sup>th</sup> June, 2023
  - ICES (2019). ICES Advice basis. In: Report of the ICES Advisory Committee, ICES Advice 2019, Introduction\_to\_advice\_2019. ICES, Copenhagen / DK, 17 pp. doi: 10.17895/ices.advice.5757
  - ICES (2021a). Advice on fishing opportunities. In: Report of the ICES Advisory Committee, 2021. ICES Advice 2021, 1-9. doi: 10.17895/ices.advice.7720
  - ICES (2021b). Cod (*Gadus morhua*) in Subarea 4, Division 7.d, and Subdivision 20 (North Sea, eastern English Channel, Skagerrak). ICES Working Group on the Assessments of Demersal Stocks in the North Sea and Skagerrak, 2 (61), 101-181. doi: 10.17895/ices.pub.6092
  - ICES (2021c). Cod (27.47d20). Benchmark Workshop on North Sea Stocks (WKNSEA), 3 (25), 5-46. doi: 10.17895/ices.pub.7922
  - ICES (2021d). ICES fisheries reference points for category 1 and 2 stocks; Technical Guidelines. In: Report of the ICES Advisory Committee, 2021. ICES Advice 2021, Section 16.4.3.1. ICES, Copenhagen / DK, 19 pp. doi: 10.17895/ices.advice.7891
  - ICES (2021e). Baltic Fisheries Assessment Working Group (WGBFAS). ICES Scientific Reports, 3 (53), 717 pp. doi: 10.17895/ices.pub.8187
  - ICES (2021f). Inter-Benchmark Process on Western Baltic cod (IBPWEB). ICES Scientific Reports, 3 (87), 76 pp. doi: 10.17895/ices.pub.5257

- ICES (2022a) Cod (*Gadus morhua*) in ICES Subarea 14 and NAFO Division 1.F (East Greenland, South Greenland). In: Report of the ICES Advisory Committee, 2022. ICES Advice 2022, cod.2127.1f14. doi: 10.17895/ices.advice.19447838
- ICES (2022b). Working Group for the Celtic Seas Ecoregion (WGCSE). ICES Scientific Reports, 4 (45), 1413 pp. doi: 10.17895/ices.pub.19863796
- ICES (2022c). Baltic Sea ecoregion – fisheries overview. In: Report of the ICES Advisory Committee, 2022. ICES Advice 2022, section 4.2, 34 pp. doi: 10.17895/ices.advice.21646934
- ICES (2022d). Cod (*Gadus morhua*) in Subdivision 5.b.1 (Faroe Plateau). In: Report of the ICES Advisory Committee, 2022. ICES Advice 2022, cod.27.5b1. doi: 10.17895/ices.advice.19772368
- ICES (2023a). ICES Guidelines for Benchmarks. Version 1. ICES Guidelines and Policies - Advice Technical Guidelines, 26 pp. doi: 10.17895/ices.pub.22316743
- ICES (2023b). Cod (*Gadus morhua*) in subdivisions 22-24, western Baltic stock (western Baltic Sea). In: Report of the ICES Advisory Committee, 2023. ICES Advice 2023, cod.27.22-24. doi: 10.17895/ices.advice.21820494
- ICES (2023c). ICES Guidelines for Benchmarks. Version 1. ICES Guidelines and Policies - Advice Technical Guidelines, 26 pp. doi: 10.17895/ices.pub.22316743
- Ingvaldsen, R. B., Gjørseter, H., Ona, E. & Michalsen, K. (2017). Atlantic cod (*Gadus morhua*) feeding over deep water in the high Arctic. Polar Biology, 40, 2105-2111. doi: 10.1007/s00300-017-2115-2
- IPCC (2021). Climate Change 2021 - the Physical Science Basis, Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, USA, 2391 pp. doi: 10.1017/9781009157896
- IPCC (2023). Climate change 2023: Synthesis report. A report of the Intergovernmental Panel on Climate Change. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva / CH, 85 pp.
- Ipkewe, I. E., Baudron, A. R., Ponchon, A. & Fernandes, P. G. (2020). Bigger juveniles and smaller adults: Changes in fish size correlate with warming seas. Journal of Applied Ecology, 58, 847-856. doi: 10.1111/1365-2664.13807
- Jacobsen, N. S., Marshall, K. N., Berger, A. M., Grandin, C. & Taylor, I. G. (2022). Climate-mediated stock redistribution causes increased risk and challenges for fisheries management. ICES Journal of Marine Science, 79, 1120-1132. doi: 10.1093/icesjms/fsac029
- Jacobsen, S., Nielsen, K. K., Kristiansen, R., Grønkjær, P., Gaard, E. & Steingrund, P. (2020). Diet and prey preferences of larval and pelagic juvenile Faroe Plateau cod (*Gadus morhua*). Marine Biology, 167, 122. doi: 10.1007/s00227-020-03727-5
- Jakobsen, T. (1987). Coastal cod in Northern Norway. Fisheries Research, 5, 223-234. doi: 10.1016/0165-7836(87)90042-7
- Jean, Y. (1964). Seasonal Distribution of Cod (*Gadus morhua* L.) Along the Canadian Atlantic Coast in Relation to Water Temperature. Journal of the Fisheries Board of Canada, 21, 429-460. doi: 10.1139/f64-038

- Jordaan, A. & Kling, L. J. (2003). Determining the optimal temperature range for Atlantic cod (*Gadus morhua*) during early life. In: Browman, H. I. & Skiftesvik, A. B. (eds.): The Big Fish Bang. Proceedings of the 26th Annual Larval Fish Conference. Institute of Marine Research, Bergen / NO, 45-62
- Kändler, R., (1944). Untersuchungen über den Ostseedorsch während der Forschungsfahrt mit dem R.F.D. "Poseidon" in den Jahren 1925–1938. Ber. DWK N.F., 9, 137–255.
- Kapturowski, S., Ostrovski, G., Quan, J., Munos, R. & Dabney, W. (2019). Recurrent experience replay in distributed reinforcement learning. Proceedings of the International Conference on Learning Representations (ICLR) 2019, 19 pp.
- Kaschner, K., Kesner-Reyes, K., Garilao, C., Segschneider, J., Rius-Barile, J. Rees, T., & Froese, R. (2019). AquaMaps: Predicted range maps for aquatic species. Retrieved from <https://www.aquamaps.org>. Last access 12<sup>th</sup> August, 2023
- Kawarazuka, N. & Béné, C. (2010). Linking small-scale fisheries and aquaculture to household nutritional security: an overview. Food Security, 2, 343-357. doi: 10.1007/s12571-010-0079-y
- Keith, D. M. & Hutchings, J. A. (2012). Population dynamics of marine fishes at low abundance. Canadian Journal of Fisheries and Aquatic Science, 69, 1150-1163. doi: 10.1139/f2012-055
- Kell, L. T., Pilling, G. M. & O'Brien, C. M. (2005). Implications of climate change for the management of North Sea cod (*Gadus morhua*). ICES Journal of Marine Science, 62, 1483-1491. doi: 10.1016/j.icesjms.2005.05.006
- King, J. R., McFarlane, G. A. & Punt, A. E. (2015). Shifts in fisheries management: adapting to regime shifts. Philosophical Transactions of the Royal Society B, 370, 20130277. doi: 10.1098/rstb.2013.0277
- Kingma, D. P. & Ba, J. (2014). Adam: a method for stochastic optimization. arXiv:1412.6980. doi: 10.48550/arXiv.1412.6980
- Kjesbu, O. S., Bogstad, B., Devine, J. A. & Skjæraasen, J. E. (2014). Synergies between climate and management for Atlantic cod fisheries at high latitudes. PNAS, 111, 3473-3483. doi: 10.1073/pnas.1316342111
- Koenigstein, S., Dahlke, F. T., Stiasny, M. H., Storch, D., Clemmesen, C. & Pörtner, H.-O. (2017). Forecasting future recruitment success for Atlantic cod in the warming and acidifying Barents Sea. Global Change Biology, 24, 526-535. doi: 10.1111/gcb.13848
- Köster, F. W. & Möllmann, C. (2000). Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES Journal of Marine Science, 57, 310-323. doi: 10.1006/jmsc.1999.0528
- Köster, F. W., Möllmann, C., Hinrichsen, H.-H., Wieland, K., Tomkiewicz, J., Kraus, G., Voss, R. et al. (2005). Baltic cod recruitment – the impact of climate variability on key processes. ICES Journal of Marine Science, 62, 1408-1425. doi: 10.1016/j.icesjms.2005.05.004
- Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V. & Aschan, M. (2015). Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists Proceedings of the Royal Society B, 282, 20151546. doi: 10.1098/rspb.2015.1546



- Kristensen, C., Nielsen, A., Berg, C. W., Skaug, H. & Bell, B. M. (2016). TMB: Automatic differentiation and Laplace approximation. *Journal of Statistical Software*, 70, 1-21. doi: 10.18637/jss.v070.i05
- Kritzer, J. P., Costello, C., Mangin, T. & Smith, S. L. (2019). Responsive harvest control rules provide inherent resilience to adverse effects of climate change and scientific uncertainty. *ICES Journal of Marine Science*, 76, 1424-1435. doi: 10.1093/icesjms/fsz038
- Kühn, B., Kempf, A., Brunel, T., Cole, H., Mathis, M., Sys, K., Trijoulet, V., Vermard, Y. & Taylor, M. (2023). Adding to the mix – Challenges of mixed-fisheries management in the North Sea under climate change and technical interactions. *Fisheries Management and Ecology*, 30, 360-377. doi: 10.1111/fme.12629
- Kuo, C.-Y., Ko, C.-Y. & Lai, Y.-Z. (2022). Assessing warming impacts on marine fishes by integrating physiology-guided distribution projections, life-history changes and food web dynamics. *Methods in Ecology and Evolution*, 13, 1343-1357. doi: 10.1111/2041-210X.13846
- Kuparinen, A., Keith, D. M. & Hutchings, J. A. (2014). Allee effect and the uncertainty of population recovery. *Conservation Biology*, 28, 790-798. doi: 10.1111/cobi.12216
- Kurlansky, M. (1997). *Cod. A Biography of the Fish that Changed the World*. Walker & Company, New York / US, 304 pp.
- Kwakkel, J. H., Haasnot, M. & Walker, W. E. (2016a). Comparing Robust Decision-Making and Dynamic Adaptive Policy Pathways for model-based decision support under deep uncertainty. *Environmental Modelling & Software*, 86, 168-183. doi: 10.1016/j.envsoft.2016.09.017
- Kwakkel, J. H., Walker, W. E. & Haasnoot, M. (2016b). Coping with the wickedness of public policy problems: approaches for decision making under deep uncertainty. *Journal of Water Resources Planning and Management*, 142, 01816001. doi: 10.1061/(ASCE)WR.1943-5452.00006
- Kwakkel, J. H. (2017). The Exploratory Modeling Workbench: An open source toolkit for exploratory modeling, scenario discovery, and (multi-objective) robust decision making. *Environmental Modelling & Software*, 96, 239-250. doi: 10.1016/j.envsoft.2017.06.054
- Lapeyrolie, M., Chapman, M. S., Norman, K. E. A. & Boettiger, C. (2022). Deep reinforcement learning for conservation decisions. *Methods in Ecology and Evolution*, 13, 2649-2662. doi: 10.1111/2041-210X.13954
- Larkin, P. A. (1977). An Epitaph for the Concept of Maximum Sustained Yield. *Transactions of the American Fisheries Society*, 106, 1-11. doi: 10.1577/1548-8659(1977)106<1:AEFTCO>2.0.CO;2
- Lauck, T., Clark, C. W., Mangel, M. & Munro, G. R. (1998). Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications*, 8, S72-S78. Doi: 10.2307/2641364
- Lear, W. H. & Parsons, L. S. (1993). History and management of the fishery for Northern cod in NAFO Divisions 2J, 3K and 3L. In: Parsons, L. S. & Lear, W. H. (eds.): *Perspectives on Canadian marine fisheries management*. Canadian Bulletin of Fisheries and Aquatic Sciences, 226, 55-90, NRC Research Press, Ottawa / CA

- Lear, W. H. (1998). History of fisheries in the northwest Atlantic: the 500-year perspective. *Journal of Northwest Atlantic Fishery Science*, 23, 41-73
- Lear, W. H. & Parsons, L. S. (1993). History and management of the fishery for Northern cod in NAFO Divisions 2J, 3K and 3L. In: Parsons, L. S. & Lear, W. H. (eds.): *Perspectives on Canadian marine fisheries management*. *Canadian Bulletin of Fisheries and Aquatic Sciences*, 226, 55-90
- Le Bris, A., Mills, K. E., Wahle, R. A., Chen, Y., Alexander, M. A., Allyn, A. J., Schuetz, J. G., Scott, J. D. & Pershing, A. J. (2018). Climate vulnerability and resilience in the most valuable North American fishery. *PNAS*, 115, 1831-1836. doi: 10.1073/pnas.1711122115
- Lehmann, A. & Hinrichsen, H.-H. (2000). On the thermohaline variability of the Baltic Sea. *Journal of Marine Systems*, 25, 233-357. doi: 10.1016/S0924-7963(00)00026-9
- Lehmann, A., Hinrichsen, H.-H. & Getzlaff, K. (2014). Identifying potentially high risk areas for environmental pollution in the Baltic Sea. *Boreal Environment Research*, 19, 140-152
- Lehmann, A., Krauss, W. & Hinrichsen, H.-H. (2002). Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. *Tellus A*, 54, 299-316
- Lemos, M. C. & Rood, R. B. (2010). Climate projections and their impact on policy and practice. *WIREs Climate Change*, 1, 670-682. doi: 10.1002/wcc.71
- Lempert, R. J., Popper, S. W. & Bankes, S. C. (2003). *Shaping the next one hundred years: New methods for quantitative, long-term policy analysis*. RAND Corporation, Santa Monica / US, 210 pp.
- Lempert, R. J., Nakicenovic, N., Sarewitz, D. & Schlesinger, M. (2004). Characterizing climate-change uncertainties for decision-makers. An editorial essay. *Climate Change*, 65, 1-9. doi: 10.1023/B:CLIM.0000037561.75281.b3
- Lempert, R. J. & Popper, S. W. (2005). High-performance government in an uncertain world. In: Klitgaard, R. & Light, P. C. (eds.): *High-performance government: Structure, leadership, incentives*, RAND Corporation, Santa Monica / US, 113-136
- Lempert, R. J., Popper, S. W., Groves, D. G., Kalra, N., Fischbach, J. R., Blankes, S. C. et al. (2013). *Making good decisions without predictions: Robust Decision Making for planning under Deep Uncertainty*. RAND Corporation, Santa Monica / US. 6 pp. doi: 10.7249/RB9701
- Lempert, R. J. (2019). Robust Decision Making (RDM). In: Marchau, V. A. W. J., Walker, W. E., Bloemen, P. J. T. M. & Popper, S. W. (eds.): *Decision Making under Deep Uncertainty: From Theory to Practice*, Springer, Cham / CH, 23-51. doi: 10.1007/978-3-030-05252-2\_2
- Lengkeek, W., Coolen, J. W. P., Gittenberger, A. & Schrieken, N. (2013). Ecological relevance of shipwrecks in the North Sea. *Nederlandse Faunistische Mededelingen*, 41, 49-57
- Lilly, G. R., Wieland, K., Rothschild, B. J., Sundby, S., Drinkwater, K. F., Brander, K., Ottersen, G. et al. (2008). Decline and recovery of Atlantic cod (*Gadus morhua*) stocks throughout the North Atlantic. In: Kruse, G. H., Drinkwater, K., Ianelli, J. N., Link, J. S., Stram, D. L., Wespestad, V. & Woodby, B. (eds.). *Resiliency of Gadid Stocks to Fishing and Climate Change*. Alaska Sea Grant College Program, Fairbanks, Alaska / US, 39-66. doi: 10.4027/rgsfcc.2008.03

- Lilly, G. R., Nakken, O. & Brattey, J. (2013). A review of the contributions of fisheries and climate variability to contrasting dynamics in two Arcto-boreal Atlantic cod (*Gadus morhua*) stocks: Persistent high productivity in the Barents Sea and collapse on the Newfoundland and Labrador Shelf. *Progress in Oceanography*, 114, 106-125. doi: 10.1016/j.pocean.2013.05.008
- Lindegren, M., Möllmann, C., Nielsen, A. & Stenseth, N. C. (2009). Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach. *PNAS*, 106, 14722-14727. doi: 10.1073/pnas.0906620106
- Lindegren, M., Möllmann, C., Nielsen, A., Brander, K., MacKenzie, B. R. & Stenseth, N. C. (2010). Ecological forecasting under climate change: the case of Baltic cod. *Proceedings of the Royal Society B*, 277, 2121-2130. doi: 10.1098/rspb.2010.0353
- Lomartire, S., Marques, J. C. & Gonçalves, A. M. M. (2021). The key role of zooplankton in ecosystem services: A perspective of interaction between zooplankton and fish recruitment. *Ecol. Indic.*, 129, 107867. doi: 10.1016/j.ecolind.2021.107867
- Lomond, T. M., Schneider, D. C. & Methven, D. A. (1998). Transition from pelagic to benthic prey for age group 0-1 Atlantic cod, *Gadus morhua*. *Fishery Bulletin*, 96, 908-911
- Lotze, H. K., Tittensor, D. P., Bryndum-Buchholz, A., Eddy, T. D., Cheung, W. W. L., Gailbraith, E. D., Barange, M. et al. (2019). Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *PNAS*, 116, 12907-12912. doi: 10.1073/pnas.1900194116
- Ludwig, D., Hilborn, R. & Walters, C. (1993). Uncertainty, resource exploitation, and conservation: lessons from history. *Science*, 260, 17-36. doi: 10.1126/science.260.5104.17
- Lundström, K., Hjerne, O., Lunneryd, S.-G. & Karlsson, O. (2010). Understanding the diet composition of marine mammals: grey seals (*Halichoerus grypus*) in the Baltic Sea. *ICES Journal of Marine Science*, 67, 1230-1239. doi: 10.1093/icesjms/fsq022
- Lynam, C. P. & Mackinson, S. (2015). How will fisheries management measures contribute towards the attainment of Good Environmental Status for the North Sea ecosystem? *Global Ecology and Conservation*, 4, 160-175. doi: 10.1016/j.gecco.2015.06.005
- Mace, P. (2001). A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. *Fish and Fisheries*, 2, 2-32. doi: 10.1046/j.1467-2979.2001.00033.x
- MacKenzie, B. R., Myers, R. A. & Bowen, K. G. (2003). Spawner-Recruit relationship and fish stock carrying capacity in aquatic ecosystems. *Marine Ecology Progress Series*, 248, 209-220. doi: 10.3354/meps248209
- MacKenzie, B. R., Gislason, H., Möllmann, C. & Köster, F. W. (2007). Impact of 21st century climate change on the Baltic Seafish community and fisheries. *Global Change Biology*, 13, 1348-1367. doi: 10.1111/j.1365-2486.2007.01369.x
- Macura, B., Byström, P., Airoidi, L., Eriksson, B. K., Rudstam, L. & Støttrup, J. G. (2019). Impact of structural habitat modifications in coastal temperate systems on fish recruitment: a systematic review. *Environmental Evidence*, 8, 14 (2019). doi: 10.1186/s13750-019-0157-3
- Magnussen, E. (2011). Food and feeding habits of cod (*Gadus morhua*) on the Faroe Bank. *ICES Journal of Marine Science*, 68, 1909-1917. doi: 10.1093/icesjms/fsr104

- Mansfield, B. (2010). "Modern" industrial fisheries and the crisis of overfishing. In: Peet, R., Robbins, P. & Watts, M. (eds.). *Global Political Ecology*. Taylor & Francis, Oxfordshire / UK, 84-99. doi: 10.4324/9780203842249
- Maraun, D. (2016). Bias correcting climate change simulations – a critical review. *Current Climate Change Reports*, 2, 211-2020. 10.1007/s40641-016-0050-x
- Marchau, V. A. W. J., Walker, W. E., Bloemen, P. J. T. M. & Popper, S. W. (2019a). Introduction. In: Marchau, V. A. W. J., Walker, W. E., Bloemen, P. J. T. M. & Popper, S. W. (eds.): *Decision Making under Deep Uncertainty: From Theory to Practice*. Springer, Cham / CH, 1-20. doi: 10.1007/978-3-030-05252-2\_1
- Marchau, V. A. W. J., Walker, W. E., Bloemen, P. J. T. M. & Popper, S. W. (2019b). Conclusions and Outlook. In: Marchau, V. A. W. J., Walker, W. E., Bloemen, P. J. T. M. & Popper, S. W. (eds.): *Decision Making under Deep Uncertainty: From Theory to Practice*. Springer, Cham / CH, 393-400. doi: 10.1007/978-3-030-05252-2\_17
- Marteinsdóttir, G. & Rose, G. A. (2018). Atlantic Cod: Origin and Evolution. In: Rose, G. A. (ed.). *Atlantic cod: a bio-ecology*. John Wiley & Sons, Hoboken / US, 7-26. doi: 10.1002/9781119460701.ch1
- Maunder, M. N. (2008). Maximum Sustainable Yield. Reference Module in Earth Systems and Environmental Sciences, *Encyclopedia of Ecology*, 2292-2296. doi: 10.1016/B978-008045405-4.00522-X
- Maunder, M. N., Hamel, O. S., Lee, H.-H., Piner, K. R., Cope, J. M., Punt, A. E., Ianelli, J. N., Castillo-Jordán, C., Kapur, M. S. & Methot, R. D. (2023). A review of estimation methods for natural mortality and their performance in the context of fishery stock assessment. *Fisheries Research*, 275, 106489. doi: 10.1016/j.fishres.2022.106489
- McIlgorm, A., Hanna, S., Knapp, G., Le Floc'H, P., Millerd, F. & Pan, M. (2010). How will climate change alter fishery governance? Insights from seven international case studies. *Marine Policy*, 34, 170-177. doi: 10.1016/j.marpol.2009.06.004
- Meier, H. E. M., Andersson, H. C., Eilola, K., Gustafsson, B. G., Kuznetsov, I., Müller-Karulis, B., Neumann, T. & Savchuk, O. P. (2011). Hypoxia in future climates: A model ensemble study for the Baltic Sea. *Geophysical Research Letters*, 38, L24608. doi: 10.1029/2011GL049929
- Meier, H. E. M., Edman, M., Eilola, K., Placke, M., Neumann, T., Andersson, H. C., Brunabend, S.-E. et al. (2019). Assessment of uncertainties in scenario simulations of biogeochemical cycles in the Baltic Sea. *Frontiers in Marine Science*, 6, 46. doi: 10.3389/fmars.2019.00046
- Melnychuk, M. C., Kurota, H., Mace, P. M., Pons, M., Minto, C., Osio, G. C., Jensen, O. P. (2021). Identifying management actions that promote sustainable fisheries. *Nature Sustainability*, 4, 440-449. doi: 10.1038/s41893-020-00668-1
- Memarzadeh, M., Britten, G. L., Worm, B. & Boettiger, C. (2019). Rebuilding global fisheries under uncertainty. *PNAS*, 116, 15985-15990. doi: 10.1073/pnas.1902657116
- Mildenerger, T. K., Berg, C. W., Kokkalis, A., Hordyk, A. R., Wetzal, C., Jacobsen, N. S., Punt, A. E. & Nielsen, J. R. (2021). Implementing the precautionary approach into fisheries management: Biomass reference points and uncertainty buffers. *Fish and Fisheries*, 23, 73-92. doi: 10.1111/faf.12599

- Miller, K., Charles, A., Barange, M., Brander, K., Gallucci, V. F., Gasalla, M. A., Khan, A., Munro, G., Murtugudde, R., Ommer, R. E. & Perry, R. I. (2010). Climate change, uncertainty, and resilient fisheries: Institutional responses through integrative science. *Progress in Oceanography*, 57, 338-346. doi: 10.1016/j.pocean.2010.09.014
- Mills, D. J., Westlund, L., de Graaf, G., Kura, Y., Willman, R. & Kelleher, K. (2011). Under-reported and undervalued: small-scale fisheries in the developing world. In: Pomeroy, R. S. & Andrew, N. L. (eds.). *Small-scale Fisheries Management: Frameworks and Approaches for the Developing World*. CABI, Wallingford / UK, 1-16. doi: 10.1079/9781845936075.0001
- Möllmann, C., Folke, C., Edwards, M. & Conversi, A., (2015). Marine regime shifts around the globe: theory, drivers and impacts. *Philosophical Transactions of the Royal Society B*, 368, 20130260. doi: 10.1098/rstb.2013.0260
- Möllmann, C., Cormon, X., Funk, S., Otto, S. A., Schmidt, J. O., Schwermer, H., Sguotti, C., Voss, R. & Quaas, M. (2021). Tipping point realized in cod fishery. *Scientific Reports*, 11, 14259. doi: 10.1038/s41598-021-93843-z
- Mohn, R. (1999). The retrospective problem in sequential population analysis: An investigation using cod fishery and simulated data. *ICES Journal of Marine Science*, 56, 473-488. doi: 10.1006/jmsc.1999.0481
- Moss, R. H., Edmonds, J. A., Hibbard, K. A., Manning, M. R., Rose, S. K., van Vuuren, D. P., Carter, T. R. et al. (2010). The next generation of scenarios for climate change research and assessment. *Nature*, 463, 747-756. doi: 10.1038/nature08823
- Murawski, S. A. (2005). The New England Groundfish Resource: A history of population change in relation to harvesting. In: Buchsbaum, R. Pederson, J. & Robinson, W. E. (eds.). *The Decline of Fisheries Resources in New England. Evaluating the Impact of Overfishing, Contamination, and Habitat Degradation*. MIT Sea Grant College Program, Cambridge, Massachusetts / US, 11-24
- Myers, R. A. & Barrowman, N. J. (1996). Is fish recruitment related to spawner abundance? *Fishery Bulletin*, 94, 707-724
- Myers, R. A., Hutchings, J. A. & Barrowman, N. J. (1996). Hypotheses for the decline of cod in the North Atlantic. *Marine Ecology Progress Series*, 138, 293-308. doi: 10.3354/meps138293
- Myers, R. A. (1998). When do environment–recruitment correlations work? *Reviews in Fish Biology and Fisheries*, 8, 285-305. doi: 10.1023/A:1008828730759
- NAFO (2004). NAFO Precautionary Approach Framework. NAFO Fisheries Commission Document 04/18, Serial No. N5069, 5 pp.
- NAFO (2017). Convention on Cooperation in the Northwest Atlantic Fisheries. NAFO, Dartmouth / CA, 46 pp.
- NAFO (2021). Achieving NAFO Convention Objectives with a Precautionary Approach Framework Precautionary Approach Working Group (PA-WG). NAFO Scientific Council Summary Document 22/02, 20 pp. <https://www.nafo.int/Portals/0/PDFs/sc/2022/scs22-02.pdf>. Last access 22<sup>nd</sup> June, 2023
- Nakken, O. (1994). Causes of trends and fluctuations in the Arcto-Norwegian cod stock. *ICES Marine Science Symposia*, 198, 212-228

- National Research Council (1998). Improving Fish Stock Assessments. The National Academies Press, Washington, DC / US, 188 pp. doi: 10.17226/5951
- Neuenhoff, R. D., Swain, D. P., Cox, S. P., McAllister, M. K., Trites, A. W., Walters, C. J. & Hammill, M. O. (2019). Continued decline of a collapsed population of Atlantic cod (*Gadus morhua*) due to predation-driven Allee effects. Canadian Journal of Fisheries and Aquatic Sciences, 76, 168-184. doi: 10.1139/cjfas-2017-0190
- Nicol, S. J., Allain, V., Pilling, G. M., Polovina, J., Coll, M., Bell, J., Dalzell, P. et al. (2013). An ocean observation system for monitoring the affects of climate change on the ecology and sustainability of pelagic fisheries in the Pacific Ocean. Climate Change, 119, 131-145. doi: 10.1007/s10584-012-0598-y
- Nilssen, E. M., Pedersen, T., Hopkins, C. C. E., Thyholt, K. & Pope, J. G. (1994). Recruitment variability and growth of Northeast Arctic cod: influence of physical environment, demography and predator-prey energetics. ICES Marine Science Symposia, 198, 449-470
- Nissling, A. & Vallin, L. (1996). The ability of Baltic cod eggs to maintain neutral buoyancy and the opportunity for survival in fluctuating conditions in the Baltic Sea. Journal of Fish Biology, 48, 217-227. doi: 10.1111/j.1095-8649.1996.tb01114.x
- Northeast Fisheries Science Center (2013). 55<sup>th</sup> Northeast Regional Stock Assessment Workshop (55<sup>th</sup> SAW) Assessment Report. US Department of Commerce, Northeast Fisheries Science Center Reference Document 13-11. 845 pp.
- Norström, A. V., Nyström, M., Jouffray, J.-B., Folke, C., Graham, N. A. J., Moberg, F., Olsson, P. & Williams, G. J. (2016). Guiding coral reef futures in the Anthropocene. Frontiers in Ecology and the Environment, 14, 490-498. doi: 10.1002/fee.1427
- NRC (2009). Informing decisions in a changing climate, The National Academy Press, Washington, DC / US, 200 pp. doi: 10.17226/12626
- O'Brien, C. M., Fox, C. J., Planque, B. & Casey, J. (2000). Climate variability and North Sea cod. Nature, 404, 142. doi: 10.1038/35004654
- O'Connor, M. I., Piehler, M. F., Leech, D. M., Anton, A. & Bruno, J. F. (2009). Warming and Resource Availability Shift Food Web Structure and Metabolism. PLOS Biology, 7, e1000178. doi: 10.1371/journal.pbio.1000178
- OECD (2022). OECD Review of Fisheries 2022. OECD, Paris / FR, 124 pp. doi: 10.1787/9c3ad238-en
- Ofir, E., Silver, T., Steenbeek, J., Shachar, N. & Gal, G. (2022). Applying the safe operating space (SOS) approach to sustainable commercial fishing under varying lake levels and littoral zone conditions. Fisheries Magazine, 48, 107-120. doi: 10.1002/fsh.10869
- Ohlberger, J., Langangen, Ø. & Stige, L. C. (2022). Age structure affects population productivity in an exploited fish species. Ecological Applications, 32, e2614. doi: 10.1002/eap.2614
- Olsen, E., Aanes, S., Mehl, S., Holst, J. C., Aglen, A. & Gjøsæter, H. (2010). Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the biological value of the area. ICES Journal of Marine Science, 67, 87-101. doi: 10.1093/icesjms/fsp229

- Olsen, E. M., Ottersen, G., Llope, M., Chan, K.-S., Beaugrand, G. & Stenseth, N. C. (2011). Spawning stock and recruitment in North Sea cod shaped by food and climate. *Proceedings of the Royal Society B*, 278, 504-510. doi: 10.1098/rspb.2010.1465
- Orío, A., Heimbrand, Y. & Limburg, K. (2022). Deoxygenation impacts on Baltic Sea cod: Dramatic declines in ecosystem services of an iconic keystone predator. *Ambio*, 51, 626-637. doi: 10.1007/s13280-021-01572-4
- Ottersen, G., Stige, L. C., Durant, J. M., Chan, K.-S., Rouyer, T. A., Drinkwater, K. F. & Stenseth, N. C. (2013). Temporal shifts in recruitment dynamics of North Atlantic fish stocks: effects of spawning stock and temperature. *Marine Ecology Progress Series*, 480, 205-225. doi: 10.3354/meps10249
- Ottersen, G., Bogstad, B., Yaragina, N. A., Stige, L. C., Vikebø, F. O. & Dalpadado, P. (2014). A review of early life history dynamics of Barents Sea cod (*Gadus morhua*). *ICES Journal of Marine Science*, 71, 2064-2087. doi: 10.1093/icesjms/fsu037
- Ottersen, G. & Holt, R. E. (2022). Long-term variability in spawning stock age structure influences climate–recruitment link for Barents Sea cod. *Fisheries Oceanography*, 32, 91-105. doi: 10.1111/fog.12605
- Palacios-Abrantes, J., Sumaila, U. R. & Cheung, W. W. L. (2020). Challenges to trans-boundary fisheries management in North America under climate change. *Ecology & Society*, 25, 41. doi: 10.5751/ES-11743-250441
- Pankhurst, N. W. & Munday, P. L. (2011). Effects of climate change on fish reproduction and early life history stages. *Marine and Freshwater Research*, 62, 1015-1026. doi: 10.1071/MF10269
- Patterson, K., Cook, R., Darby, C., Gavaris, S., Kell, L., Lewy, P., Mesnil, B., Punt, A., Restrepo, V., Skagen, D. W. & Stefánsson, G. (2001). Estimating uncertainty in fish stock assessment and forecasting. *Fish and Fisheries*, 2, 125-157. doi: 10.1046/j.1467-2960.2001.00042.x
- Payne, M. R., Barange, M., Cheung, W. W. L., MacKenzie, B., Batchelder, H. P., Cormon, X., Eddy, T. D. et al. (2016). Uncertainties in projecting climate-change impacts in marine ecosystems. *ICES Journal of Marine Science*, 73, 1272-1282. doi: 10.1093/icesjms/fsv231
- Peck, M. A. & Pinnegar, J. K. (2019). Chapter 5: Climate change impacts, vulnerabilities and adaptations: North Atlantic and Arctic marine fisheries. In: Barange, M., Bahri, T., Beveridge, M. C. M., Cochrane, K. L., Funge-Smith, S. & Poulain, F. (eds.): *Impact of climate change on fisheries and aquaculture*. FAO Fisheries and Aquaculture Technical Paper, 627, FAO, Rome / IT, 87-112
- Peck, M. A., Catalán, I. A., Damalas, D., Elliott, M., Ferreira, J. G., Hamon, K. G., Kamer-mans, P. et al. (2020). Climate change and European fisheries and aquaculture. CERES Project Synthesis Report, Universität Hamburg, Hamburg / DE, 110 pp. doi: 10.25592/uuhfdm.804
- Pedregosa, F., Varoquaux, G., Gramfort, A., Michel, V., Thirion, B., Grisel, O., Blondel, M. et al. (2011). Scikit Learn: Machine Learning in Python. *Journal of Machine Learning Research*, 12, 2825-2830
- Perälä, T., Hutchings, J. A. & Kuparinen, A. (2022). Allee effects and the Allee-effect zone in northwest Atlantic cod. *Biology Letters*, 18, 20210439. doi: 10.1098/rsbl.2021.0439

- Pereira, L. S., Agosthino, A. A. & Winemiller, K. O. (2017). Revisiting cannibalism in fishes. *Reviews in Fish Biology and Fisheries*, 27, 499-513. doi: 10.1007/s11160-017-9469-y
- Perry, A. L., Low, P. J., Ellis, J. R. & Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science*, 308, 1912-1915. doi: 10.1126/science.1111322
- Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Le Bris, A., Mills, K. E., Nye, J. A. et al. (2015). Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Science*, 350, 809-812. doi: 10.1126/science.aac981
- Petersen, M. F. & Steffensen, J. F. (2003). Preferred temperature of juvenile Atlantic cod *Gadus morhua* with different haemoglobin genotypes at normoxia and moderate hypoxia. *Journal of Experimental Biology*, 206, 359-364. doi: 10.1242/jeb.00111
- Pethybridge, H. R., Fulton, E. A., Hobday, A. J., Blanchard, J., Bulman, C. M., Butler, I. R., Cheung, W. W. L. et al. (2020). Contrasting futures for Australia's fisheries stocks under IPCC RCP8.5 emissions – a multi-ecosystem model approach. *Frontiers in Marine Science*, 7, 577964. doi: 10.3389/fmars.2020.577964
- Pielke jr., R. A., Sarewitz, D. & Byerly jr., R. (2000). Decision making and the future of nature: Understanding and using predictions. In: Sarewitz, D., Pielke, R. A. jr. & Byerly, R. jr. (eds.). *Prediction: Science, decision making, and the future of nature*. Island Press, Washington, D.C. / US, 361-387
- Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P. et al. (2004). Ecosystem-Based Fishery Management. *Science*, 305, 346-347. doi: 10.1126/science.1098222
- Pilling, G. M., Millner, R. S., Easey, M. W., Maxwell, D. L. & Tidd, A. N. (2007). Phenology and North Sea cod *Gadus morhua* L.: has climate change affected otolith annulus formation and growth? *Journal of Fish Biology*, 70, 584-599. doi: 10.1111/j.1095-8649.2007.01331.x
- Pineda, J., Reyns, N. B. & Starczak, V. R. (2009). Complexity and simplification in understanding recruitment in benthic populations. *Population Ecology*, 51, 17-32. doi: 10.1007/s10144-008-0118-0
- Pinsky, M. L. & Mantua, N. J. (2015). Emerging adaptation approaches for climate-ready fisheries management. *Oceanography*, 27, 146-159. doi: 10.5670/oceanog.2014.93
- Pitcher, T. J. & Cheung, W. W. L. (2013). Fisheries – Hope or despair? *Marine Pollution Bulletin*, 75, 506-516. doi: 10.1016/j.marpolbul.2013.05.045
- Plagányi, É. E., Haywood, M. D. E., Gorton, R. J., Siple, M. C. & Deng, R. A. (2019). Management implications of modelling fisheries recruitment. *Fisheries Research*, 217, 169-184. doi: 10.1016/j.fishres.2019.03.007
- Planque, B. & Frédou, T. (1999). Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 56, 2069-2077. doi: 10.1139/f99-114
- Pörtner, H.-O. & Peck, M. A. (2010). Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology*, 77, 1745-1779. doi: 10.1111/j.1095-8649.2010.02783.x



- Prime, J. H. & Hammond, P. (1990). The diet of grey seals from the south-western North Sea assessed from analyses of hard parts found in faeces. *Journal of Applied Ecology*, 27, 435-447. doi: 10.2307/2404292
- Punt, A. E. (2010). Harvest control rules and fisheries management. In: Grafton, R. Q., Hilborn, R., Squires, D., Tait, M. & Williams, M. J. (eds.). *Handbook of Marine Fisheries Conservation and Management*. Oxford University Press, New York / US, 582-594
- Punt, A. E., A'mar, T., Bond, N. A., Butterworth, D. S., de Moor, C. L., De Oliveira, J. A. A., Haltuch, M. A., Hollowed, A. B. & Szuwalski, C. (2014). Fisheries management under climate and environmental uncertainty: control rules and performance simulation. *ICES Journal of Marine Science*, 71, 2208-2220. doi: 10.1093/icesjms/fst057
- Punt, A. E., Butterworth, D. S., de Moor, C. L., de Oliveira, J. A. A. & Haddon, M. (2016). Management strategy evaluation: best practices. *Fish and Fisheries*, 17, 303-334. doi: 10.1111/faf.12104
- Punt, A. E. (2017). Strategic management decision-making in a complex world: quantifying, understanding, and using trade-offs. *ICES Journal of Marine Science*, 74, 499-510. doi: 10.1093/icesjms/fsv193
- Punt, A. E., Castillo-Jordán, C., Hamel, O., Cope, J. M., Maunder, M. & Ianelli, J. (2021). Consequences of error in natural mortality and its estimation in stock assessment models. *Fisheries Research*, 233, 105759. doi: 10.1016/j.fishres.2020.105759
- Punt, A. E. (2023). Those who fail to learn from history are condemned to repeat it: A perspective on current stock assessment good practices and the consequences of not following them. *Fisheries Research*, 261, 106642. doi: 10.1016/j.fishres.2023.106642
- Punt, A. E., Tuck, G. N., Day, J., Canales, C. M., Cope, J. M., de Moor, C. L., De Oliveira, J. A. A. et al. (2023). When are model-based stock assessments rejected for use in management and what happens then? *Fisheries Research*, 224, 105465. doi: 10.1016/j.fishres.2019.105465
- R Core Team (2020). *R: an environment for statistical computing*. R Foundation for Statistical Computing, Vienna
- Rademeyer, R. A., Plagányi, É. E. & Butterworth, D. S. (2007). Tips and tricks in designing management procedures. *ICES Journal of Marine Science*, 64, 618-625. doi: 10.1093/icesjms/fsm050
- Rätz, H.-J. & Lloret, J. (2003). Variation in fish condition between Atlantic cod (*Gadus morhua*) stocks, the effect on their productivity and management implications. *Fisheries Research*, 60, 369-380. doi: 10.1016/S0165-7836(02)00132-7
- Ramírez, F., Coll, M., Navarro, J., Bustamante, J. & Green, A. J. (2018). Spatial congruence between multiple stressors in the Mediterranean Sea may reduce its resilience to climate impacts. *Scientific Reports*, 8, 14871. doi: 10.1038/s41598-018-33237-w
- Raworth, K. (2012). A Safe and Just Space for Humanity: Can we live within the doughnut? *Oxfam Discussion Papers*, 26 pp. [https://www-cdn.oxfam.org/s3fs-public/file\\_attachments/dp-a-safe-and-just-space-for-humanity-130212-en\\_5.pdf](https://www-cdn.oxfam.org/s3fs-public/file_attachments/dp-a-safe-and-just-space-for-humanity-130212-en_5.pdf). Last access 13<sup>th</sup> June, 2023

- Receveur, A., Bleil, M., Funk, S., Stötera, S., Gräwe, U., Naumann, M., Dutheil, C. & Krumme, U. (2022). Western Baltic cod in distress: decline in energy reserves since 1977. *ICES Journal of Marine Science*, 79, 1187-1201. doi: 10.1093/icesjms/fsac042
- Renaud, P. E., Berge, J., Varpe, Ø., Lønne, O. J., Nahrgang, J., Ottesen, C. & Hallanger, I. (2012). Is the poleward expansion by Atlantic cod and haddock threatening native polar cod, *Boreogadus saida*? *Polar Biology*, 35, 401-412. doi: 10.1007/s00300-011-1085-z
- Restrepo, V. R., Thompson, G. G., Mace, P. M., Gabriel, W. L., Low, L. L., MacCall, A. D., Methot, R. D. et al. (1998). Technical guidance on the use of precautionary approaches to implementing National Standard 1 of the Magnuson-Stevens Fishery Conservation and Management Act. NOAA Technical Memorandum, NMFS-F/SPO-31, 56 pp.
- Restrepo, V. R. & Powers, J. E. (1999). Precautionary control rules in US fisheries management: specification and performance. *ICES Journal of Marine Science*, 56, 846-852. doi: 10.1006/jmsc.1999.0546
- Riahi, K., van Vuuren, D. P., Kriegler, E., Edmonds, J., O'Neill, B. C., Fujimori, S., Bauer, N. et al. (2017). The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. *Global Environmental Change*, 42, 153-168. doi: 10.1016/j.gloenvcha.2016.05.009
- Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, 11, 559-623. doi: 10.1139/f54-039
- Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin - Fisheries Research Board of Canada*, 191, 382 doi: 10.2307/3800109
- Righton, D. A., Andersen, K. H., Neat, F., Thorsteinsson, V., Steingrund, P., Svedäng, H., Michalsen, K. et al. (2010). Thermal niche of Atlantic cod *Gadus morhua*: limits, tolerance and optima. *Marine Ecology Progress Series*, 420, 1-13. doi: 10.3354/meps08889
- Rindorf, A., Dichmont, C. M., Levin, P. S., Mace, P., Pascoe, S., Prellezo, R., Punt, A. E., Reid, D. G., Stephenson, R., Ulrich, C., Vinther, M. & Clausen, L. W. (2017). Food for thought: pretty good multispecies yield. *ICES Journal of Marine Science*, 74, 475-486. doi: 10.1093/icesjms/fsw071
- Robert, D., Shoji, J., Sirois, P., Takasuka, A., Catalán, I. A., Folkvord, A., Ludsin, S. A. et al. (2023). Life in the fast lane: Revisiting the fast growth—High survival paradigm during the early life stages of fishes. *Fish and Fisheries (early view)*. doi: 10.1111/faf.12774
- Rocha, J., Yletyinen, J., Biggs, R., Blenckner, T. & Peterson, G. (2015). Marine regime shifts: drivers and impacts on ecosystems services. *Philosophical Transactions of the Royal Society B*, 370, 20130273. doi: 10.1098/rstb.2013.0273
- Rockström, J., Steffen, W., Noone, K., Persson, A., Chapin III, F. S., Lambin, E. F., Lenton, T. M. et al. (2009). A safe operating space for humanity. *Nature*, 461-472-475. doi: doi.org/10.1038/461472a
- Rogers, L. A., Stige, L. C., Olsen, E. M., Knutsen, H., Chan, K.-S. & Stenseth, N. C. (2011). Climate and population density drive changes in cod body size throughout a century on the Norwegian coast. *PNAS*, 108, 1961-1966. doi: 10.1073/pnas.101031410

- Roscher, M. B., Allison, E. H., Mills, D. J., Eriksson, H., Hellebrandt, D. & Andrew, N. L. (2022). Sustainable development outcomes of livelihood diversification in small-scale fisheries.
- Rose, G. A. & Rowe, S. (2015). Northern cod comeback. *Canadian Journal of Fisheries and Aquatic Sciences*, 72, 1789-1798. doi: 10.1139/cjfas-2015-0346
- Rose, G. A. (2018a). Atlantic cod: a bio-ecology - Introduction. In: Rose, G. A. (ed.). *Atlantic cod: a bio-ecology*. John Wiley & Sons, Hoboken, US, 287-336. doi: 10.1002/9781119460701
- Rose, G. A. (2018b). The future of wild cod and their fisheries. In: Rose, G. A. (ed.). *Atlantic cod: a bio-ecology*. John Wiley & Sons, Hoboken, US, 287-336. doi: 10.1002/9781119460701.ch9
- Rose, G. A. (2018c). *Atlantic Cod: a Bio-Ecology*. John Wiley & Sons, Ltd., Hoboken, NJ, USA and Chichester, West Sussex, UK, 397 pp.
- Rose, G. A. (2018d). The future of wild cod and their fisheries. In: Rose, G. A. (ed.): *Atlantic Cod: A Bio-Ecology*. John Wiley & Sons, Ltd., Hoboken, NJ, USA and Chichester, West Sussex, UK, 397 pp.
- Rose, G. A., Marteinsdóttir, G. & Godø, O.-R. (2018). Exploitation: Cod is Fish and Fish is Cod. In: Rose, G. A. (ed.). *Atlantic cod: a bio-ecology*. John Wiley & Sons, Hoboken / US, 287-336. doi: 10.1002/9781119460701.ch7
- Rose, K. A., Cowan Jr., J. H., Winemiller, K. O., Myers, R. A. & Hilborn, R. (2001). Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries*, 2, 293-327. doi: 10.1046/j.1467-2960.2001.00056.x
- Rosenberg, A. A. & Restrepo, V. R. (1995). Precautionary management reference points and management strategies. In: FAO (ed.). *Precautionary approach to fisheries. Part 2: scientific papers*. Prepared for the Technical Consultation on the Precautionary Approach to Capture Fisheries (Including Species Introductions). Lysekil, Sweden, 6–13 June 1995. (A scientific meeting organized by the Government of Sweden in cooperation with FAO). *FAO Fisheries Technical Paper*, 350, Part 2, FAO, Rome / IT, 210 pp.
- Rounsevell, M. D. A., Arneth, A., Brown, C., Cheung, W. W. L., Girmenez, O., Holman, I., Leadley, P. et al. (2021). Identifying uncertainties in scenarios and models of socio-ecological systems in support of decision-making. *One Earth*, 4, 967-985. doi: 10.1016/j.oneear.2021.06.003
- Roux, M.-J., Duplisea, D. E., Hunter, K. L. & Rice, J. (2022). Consistent risk management in a changing world: risk equivalence in fisheries and other human activities affecting marine resources and ecosystems. *Frontiers in Climate*, 3, 781559. doi: 10.3389/fclim.2021.781559
- Rowe, S. & Rose, G. A. (2017). Don't derail cod's comeback in Canada. *Nature*, 545, 412. doi: 10.1038/545412b
- Rowe, S., Hutchings, J. A., Bekkevold, D. & Rakitin, A. (2004). Depensation, probability of fertilization, and the mating system of Atlantic cod (*Gadus morhua* L.). *ICES Journal of Marine Science*, 61, 1144-1150. doi: 10.1016/j.icesjms.2004.07.007

- Sainsbury, K. J., Punt, A. E. & Smith, A. D. M. (2000). Design of operational management strategies for achieving fishery ecosystem objectives. *ICES Journal of Marine Science*, 57, 731-741. doi: 10.1006/jmsc.2000.0737
- Saraiva, S., Meier, H. E. M., Andersson, H., Höglund, A., Dieterich, C., Gröger, M., Hordoir, R. & Eilola, K. (2018). Baltic Sea ecosystem response to various nutrient load scenarios in present and future climates. *Climate Dynamics*, 52, 3369-3387. doi: 10.1007/s00382-018-4330-0
- Scarborough, J. B. (1930). The weight of sea water and its variation with salinity and temperature. *United States Naval Institute Proceedings*, 56/4/326, 299-300
- Schaefer, M. B. (1991). Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. *Bulletin of Mathematical Biology*, 53, 253-279. doi: 10.1016/S0092-8240(05)80049-7
- Scheffer, M., Barrett, S., Carpenter, S. R., Folke, C., Green, A. J., Holmgren, M., Hughes, T. P., Kosten, S., van de Leemput, I. A., Nepstad, D. C., van Nes, E. H., Peeters, E. T. H. M. & Walker, B. (2015). Creating a safe operating space for iconic ecosystems. *Science*, 347, 1317-1319. doi: 10.1126/science.aaa37
- Schenk, H., Zimmermann, F. & Quaas, M. (2023). The economics of reversing fisheries-induced evolution. *Nature Sustainability*, 6, 706-711. doi: 10.1038/s41893-023-01078-9
- Schindler, D. E. & Hilborn, R. (2015). Prediction, precaution, and policy under global change. *Science*, 347, 953-954. doi: 10.1126/science.1261824
- Schnute, J. T. & Richards, L. J. (2001). Use and abuse of fishery models. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 10-17. doi: 10.1139/f00-150
- Schwermer, H., Aminpour, P. Reza, C., Funk, S., Möllmann, C. & Gray, S. (2021a). Modeling and understanding social–ecological knowledge diversity. *Conservation Science and Practice*, 3, e396. doi: 10.1111/csp2.396
- Schwermer, H., Blöcker, A. M., Möllmann, C. & Döring, M. (2021b). The ‘cod-multiple’: modes of existence of fsh, science and people. *Sustainability*, 13, 12229. doi: 10.3390/su132112229
- Selkoe, K. A., Blenckner, T., Caldwell, M. R., Crowder, L. B., Erickson, A. L., Essington, T. E., Estes, J. A. et al. (2015). Principles for managing marine ecosystems prone to tipping points. *Ecosystem Health and Sustainability*, 1, 1-18. doi: 10.1890/EHS14-0024.1
- Serchuk, F. M. & Wigley, S. E. (1992). Assessment and management of the Georges Bank cod fishery: an historical review and evaluation. *Journal of Northwest Atlantic Fishery Science*, 13, 25-52. doi: 10.2960/J.v13.a3
- Serpetti, N., Baudron, R. A., Burrows, M. T., Payne, B. L., Helaouët, E., Fernandes, P. G. & Heymans, J. J. (2017). Impact of ocean warming on sustainable fisheries management informs the Ecosystem Approach to Fisheries. *Scientific Reports*, 7, 13438. doi: 10.1038/s41598-017-13220-7
- Sguotti, C., Otto, S. A., Frelat, R., Langbehn, T. J., Plambech Ryberg, M., Lindegren, M., Durant, J. M., Stenseth, N. C. & Möllmann, C. (2019). Catastrophic dynamics limit Atlantic cod recovery. *Proceedings of the Royal Society B*, 286, 1898. doi: 10.1098/rspb.2018.2877

- Sguotti, C., Otto, S. A., Cormon, X., Werner, K. M., Deyle, E., Sugihara, G. & Möllmann, C. (2020). Non-linearity in stock–recruitment relationships of Atlantic cod: insights from a multi-model approach. *ICES Journal of Marine Science*, 77, 1492-1502. doi: 10.1093/icesjms/fsz113
- Sguotti, C., Bischoff, A., Conversi, A., Mazzoldi, C., Möllmann, C. & Barausse, A. (2022a). Stable landings mask irreversible community reorganizations in an overexploited Mediterranean ecosystem. *Journal of Animal Ecology*, 91, 2465-2479. doi: 10.1111/1365-2656.13831
- Sguotti, C., Färber, L. and Romagnoni, G. (2022b). Regime Shifts in Coastal Marine Ecosystems: Theory, Methods and Management Perspectives. In: Reference Module in Earth Systems and Environmental Sciences. Elsevier BV, Amsterdam / NL. doi: 10.1016/B978-0-323-90798-9.00004-4
- Shelton, P. A., Sinclair, A. F., Chouinard, G., Mohn, R. & Duplisea, D. E (2006). Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 63, 235-238. doi: 10.1139/f05-253
- Skern-Mauritzen, M., Ottersen, G., Handegard, N. O., Huse, G., Dingsør, G. E., Stenseth, N. C. & Kjesbu, O. S. (2016). Ecosystem processes are rarely included in tactical fisheries management. *Fish and Fisheries*, 17, 165-175. doi: 10.1111/faf.12111
- Skreslet, S. (1989). Spatial match and mismatch between larvae of cod (*Gadus morhua* L.) and their principal prey, nauplii of *Calanus finmarchicus* (Gunnerus). *Rapports et procès-verbaux des réunions*, 191, 258-263
- Smalås, A., Primicerio, R., Kahilainen, K. K., Terentyev, P. M., Kashulin, N. A., Zubova, E. M. & Amundsen, P.-A. (2023). Increased importance of cool-water fish at high latitudes emerges from individual-level responses to warming. *Ecology and Evolution*, 13, e10185. doi: 10.1002/ece3.10185
- Smedbol, R. K. & Wroblewski, J. S. (2002). Metapopulation theory and northern cod population structure: interdependency of subpopulations in recovery of a groundfish population. *Fisheries Research*, 55, 161-174. doi: 10.1016/S0165-7836(01)00289-2
- Smith, A. D. M. (1993). Risk assessment or management strategy evaluation: what do managers need and want? *ICES C.M. 1993/D:18*, 6 pp.
- Smith, A. D. M. (1994). Management strategy evaluation: the light on the hill. *Population Dynamics for Fisheries Management, Australian Society for Fish Biology Workshop Proceeding*, 249-253
- Smith, A. D. M., Sainsbury, K. J. & Stevens, R. A. (1999). Implementing effective fisheries-management systems – management strategy evaluation and the Australian partnership approach. *ICES Journal of Marine Science*, 56, 967-979. doi: 10.1006/jmsc.1999.0540
- Smith, R., Zagona, E., Kasprzyk, J., Bonham, N., Alexander, E., Butler, A., Prairie, J. & Jerla, C. (2022). Decision science can help address the challenges of long-term planning in the Colorado River basin. *JAWRA*, 58, 735-745. doi: 10.1111/1752-1688.12985
- Soares, P. M. M., Lemos, G. & Lima, D. C. A. (2022). Critical analysis of CMIPs past climate model projections in a regional context: The Iberian climate. *International Journal of Climatology*, 43, 2250-2270. doi: 10.1002/joc.7973

- Song, K. H., Oh, J. H., Jung, M. J., Park, J. H. & Hong, D. H. (2017). Application of DMDU (Decision Making Under Uncertainty Methodology) on Korean transportation infrastructure feasibility study. Korea Transport Institute (KOTI), GGKP Annual Conference, 19 pp.
- Sparholt, H. (1994). Fish species interactions in the Baltic Sea. *Dana*, 10, 131-162
- Steele, D. H., Andersen, R. & Green, J. M. (1992). The managed commercial annihilation of Northern cod. *Newfoundland Studies*, 8, 34-68
- Steele, J. H., Gifford, D. J. & Collie, J. S. (2011). Comparing species and ecosystem-based estimates of fisheries yields. *Fisheries Research*, 111, 139-144. doi: 10.1016/j.fishres.2011.07.009
- Steffen, W., Richardson, K., Rockström, J., Cornell, S. E., Fetzer, I., Bennett, E. M., Biggs, R. et al. (2015). Planetary boundaries: Guiding human development on a changing planet. *Science*, 347, 6223. doi: 10.1126/science.1259855
- Steingrund, P., Mouritsen, R., Reinert, J., Gaard, E. & Hátún, H. (2010). Total stock size and cannibalism regulate recruitment in cod (*Gadus morhua*) on the Faroe Plateau. *ICES Journal of Marine Science*, 67, 111-124. doi: 10.1093/icesjms/fsp240
- Stroustrup, B. (1996). A history of C++: 1979-1991. <https://www.stroustrup.com/hopl2.pdf>. Last access 29th August, 2023
- Stanton, M. C. B. & Roelich, K. (2021). Decision making under deep uncertainties: A review of the applicability of methods in practice. *Technological Forecasting and Social Change*, 171, 120939. doi: 10.1016/j.techfore.2021.120939
- Steffen, W., Richardson, K., Rockström, J., Cornell, S. E., Fetzer, I., Bennett, E. M. et al. (2015). Planetary boundaries: Guiding human development on a changing planet. *Science*, 347, 6223. doi: 10.1126/science.1259855
- Stenevik, E. K. & Sundby, S. (2007). Impacts of climate change on commercial fish stocks in Norwegian waters. *Marine Policy*, 31, 19-31. doi: 10.1016/j.marpol.2006.05.001
- Strnad, F. M., Barfuss, W., Donges, J. F. & Heitzig, J. (2019). Deep reinforcement learning in World-Earth system models to discover sustainable management strategies. *Chaos*, 29, 123122, doi: 10.1063/1.5124673
- Subbey, S., Devine, J. A., Schaarschmidt, U. & Nash, R. D. M. (2014). Modelling and forecasting stock–recruitment: current and future perspectives. *ICES Journal of Marine Science*, 71 (8), 2307-2322. doi: 10.1093/icesjms/fsu148
- Sumaila, U. R., Cheung, W. W. L., Lam, V. W. Y., Pauly, D. & Herrick, S. (2011). Climate change impacts on the biophysics and economics of world fisheries. *Nature Climate Change*, 1, 449-456. doi: 10.1038/nclimate1301
- Sundby, S. (2000). Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia*, 85, 277-298. doi: 10.1080/00364827.2000.10414580
- Sundby, S. & Nakken, O. (2008). Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. *ICES Journal of Marine Science*, 65, 953-962. doi: 10.1093/icesjms/fsn085

- Swain, D. P. (2011). Life-history evolution and elevated natural mortality in a population of Atlantic cod (*Gadus morhua*). *Evolutionary Applications*, 4, 18-29. doi: 10.1111/j.1752-4571.2010.00128.x
- Swain, D. P. & Sinclair, A. F. (2000). Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 1321-1325. doi: 10.1139/f00-104
- Swain, D. P., Benoît, H. P. & Hammill, M. O. (2015). Spatial distribution of fishes in a Northwest Atlantic ecosystem in relation to risk of predation by a marine mammal. *Journal of Animal Ecology*, 84, 1286-1298. doi: 10.1111/1365-2656.12391
- Swain, D. P., Ricard, D., Rolland, N. & Aubrey, É. (2019). Assessment of the southern Gulf of St. Lawrence Cod (*Gadus morhua*) stock of NAFO Div. 4T and 4Vn (November to April), March 2019. DFO Canadian Science Advisory Secretariat Research Document 2019/038, iv+105 pp.
- Szuwalski, C. S. & Punt, A. E. (2013). Fisheries management for regime-based ecosystems: a management strategy evaluation for the snow crab fishery in the eastern Bering Sea. *ICES Journal of Marine Science*, 70, 955-967. doi: 10.1093/icesjms/fss182
- Szuwalski, C. S., Vert-Pre, K. A., Punt, A. E., Branch, T. A. & Hilborn, R. (2014). Examining common assumptions about recruitment: a meta-analysis of recruitment dynamics for worldwide marine fisheries. *Fish and Fisheries*, 16, 633-648. doi: 10.1111/faf.12083
- Szuwalski, J. S. & Hollowed, A. B. (2016). Climate change and non-stationary population processes in fisheries management. *ICES Journal of Marine Science*, 73, 1297-1305. doi: 10.1093/icesjms/fsv229
- Szuwalski, C. S., Britten, G. L., Licandeo, R., Amoroso, R. O., Hilborn, R. & Walters, C. (2019). Global forage fish recruitment dynamics: A comparison of methods, time-variation, and reverse causality. *Fisheries Research*, 214, 56-64. doi: 10.1016/j.fishres.2019.01.007
- Szuwalski, C. S., Hollowed, A. B., Holsman, K. K., Ianelli, J. N., Legault, C. M., Melnychuk, M. C., Ovando, D. & Punt, A. E. (2023). Unintended consequences of climate-adaptive fisheries management targets. *Fish and Fisheries*, 24, 439-453. doi: 10.1111/faf.12737
- Taggart, C. T., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J. et al. (1994). Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. *ICES Marine Science Symposia*, 198, 140-157
- Taylor, G. D. (1995). The collapse of the northern cod fishery: a historical perspective. *Dalhousie Law Journal*, 18, 13-22
- Thilsted, S. H., Thorne-Lyman, A., Webb, P., Bogard, J. R., Subasinghe, R., Phillips, M. J. & Allison, E. H. (2016). Sustaining healthy diets: The role of capture fisheries and aquaculture for improving nutrition in the post-2015 era. *Food Policy*, 61, 126-131. doi: 10.1016/j.foodpol.2016.02.005
- Thorson, J. T., Monnahan, C. C. & Cope, J. M. (2015). The potential impact of time-variation in vital rates on fisheries management targets for marine fishes. *Fisheries Research*, 169, 8-17. doi: 10.1016/j.fishres.2015.04.007

- Tiedemann, M., Slotte, A., Nash, R. D. M., Stenevik, E. K. & Kjesbu, O. S. (2021). Drift indices confirm that rapid larval displacement is essential for recruitment success in high-latitude oceans. *Frontiers in Marine Science*, 8, 679900. doi: 10.3389/fmars.2021.679900
- Tirronen, M., Perälä, T. & Kuparinen, A. (2022). Temporary Allee effects among non-stationary recruitment dynamics in depleted gadid and flatfish populations. *Fish and Fisheries*, 23, 392-406. doi: 10.1111/faf.12623
- Tittensor, D. P., Novaglio, C., Harrision, C. S., Heneghan, R. F., Barrier, N., Bianchi, D., Bopp, L. et al. (2021). Next-generation ensemble projections reveal higher climate risks for marine ecosystems. *Nature Climate Change*, 11, 973–981. doi: 10.1038/s41558-021-01173-9
- Travers-Trolet, M., Bourdaud, P., Genu, M., Velez, L. & Vermard, Y. (2020). The risky decrease of fishing reference points under climate change. *Frontiers in Marine Science*, 7, 568232. doi: 10.3389/fmars.2020.568232
- Trzcinsky, M. K., Mohn, R. & Bowen, W. D. (2006). Continued decline of an Atlantic cod population: how important is gray seal predation? *Ecological Applications*, 16, 2276-2292. doi: 10.1890/1051-0761(2006)016[2276:CDOAAC]2.0.CO;2
- Tsikliras, A. C. & Froese, R. (2019). Maximum Sustainable Yield. *Encyclopedia of Ecology (Second Edition)*, 1, 108-115. doi: 10.1016/B978-0-12-409548-9.10601-3
- Tupper, M. & Butilier, R. G. (1995). Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 52, 1834-1841. doi: 10.1139/f95-176
- U.S. Department of Commerce (2007). Magnuson-Stevens Fishery Conservation and Management Act. As amended through January 12, 2007. 178 pp.
- Vaghefi, S. A., Muccione, V., van Ginkel, K. C. H. & Haasnoot, M. (2021): Using Decision Making under Deep Uncertainty (DMDU) approaches to support climate change adaptation of Swiss Ski Resorts. *Environmental Science and Policy*, 126, 65-78. doi: 10.1016/j.envsci.2021.09.005
- Van Beveren, E., Benoît, H. P. & Duolisea, H. E. (2021). Forecasting fish recruitment in age-structured population models. *Fish and Fisheries*, 22, 941-954. doi: 10.1111/faf.12562
- van Leeuwen, A., De Roos, A. M. & Persson, L. (2008). How cod shapes its world. *Journal of Sea Research*, 60, 89-104. doi: 10.1016/j.seares.2008.02.008
- van Rossum, G. (1995). Python tutorial. Technical Report CS R9526. Centrum voor Wiskunde en Informatica (CWI), Amsterdam, 71 pp.
- van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G. C. et al. (2011). The representative concentration pathways: an overview. *Climatic Change*, 109, 5-31. doi: 10.1007/s10584-011-0148-z
- Vert-pre, K. A., Amoroso, R. O., Jensen, O. P. & Hilborn, R. (2013). Frequency and intensity of productivity regime shifts in marine fish stocks. *PNAS*, 110, 1779-1784. doi: 10.1073/pnas.1214879110
- Villasante, S., Rodríguez-González, D. & Antelo, M. (2013). On the non-compliance in the North Sea cod stock. *Sustainability*, 5, 1974-1993. doi: 10.3390/su5051974



- Voss, R., Quaas, M. F., Stiasny, M. H., Hänsel, M., Stecher Justiniano Pinto, G. A., Lehmann, A., Reusch, T. B. H. & Schmidt, J. O. (2019). Ecological-economic sustainability of the Baltic cod fisheries under ocean warming and acidification. *Journal of Environmental Management*, 238, 110-118. doi: 10.1016/j.jenvman.2019.02.105
- Wainger, L. A., Johnston, R. J., Rose, K. A., Castellini, M. A., McCammon, M. & Newton, J. (2021). Decision Making under Deep Uncertainty – What is it and how might NOAA use it? Report to the Science Advisory Board from the Ecosystem Science and Management Working Group, NOAA, Washington, D.C. / US, 16 pp
- Walker, W. E., Rahman, S. A. & Cave, J. (2001). Adaptive policies, policy analysis, and policy-making. *European Journal of Operational Research*, 128, 282-289. doi: 10.1016/S0377-2217(00)00071-0
- Walker, W. E., Harremoës, P., Rotmans, J., van der Sluis, J. P., van Asselt, M. B. A., Janssen, P. & Kraymer von Krauss, M. P. (2003). Defining uncertainty: a conceptual basis for uncertainty management in model-based decision support. *Integrated Assessment*, 4, 5-7. doi: 10.1076/iaij.4.1.5.16466
- Walker, W. E., Lempert, R. J. & Kwakkel, J. H. (2013). Deep Uncertainty. In: Gass, S. I. & Fu, M. C. (eds.): *Encyclopedia of Operations Research and Management Science*, Springer, New York / US, 395-402. doi: 10.1007/978-1-4419-1153-7\_1140
- Walker, W. E., Marchau, V. A. W. J. and Kwakkel, J. H. 2019. Dynamic Adaptive Planning (DAP). In: Marchau, V. A. W. J., Walker, W. E., Bloemen, P. J. T. M. & Popper, S. (eds.): *Decision Making under Deep Uncertainty: From Theory to Practice*, Springer, Cham / CH, 53-69. doi: 10.1007/978-3-030-05252-2\_3
- Walters, C. & Maguire, J. (1996). Lessons for stock assessment from the northern cod collapse. *Reviews in Fish Biology and Fisheries*, 6, 125-137. doi: 10.1007/BF00182340
- Walters, C. J. & Martell, S. J. D. (2005). *Fisheries Ecology and Management*, Princeton University Press, Princeton / US. 448 pp.
- Walters, C. & Kitchell, J. F. (2001). Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 39-50. doi: 10.1139/f00-160
- Walters, C. & Parma, A. M. (1996). Fixed exploitation rate strategies for coping with effects of climate change. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 148-158. doi: 10.1139/f95-151
- Wang, F. S. & Chen, L. H. (2013). Heuristic optimization. In: Dubitzky, W., Wolkenhauer, O., Cho, K. H. & Yokota, H. (eds.): *Encyclopedia of Systems Biology*, Springer, New York / US. doi: 10.1007/978-1-4419-9863-7\_411
- Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M. L., Hop, H., Gabrielsen, G. W. et al. (2006). Food webs and carbon flux in the Barents Sea. *Progress in Oceanography*, 71, 232-287. doi: 10.1016/j.pocean.2006.10.003
- Webber, M. K. & Samaras, C. (2022). A review of Decision Making Under Deep Uncertainty applications using green infrastructure for flood management. *Earth's Future*, 10, e2021EF002322. doi: 10.1029/2021EF002322

- Westin, L. & Nissling, A. (1991). Effects of salinity on spermatozoa motility, percentage of fertilized eggs and egg development of Baltic cod (*Gadus morhua*), and implications for cod stock fluctuations in the Baltic. *Marine Biology*, 108, 5-9. doi: 10.1007/BF01313465
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer, Cham / CH, 213 pp. doi: 10.1007/978-0-387-98141-3
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G. et al. (2019). Welcome to the Tidyverse. *Journal of Open Source Software*, 4, 1686. doi: 10.21105/joss.01686
- Wiedenmann, J. & Jensen, O. P. (2017). Uncertainty in stock assessment estimates for New England groundfish and its impact on achieving target harvest rates. *Canadian Journal of Fisheries and Aquatic Sciences*, 75, 342–356. doi: 10.1139/cjfas-2016-0484
- Wiedenmann, J., Wilberg, M. J. & Miller, T. J. (2013). An evaluation of harvest control rules for data-poor fisheries. *Fisheries Management*, 33, 845-860. doi: 10.1080/02755947.2013.811128
- Wiedenmann, J., Wilberg, M., Sylvia, A. & Miller, T. (2017). An evaluation of acceptable biological catch (ABC) harvest control rules designed to limit overfishing. *Canadian Journal of Fisheries and Aquatic Sciences*, 74, 1028-1040. doi: 10.1139/cjfas-2016-0381
- Williams, J. W. & Jackson, S. T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, 5, 475-482. doi: 10.1890/070037
- Winter, A.-M., Richter, A. & Elkeset, A. M. (2019). Implications of Allee effects for fisheries management in a changing climate: evidence from Atlantic cod. *Ecological Applications*, 30, e01994. doi: 10.1002/eap.1994
- Zhang, F., Regular, P. M., Wheeland, L., Rideout, R. M. & Mogan, J. M. (2021). Accounting for non-stationary stock–recruitment relationships in the development of MSY-based reference points. *ICES Journal of Marine Science*, 78, 2233-2243. doi: 10.1093/icesjms/fs

## 7. Supplementary material for Chapter I “Robust fisheries management strategies under deep uncertainty”

Jan Conradt<sup>1\*</sup>, Steffen Funk<sup>1</sup>, Camilla Sguotti<sup>1,2</sup>, Rudi Voss<sup>3,4</sup>, Thorsten Blenckner<sup>5</sup>, Christian Möllmann<sup>1</sup>

<sup>1</sup>Institute of Marine Ecosystem and Fishery Science, Universität Hamburg, Hamburg, Germany

<sup>2</sup>Department of Biology, University of Padova, Via Bassi, Padova, Italy.

<sup>3</sup>German Centre for Integrative Biodiversity Research (iDiv), Leipzig, Germany

<sup>4</sup>Center for Ocean and Society (CeOS), Christian-Albrechts-University Kiel, Kiel, Germany.

<sup>5</sup>Stockholm Resilience Centre, Stockholm University, Stockholm, Sweden

\*Principal author

### 7.1 SI CI.1: Description of the population model

#### 1.1 General overview

We used a population model that is essentially a forward simulation of the catch-at-age stock-assessment model (Allen, 1975), which itself is based on the founding theories of fish population dynamics by Baranov (1918). The population model is climate-forced via a stock-recruitment model that is driven by sea-surface temperature (SST) in addition to spawning-stock biomass (SSB). A similar setup was originally used by Lindegren *et al.* (2013) to model the climate-driven population dynamics of sardine and anchovy stocks in the California-Current. In our case, we omitted the addition of random Gaussian noise to the recruitment process ecosystem used by those authors. An overview is given in fig. SI CI.1 / 1.

We started model projections from the year 2029 (with 2030 as the first year of projected stock) and assuming a population equalling  $B_P$  (97.78 kt) in terms of SSB as a result of a hypothetical successful stock recovery until that year. Distribution of stock size (in numbers) over age classes was assumed to equal the median distribution pattern over years 2014-2018.

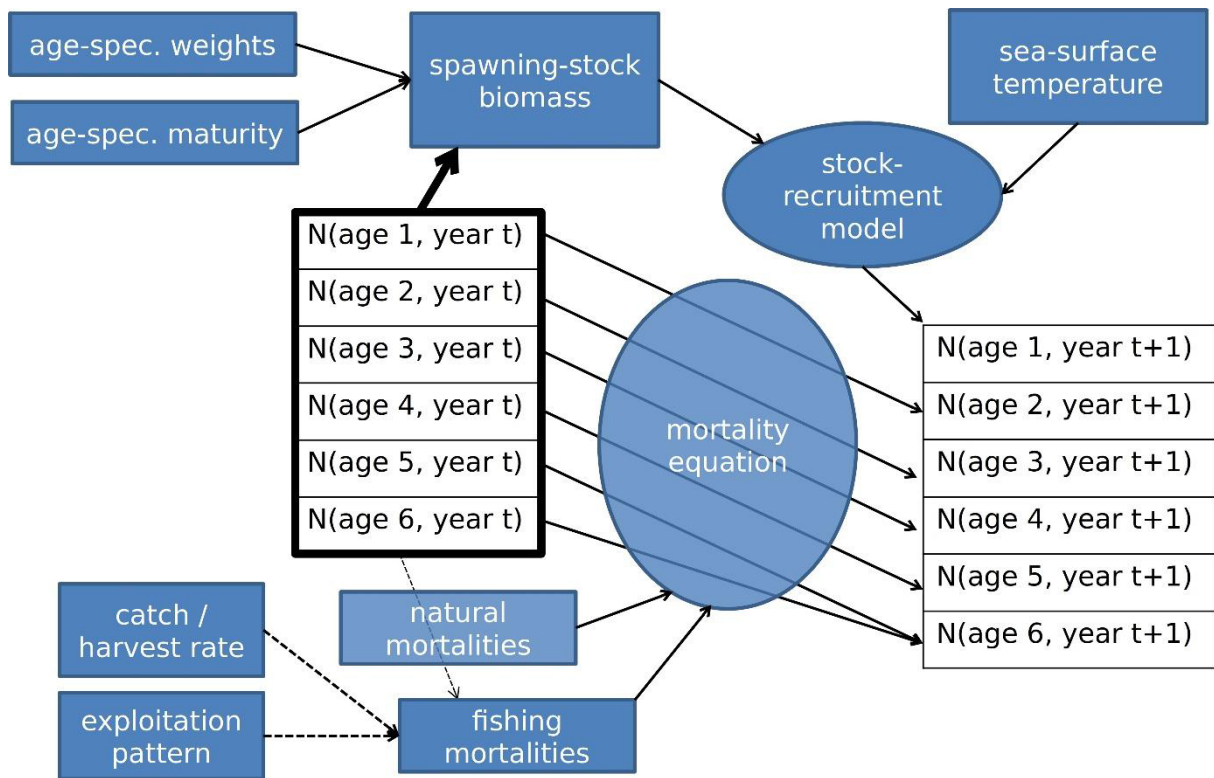


Figure SI CI.1 / 1: Overview of the population model. Catch (or harvest rate converted to catch via stock biomass) and population numbers are used to estimate fishing mortality, which in conjunction with natural mortality reduces fish in a given cohort in the course of one year. The year-class strength (number of age-1 fish) is estimated via the stock-recruitment function, which integrates SSB (calculated from population numbers and age-specific weights and maturity rates) and SST

## 1.2 Calculation of population numbers

For each age class (five plus the plus-group, which collects fish aged six years and older) and each year, the number of fish surviving to the next year and age-class is calculated via the mortality equation, which integrates natural mortality (death through predation or other natural courses) and fishing mortality (F) (death through fishing) (eq. SI CI.1 / 1). Both the fifth age-class and the plus-group of a given year contribute to the number of fish in the plus group of the following year. The number of age-1 fish added to the population is predicted from SSB and SST via the stock-recruitment function (Supplementary Material 2).

$$N_{t+1,a+1} = N_{t,a} e^{-(F_{t,a} + M_{t,a})} \text{ for } a \in [2, 5]$$

$$N_{t+1,A} = N_{t,a} e^{-(F_{t,a} + M_{t,a})} + N_{t,A} e^{-(F_{t,A} + M_{t,A})} \text{ for } a = A - 1 = 5$$

Equation SI CI.1 / 1: Mortality equation. N = population number, F = fishing mortality, M = natural mortality, a = age class, t = time (1 year)

### 1.3 Exploitation pattern

Forcing the population model with catch requires calculating age-specific catch from a total catch in kilo-tonnes. The application of an age-specific exploitation pattern for the distribution of catches over age classes is thus necessary. To determine an exploitation pattern, for each projection year, we initially calculated a reference catch in numbers from age-specific stock sizes after half a year of natural mortality only and age-specific catchability (eq. SI CI.1 / 3), as given by the ratio of F to the maximum F over age classes (eq. SI CI.1 / 2). The latter was calculated as the median over the last five used assessment years (2014-2018).

$$\gamma_a = \frac{F_a}{\max_{1 \rightarrow A} F}$$

Equation SI CI.1 / 2: Calculation of age-specific catchability.  $\gamma$  = catchability, F = fishing mortality, median over assessment years 2014-2018, a = age class, A = number of age classes

$$C_{ref,a,t}^N = \gamma_a N_{a,t} e^{-0.5M_a}$$

Equation SI CI.1 / 3: Calculation of reference catch.  $C_{ref}^N$  = reference catch in numbers,  $\gamma$  = catchability, N = size of the age class at the beginning of the year, M = natural mortality, a = age class, t = time in years

The reference catch was multiplied with weight in the catch (median over the last five used assessment years) to obtain age-specific reference catch in kilo-tonnes (eq. SI CI.1 / 4).

$$C_{ref,a,t}^W = C_{ref,a,t}^N w_a^C$$

Equation SI CI.1 / 4: Calculation of reference catch in weight.  $C_{ref}^W$  = reference catch in weight,  $C_{ref}^N$  = reference catch in numbers,  $w^c$  = weight in the catch, median over assessment years 2014-2018, a = age class, t = time in years

Age-specific reference catch in weight was then used to calculate an exploitation pattern that allows spreading a given total catch over age classes (eq. SI CI.1 / 5).

$$E_{a,t} = \frac{C_{ref,a,t}^W}{\sum_{a=1}^A C_{ref,a,t}^W}$$

Equation SI CI.1 / 5: Calculation of exploitation pattern for generating age-specific catch in weight. E = exploitation pattern (relative value),  $C_{ref}^W$  = reference catch in weight, a = age class, t = time in years, A = number of age classes

It was verified that this approach, when calculating F from age-specific catches (see below) recreates the current F pattern in the projections when age class strengths support the intended level of catch. When some age classes were depleted (i.e., contained zero individuals in the model context), the procedures above yielded notably higher relative exploitation for the remaining classes, leading to much-increased realized catchabilities compared to those resulting from eq. SI CI.1 / 2. This change bears some lack of realism from a fisheries logistics point of view, but is required in our model in order to stress-test a given level of catch. Adopting a general scheme of correcting for a more realistic exploitation pattern could lead to a high discrepancy between intended- and realized catch, and thus reduce the meaningfulness of our analyses. The changed exploitation pattern in the model could be interpreted, to some extent, as fishers adapting their strategies (e.g. spending more days at sea) in order to maintain annual catch levels.

#### 1.4 Estimation of F

Stock exploitation, was integrated into the population model by estimating age-specific fishing mortalities from catch or harvest rate. Since mortalities are calculated on the level of population numbers, not biomass, catch values given in tonnes were converted to catches in numbers (in thousands) via age-specific weights-in-the-catch (eq. SI CI.1 / 6, top). In our definition, harvest rate is the percentage of stock biomass available after half a year of natural mortality and individual growth; hence we use average individual weight-in-the-catch to calculate that biomass, and apply the harvest rate on this value to derive catch. Age-specific catch was calculated by multiplying total catch by the respective value of the exploitation-pattern (eq. SI CI.1 / 6).

$$C_a^N = \frac{E_a C^W}{w_a^c}$$

$$C_{a,t}^N = \frac{E_a h \sum_{a=1}^A N_{a,t} e^{-0.5M_a} w_a^c}{w_a^c} = \frac{E_a C^W}{w_a^c}$$

Equation SI CI.1 / 6: Calculation of age-specific catch in numbers. Top, calculation for catch-based projections; bottom, calculation for harvest-rate-based projections.  $C^N$  = catch in numbers,  $C^W$  = catch in tonnes,  $E$  = exploitation pattern (relative value),  $h$  = harvest rate,  $N$  = population number,  $a$  = age class,  $w^c$  = weight in the catch,  $t$  = time (1 year)

In case age-specific catch was larger than the age-specific number of fish in the stock, reduced by half a year of natural mortality, age-specific catch was set to that number (eq. SI

CI.1 / 7). In this case, F is infinite, and the cohort collapses. The procedure results in a lower-than-intended total catch (eq. SI CI.1 / 7, bottom); and often in the collapse of the entire stock and catch reduction to zero kt within few years or in the recovery of the catch to intended levels after a few years. A lower-than-intended harvest rate can also occur, when the age-specific catches resulting from total catch (derived from stock biomass and harvest rate) exceed the population size of the individual age classes. In any case, stabilization on a lower-than-intended exploitation level was prevented (Supplementary Material 11). Analyses of the projection outcomes refer to the non-adjusted, “intended”, catch- and harvest-rate levels, as these are the exploitation levels originally intended to be applied over the whole time series, and as realized exploitation varies with the uncertain scenarios simulated. The percentage of uncertain scenarios in which intended exploitation exceeded realized exploitation was calculated (employing methods used in risk analysis; see *Material & Methods*, section 2.5 / *Exploratory Modeling*). It increased steadily with intended catch up to a level of 80-90 % at maximum intended catch (with no catch level yielding a risk of zero %), and remained relatively close to zero over the full range of harvest rate employed (fig. SI CI.11 / 1).

$$C_{a,t}^N = \min(C_{a,t}^N, N_{a,t}e^{-0.5M_{a,t}})$$

$$C_t^W = \sum_{a=1}^A C_{a,t}^N w_a^c$$

Equation SI CI.1 / 7: Calculation of realized age-specific (top) and total catches (bottom).  $C^W$ = catch in tonnes,  $C^N$  = catch in thousands, N = population number, a = age class,  $w^c$  = weight in the catch, M = natural mortality, t = time (1 year)

Age-specific fishing mortalities were estimated by minimizing the squared difference between observed catch and the prediction of the catch equation (eq. SI CI.1 / 8), using the “nlminb” optimizer in R. The initial estimate of F required for starting the optimizer was set to the F estimated via the Pope equation (Pope, 1972.) The Pope equation is a simplified procedure for calculating population numbers that assumes that all annual catch is taken in the middle of the year, and that only natural mortality reduces the stock before and after (eq. SI CI.1 / 9). It can thus be used to estimate population numbers without the need to calculate F, but gives slightly biased results. F can be estimated afterwards by re-arranging the mortality equation, and inserting the population number estimated via the Pope equation (eq. SI CI.1 / 10). In cases where the optimizer did not converge on a final estimate, we supplied the Pope estimate instead.

$$C_{a,t}^N = N_{a,t}(1 - e^{-(F_{a,t}+M_{a,t})}) \frac{F_{a,t}}{F_{a,t} + M_{a,t}}$$

Equation SI CI.1 / 8: Catch equation.  $C^N$  = catch in numbers,  $N$  = population number,  $F$  = fishing mortality,  $M$  = natural mortality,  $a$  = age class,  $t$  = time (1 year)

$$N_{a+1,t+1} \approx ((N_{a,t}e^{-0.5M_{a,t}}) - C_{a,t}^N)e^{-0.5M_{a,t}}$$

Equation SI CI.1 / 9: Pope's (1972) approximation of the mortality equation.  $C_N$  = catch in numbers,  $N$  = population number,  $F$  = fishing mortality,  $M$  = natural mortality,  $a$  = age class,  $t$  = time (1 year)

$$F_{a,t} = -((\log N_{a+1,t+1} - \log N_{a,t}) + M_{a,t})$$

Equation SI CI.1 / 10: Mortality equation solved for fishing mortality.  $N$  = population number,  $F$  = fishing mortality,  $M$  = natural mortality,  $a$  = age class,  $t$  = time (1 year)

#### 1.4 Model constants

Parameters of the population model aside from those of the stock-recruitment model were set to the median of the values of the years 2014 to 2018, as given by the ICES stock assessment (ICES, 2021a). These are the age-specific natural mortalities, age-specific weights in the stock, age-specific weights in the catch age-specific maturity rates (relative amount of spawning fish) and age-specific catchabilities (tab. SI CI.1 / 1). Age-specific weights in the catch were given for all age-classes caught; weights for age classes 6 and higher were summarized as plus-group weight by taking the median weight over these age-classes. The final two assessment years (2019 and 2020) were omitted from calculating average biological parameter values due to generally higher uncertainties in later assessment years (Mohn, 1999). All parameters mentioned above were kept constant in value among years in the projections.

The population model also requires an age-resolved start population for the initial year as input. Since we assumed recovery of the stock until 2029, this was set to population numbers calculated from  $B_P$ , the above-mentioned estimates of weight in the stock and maturity and the relative distribution of weights over age classes: We assumed that the current relative proportions of age classes to the total population size remain unchanged until 2030.

In a first step, age-specific initial SSB was calculated by multiplying  $B_P$  with the ratio of current age-specific SSB values to total current SSB (eq. SI CI.1 / 12).



$$SSB_a^{ini} = MSYB_{trigger} \frac{w_a^s m_a N_a}{\sum_{a=1}^A w_a^s m_a N_a}$$

Equation SI CI.1 / 12: Calculation of age-specific initial SSB.  $SSB^{ini}$  = initial SSB,  $w^s$  = weight in the stock (median over assessment years 2014-2018),  $m$  = maturity (median over assessment years 2014-2018),  $N$  = age-specific population size (median over assessment years 2014-2018),  $a$  = age class,  $A$  = number of age classes

Age-specific SSB was then used to calculate age-specific initial population numbers (2030 start-of-the-year), by dividing the former by the age-specific product of weight and maturity (eq. SI CI.1 / 13).

$$N_a^{ini} = \frac{SSB_a^{ini}}{w_a^s m_a}$$

Equation SI CI.1 / 13: Calculation of initial age-specific population size.  $N^{ini}$  = initial population size,  $SSB^{ini}$  = initial SSB,  $w_s$  = weight in the stock ((median over assessment years 2014-2018),  $m$  = maturity (median over assessment years 2014-2018),  $a$  = age class

The first simulated year of catch was 2029, and the stock projection began in the year 2030.

Table SI CI.1 / 1 Population-model parameters

parameter	age 1	age 2	age 3	age 4	age 5	age 6+
natural mortality	1.192	0.943	0.476	0.362	0.363	0.363
weight in the stock [kg]	0.064	0.551	1.756	3.276	5.143	7.215
weight in the catch [kg]	0.366	0.927	2.138	3.803	5.624	9.218
maturity rate	0.017	0.145	0.441	0.761	0.865	1.000
catchability	0.105	0.573	0.968	0.927	1.000	0.671
initial population number [ $10^3$ ]	188928.45	95577.65	24690.36	9383.31	5500.43	3181.22

## 7.2 SI CI.2: Extended description of stock-recruitment models

### 2.1 Theoretical foundations

The Beverton-and-Holt model (Beverton & Holt, 1957; Hilborn & Walters, 1992) (eq. SI CI.2 / 1) contains two parameters related to stock biomass: the parameter  $\alpha$  describes a positive effect of the spawning-stock biomass (SSB) on recruitment strength, while the parameter  $\beta$  summarizes effects that relate to the carrying capacity of the ecosystem; these include i.a. competition for food. Effectively, this means that recruitment strength increases asymptotically with increasing SSB. An additional parameter,  $\gamma$ , describes environmental effects that act negatively on recruitment; these are usually related to physical effects affected by climate change, e.g. temperature.

$$R_{t+1} = N_{t+1,1} = e^{-\gamma E_t} \frac{\alpha SSB_t}{1 + \beta SSB_t}$$

Equation SI CI.2 / 1: Environmental Beverton-and-Holt (Hilborn & Walters, 1992) stock-recruitment-model equation. R = recruitment, N = population number, SSB = spawning-stock biomass, E = environmental variable. Same as Eq. 1 (top)

The Ricker model (Ricker, 1954; Ricker, 1975) (eq. SI CI.2 / 2) contains a similar set of parameters, with  $\alpha$  describing a positive and  $\beta$  describing a negative effect of stock size on recruitment strength. However, unlike the Beverton-and-Holt model, it assumes that recruitment strength is negatively affected by high SSB, such that highest recruitment strength is achieved at intermediate levels of SSB.

$$R_{t+1} = N_{t+1,1} = \alpha SSB_t e^{-\beta SSB_t - \gamma E_t}$$

Equation SI CI.2 / 2: Environmental Ricker (1975) stock-recruitment-model equation. R = recruitment, N = population number, SSB = spawning-stock biomass, E = environmental variable. Same as eq. 1 (bottom)

## 2.2 Calculation of spawning-stock biomass

Annual SSB was calculated by summing, over all age classes, the product of number of fish in a given age class and age-specific weight and maturity rate (eq. SI CI.2 / 3). This was then used as input for the SR model to calculate the number of age-1 fish in the following year.

$$SSB_t = \sum_a^A N_{a,t} w_{a,t} m_{a,t}$$

Equation SI CI.2 / 3: Calculation of annual spawning-stock biomass (SSB). N = population number, w = weight, m = maturity rate, a = age class, A = number of age classes, t = year

## 2.3 Fitting of the stock-recruitment models

Both the Ricker and the Beverton-and-Holt model were fitted with the nlsLM optimizer that applies the Levenberg-Marquardt algorithm to non-linear least-squares regression (Elzhov *et al.*, 2016). The original Beverton-Holt- and Ricker equations (eq. SI CI.2 / 1-2) were rearranged (eq. SI CI.2 / 4) to allow i) for a formulation closer to that of a linear equation, which can alleviate the fitting procedure, and ii) for fitting the logarithms of the SSB-related parameters ( $\alpha$  and  $\beta$ ). These parameters have no biological meaning when being negative.

Determining a mean estimate and standard deviation of the logarithms of these parameters thus ensures that no negative values will result when sampling from the uncertainty range.

The re-arranged equations necessitate a back-transformation (exponentiation and additional multiplication with SSB in the Ricker model) of the model predictions to obtain recruitment values.

$$\log(R_{t+1}) = -\gamma S S T_t + l g \alpha + \log(SSB_t) - \log(1 + e^{l g \beta + \log(SSB_t)})$$

$$\log\left(\frac{R_{t+1}}{SSB_t}\right) = \alpha' - e^{\beta'} S S B_t - \gamma S S T_t$$

where  $l g \alpha = \log(\alpha)$  and  $l g \beta = \log(\beta)$

Equation SI CI.2 / 4: Beverton-Holt- (top) and Ricker (bottom) SR functions, re-arranged equations. For details see eq. SI CI.2 / 1-2. Note that  $l g \alpha$  and  $l g \beta$  are treated as the optimizable parameters, instead of  $\alpha$  and  $\beta$  directly

Final parameter estimates for both stock-recruitment models are given in tab. SI CI.2 / 1.

Table SI CI.2 / 1: Final parameter estimates and standard errors for the two stock-recruitment models

model	parameter	estimate	standard error
Ricker	$\log(\alpha)$	10.34	1.674
Ricker	$\log(\beta)$	-12.27	0.3693
Ricker	$\gamma$	0.7952	0.1543
Beverton-Holt	$\log(\alpha)$	11.29	1.939
Beverton-Holt	$\log(\beta)$	-11.16	0.7954
Beverton-Holt	$\gamma$	0.8502	0.1616

### 7.3 SI CI.3: Stock-recruitment relationships – partial-effects of SSB and SST

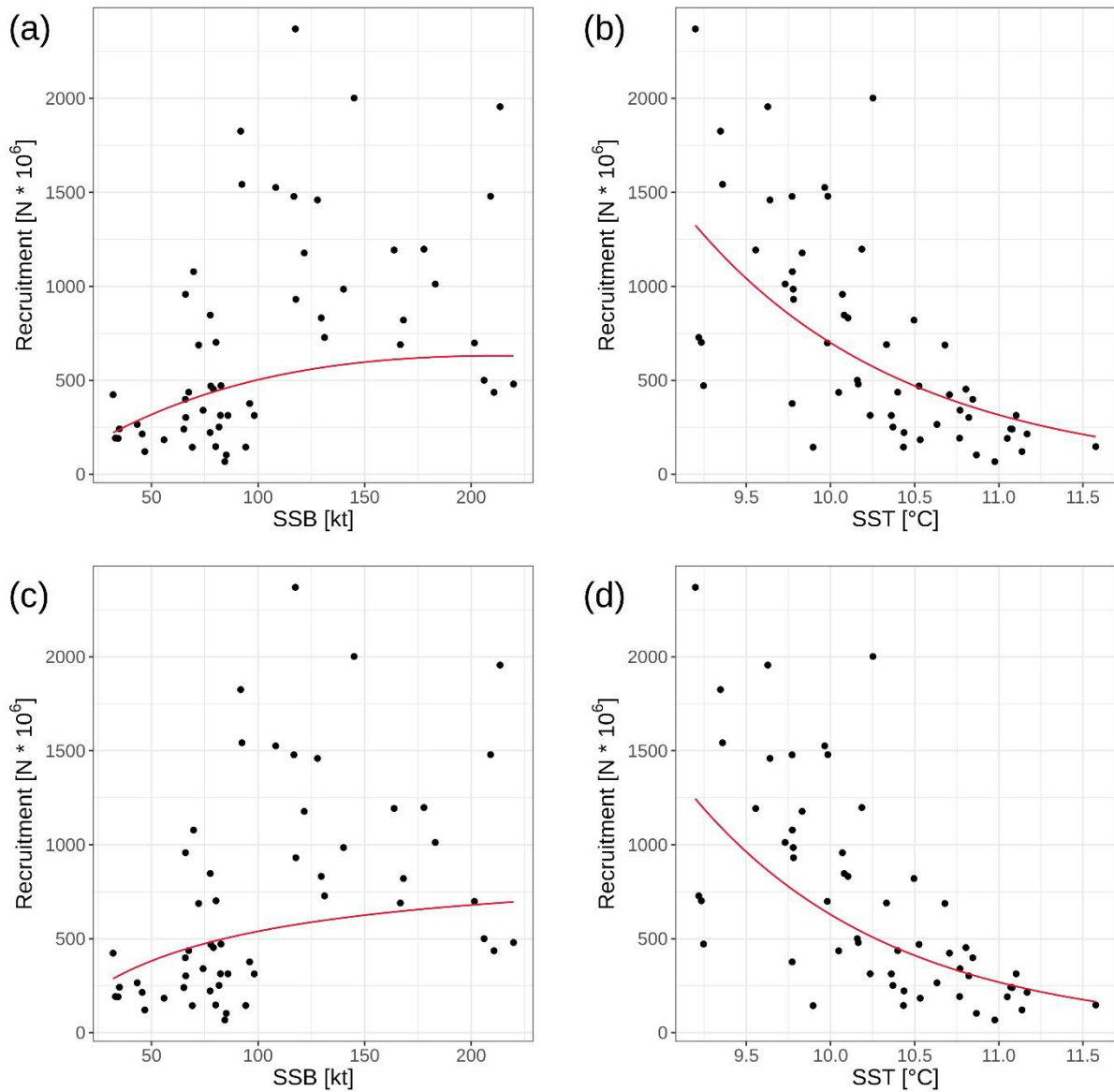


Figure SI CI.3 / 1: Partial-dependence plots showing effect strength and direction of SSB and SST on recruitment as modeled with the Ricker (a, b) and Beverton-Holt (c, d) stock-recruitment models fitted on the full time series

### 7.4 SI CI.4: Trajectories of future SST development

Trajectories of future SST development were obtained from the output of a regional physical ocean model (Peck *et al.*, 2020), which were bias-corrected against historical reconstructions of North Sea SST (which had been used in the fitting of the SR models) (NOAA Extended Reconstructed Sea Surface Temperature; ERSST [Huang *et al.*, 2017]). Bias correction was conducted by calculating the median difference between model hind-cast and early projec-

tions, and the ERSST data, and adding the offset to the future projection data (Maraun, 2016). Bias-corrected SST projections are visible in fig. SI CI.4 / 1.

With the initial projection year set to 2029 (with 2029 SSB assumed to equal  $B_P$  and the initial recruitment projection being for 2030), the SST time series were also truncated at the start such as to commence with the 2029 values.

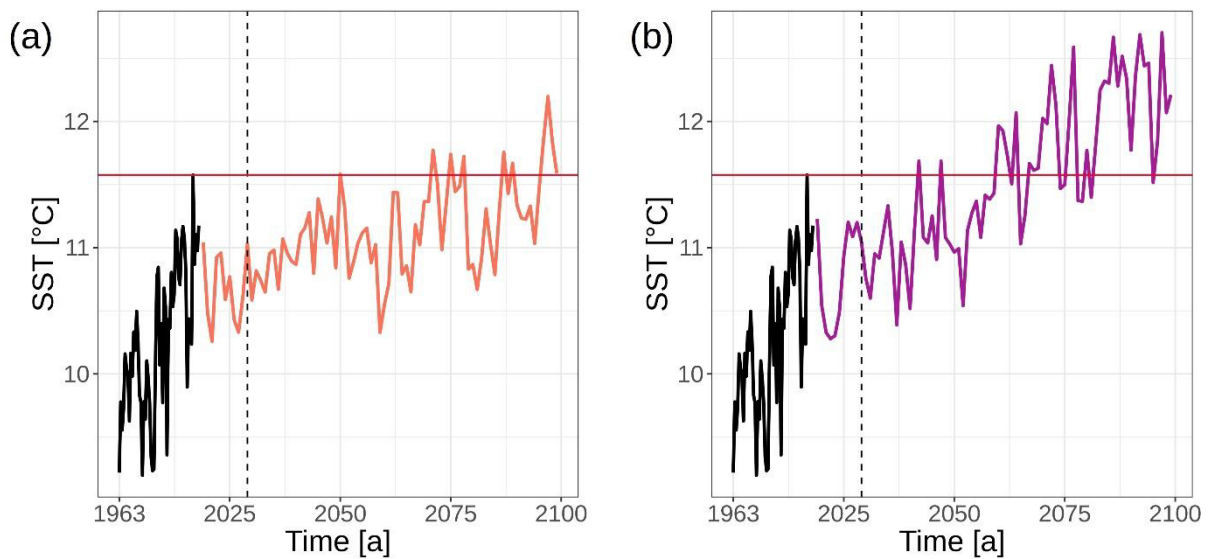


Figure SI CI.4 / 1 Trajectories of future SST for the RCP4.5 scenario (a) and the RCP8.5 scenario (b). Red horizontal line denotes maximum SST observed in the past. Dashed vertical line indicates start of the part of the time series used for stock projections

## 7.5 SI CI.5: SR relationships resulting from random parameter sampling

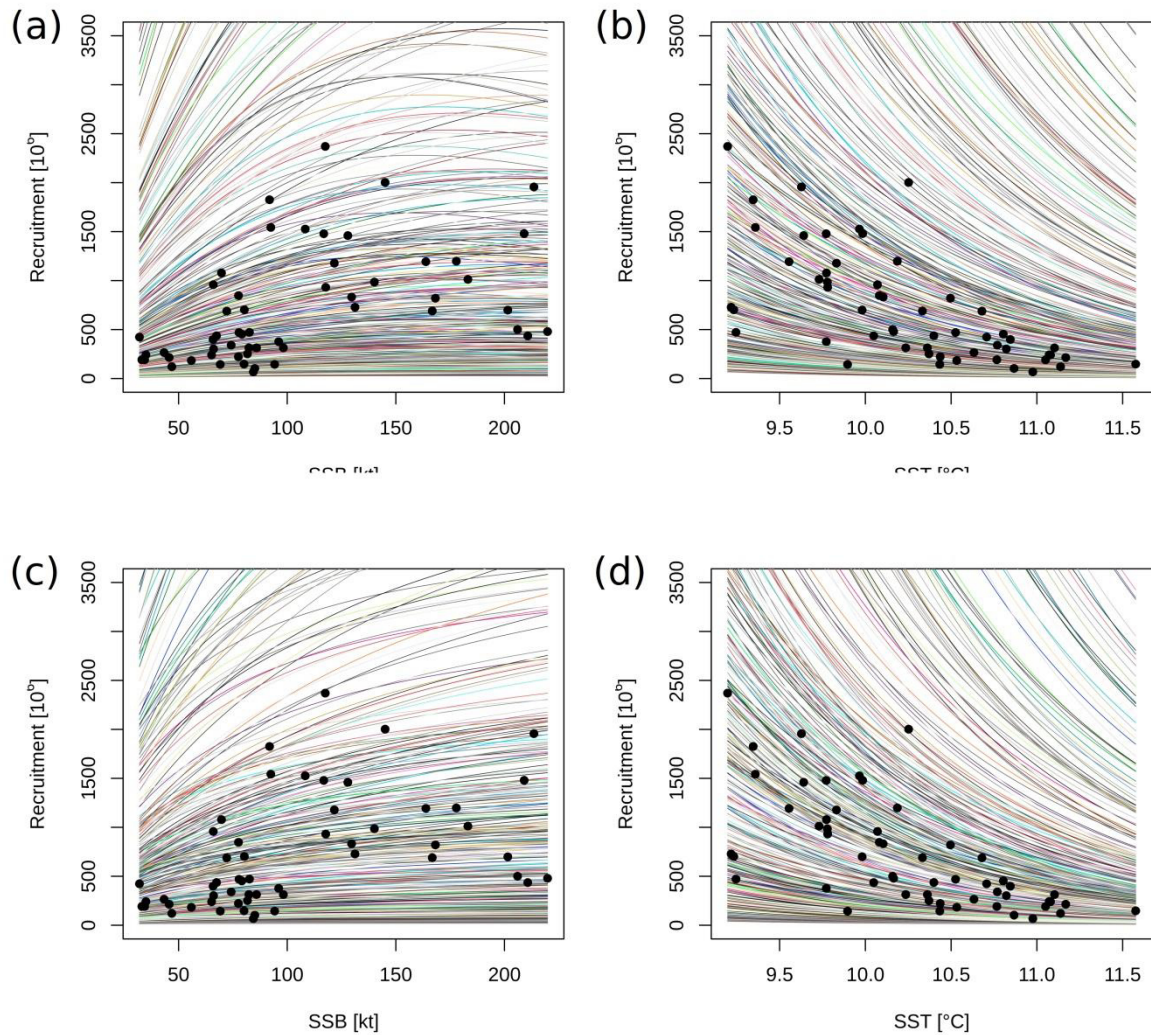


Figure SI CI.5 / 1: Assessment-estimated SSB- and recruitment data (dots) and SR relationships resulting from sampling the standard-error range of fitted SR-model parameters. Shown are the partial effects of SSB and SST for each of the 50 random parameterizations, for the Ricker (a, b) and the Beverton-Holt (c, d) models

## 7.6 SI CI.6: Description of the economic model

For the calculation of profits, we followed the procedures proposed by Schenk et al(2023):

Profits are defined as the difference of revenue and costs (eq. SI CI.6 / 1).

$$P_t = r_t - \Gamma_t$$

Equation SI CI.6 / 1: Calculation of profits. P = profits, r = revenue,  $\Gamma$  = costs, t = time

Catch revenue is calculated by assigning caught fish to a specific weight-class associated with a distinct price per weight (as obtained from the German federal office for agriculture and food (2020)). In our study, weights were set to the average age-specific weights in the catch for the period 2014-2018, thus each age class was assigned to one price level for the entire projected period (tab. SI CI.7 / 1). Revenue is then the catch in money summed over all age classes (eq. SI CI.6 / 2). We used the realized catch, i.e. the catch corrected not to exceed population numbers (see Supplementary Material 1.4) in revenue calculation.

$$r_t = \sum_{a=1}^A C_{a,t}^w * p_a * 1000 \text{ where } p_a = p_\omega \text{ for } w_{c_a} \in [\min W_\omega, \max W_\omega)$$

Equation SI CI.6 / 2: Calculation of revenue.  $r$  = revenue,  $t$  = time,  $a$  = age class,  $C^w$  = catch in weight,  $p$  = price (€ per kg),  $w_c$  = weight in the catch,  $\omega$  = weight class. Multiplication with 1000 converts catch in tonnes to catch in kg

The activity of catching also incurs costs, which are positively related to the amount of realized catch (due to e.g. wear of material and labor that increase with the amount of fish caught) (eq. SI CI.6 / 3).

$$\Gamma_t = q C_t^w * 1000$$

Equation SI CI.6 / 3: Calculation of costs.  $\Gamma$  = costs,  $q$  = baseline cost factor, equals 1.21 € per kg,  $C^w$  = catch,  $t$  = time in years. Multiplication with 1000 converts catch in tonnes to catch in kg

To calculate the profitability reference point, profits were similarly calculated for the period of observed data, using catchability coefficients calculated specifically for each year and price-class assignments based on the actual average reported weights.



## 7.7 SI CI.7: Input parameters for economic model

Table SI CI.7 / 1: Price for weighted fish

age class	weight-at-age in the catch [kg]	weight class [kg]	price [Euros * kg <sup>-1</sup> ]
1	0.37	0.3 to 1.0	1.500
2	0.93	0.3 to 1.0	1.500
3	2.14	2.0 to 4.0	2.653
4	3.80	2.0 to 4.0	2.653
5	5.62	4.0 to 7.0	3.133
6+	9.22	> 7.0	1.606

## 7.8 SI CI.8: Past profits generated by the North Sea cod stock

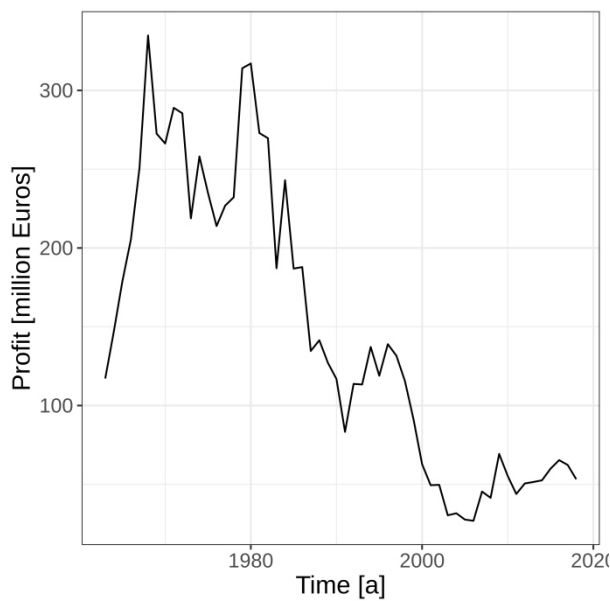


Figure SI CI.8 / 1: Past profits generated by North Sea cod for the period 1963-2018. Profits calculated using modeling approach presented by Schenk *et al.* (2023) (see Supplementary Material 7)

## 7.9 SI CI.9: Median trends of recruitment and SSB for different climate scenarios

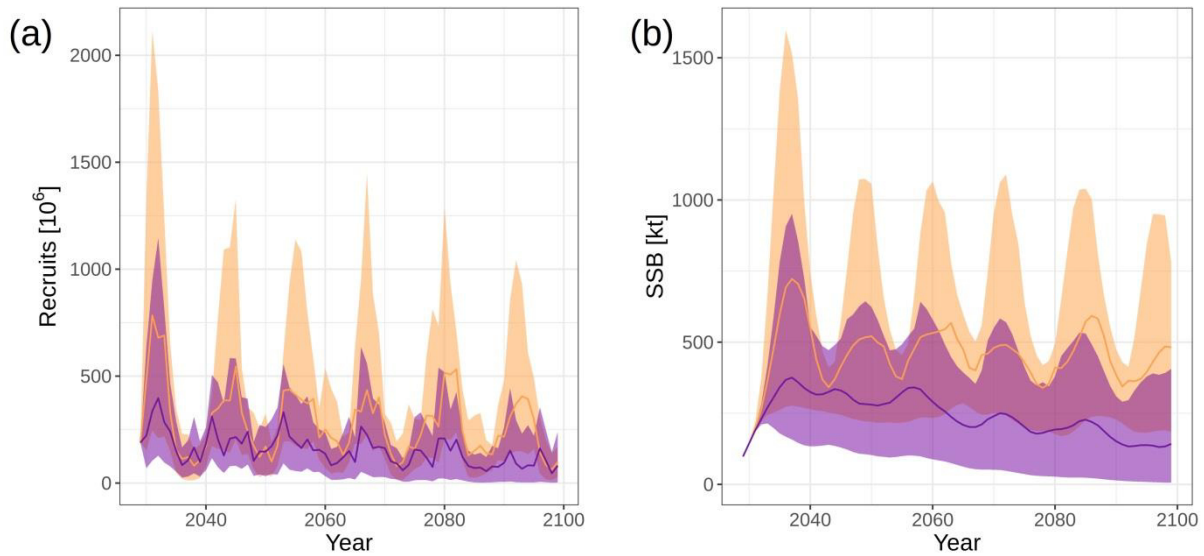


Figure SI CI.9 / 1: Projected recruitment (a) and SSB (b) under RCP4.5 (yellow) and RCP8.5 (blue). Line shows median. Shading represents range between 25- and 75-% percentiles

## 7.10 SI CI.10: Determining catch- and harvest-rate limits for sampling ranges

Lower limits for the ranges of catch and harvest rate that decision alternatives were sampled from were set to zero kt or %, respectively.

The upper limit of catch was set to current stock biomass, which was approximated as sum over population numbers derived from  $B_P$  (see Supplementary Material 1.4), reduced by half a year of natural mortality (medians over 2014-2018) and multiplied with weights in the catch (medians over 2014-2018) (eq. SI CI.10 / 1). This value represents a natural limit, as catch cannot exceed initial stock size in the first projection year.

$$C_{max} = \sum_{a=1}^A w_a^c N_{a,0} e^{-0.5M_a}$$

Equation SI CI.10 / 1: Calculation of the upper sampling limit for catch levels. C = catch,  $N_0$  = initial population size, M = natural mortality,  $w^c$  = weight in the catch, a = age class, A = number of age classes

The upper limit of harvest rate was initially set to 100 %, equaling the upper limit of the fixed-catch runs in the first projection year. An initial analysis of projection runs conducted while sampling from the range of zero to 100 % harvest rate revealed that a large part of the range yielded clearly unsustainable outcomes over virtually all uncertain scenarios (fig. SI

CI.10 / 1) (for details on the analysis procedure see *Material & Methods – Section 2.5 – Exploratory modeling*). As we were mainly interested in exploring the changing degree of sustainability in response to exploitation and uncertainty, we accordingly set a final upper limit of 25 % harvest rate (a new set of 100 random levels of harvest rate were drawn from this reduced range and used for the final analyses).

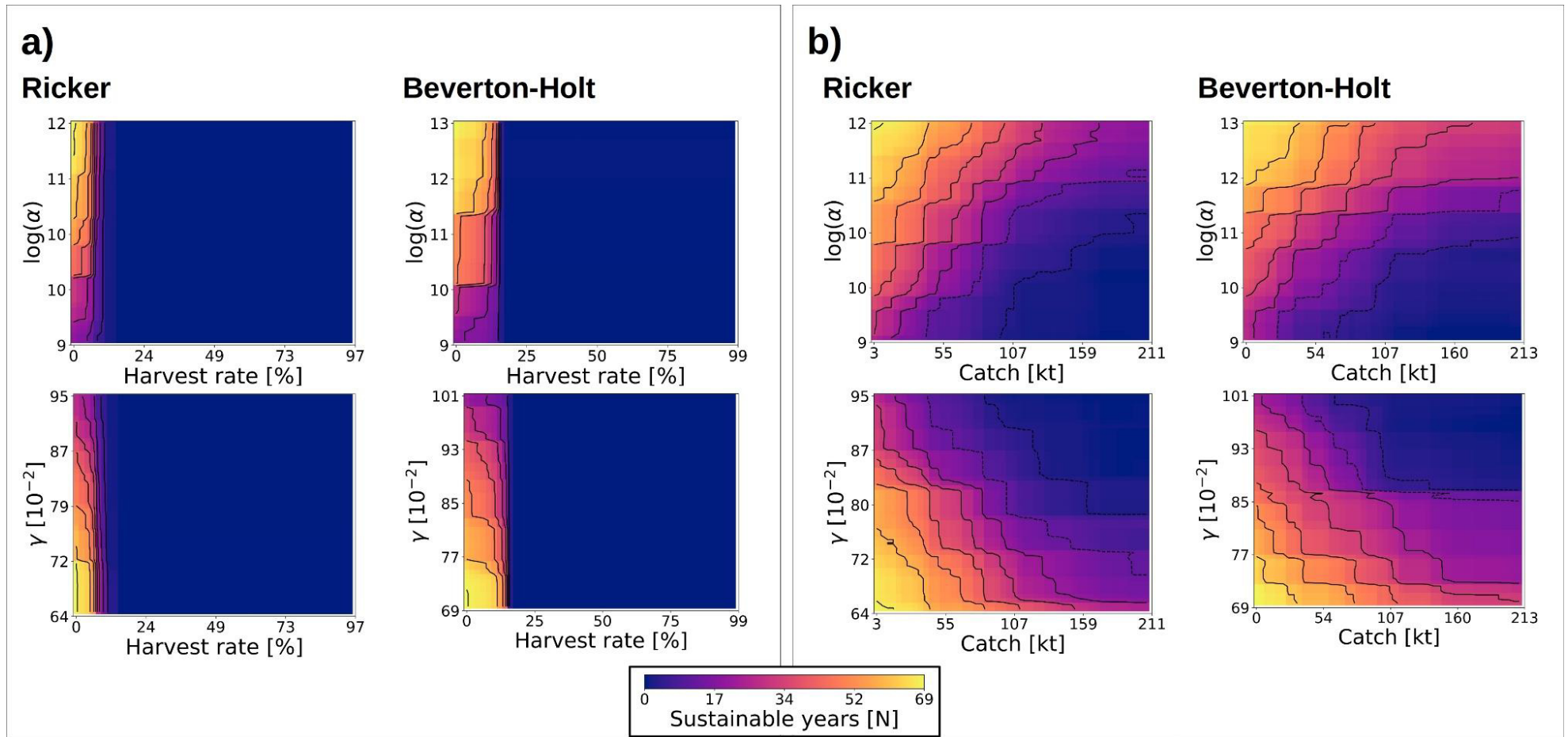


Figure SI CI.10 / 1: Outcomes of feature scoring for harvest-rate-based projections covering the full range of zero to 100 % harvest rate (a) and fixed-catch-based projections (b). For further details see fig. CI.2 in the main text.

### 7.11 SI CI.11: Relationship between intended and realized catches

Realized catch in a model projection conducted with the fixed-catch management scheme can deviate from intended catch (the level of catch taken in the first projection year, which is intended to be taken in all subsequent years, as well). This event occurs when stock size is smaller than the intended level of catch as a result of initial overexploitation and / or insufficient stock productivity. Its occurrence is therefore dependent on uncertainty about the SR relationship.

We calculated the relative amount of instances (uncertain scenarios and years) in which realized catch deviated from intended catch for each bin of catch levels (see *Material & Methods - Section 2.5 – Exploratory modeling*) and visualized the relationship to obtain information on the amount of occurrences where the results shown relate not to the actual intended catch level but to a lower catch level resulting from forced reduction.

We found that the relative amount of instances in which realized catch deviated from intended catch increased relatively linearly with intended catch, reaching a level of c. 90 % at the highest catch level (fig. SI CI.11 / 1 b). There was no clearly defined range of intended catch where there were no instances of deviation. However, realized catch in general quickly reached zero when it did deviate from intended catch (fig. SI CI.11 / 2 b), indicating that in our model, deviations are caused by relatively quick stock collapse and are terminal, i.e. realized catch does not stabilize on some lower-than-intended level.

Realized harvest rate also differed from intended harvest rate in some instances, though only in the very beginning of the time series, before it returned to the intended level (fig. SI CI.11 / 2 a)

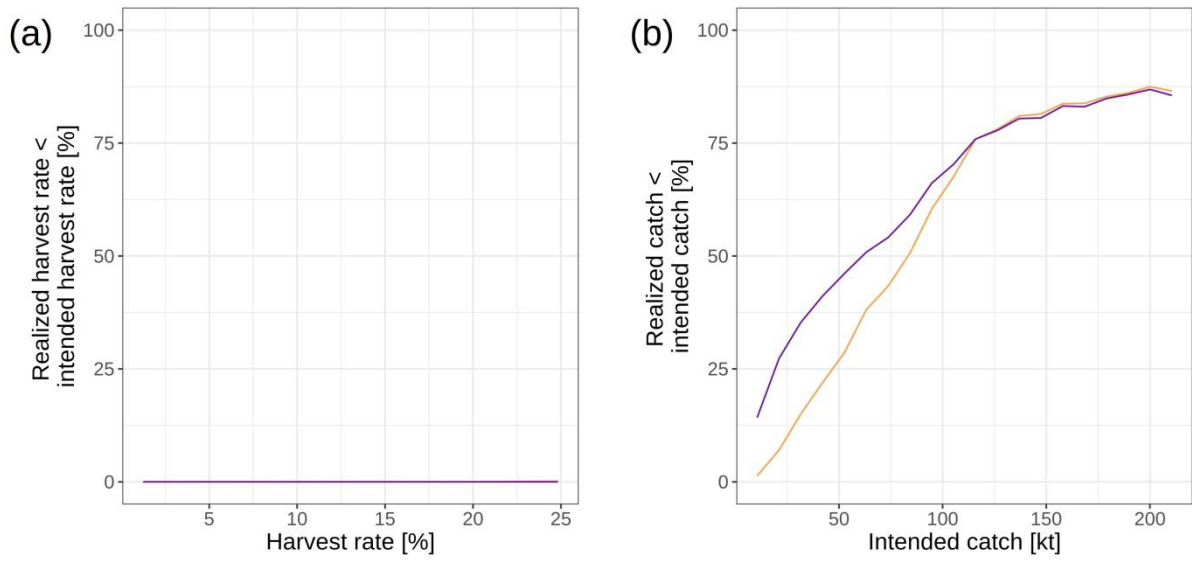


Figure SI CI.11 / 1: Relative amounts of instances where intended harvest rate exceeded realized harvest rate (a) and where intended catch exceeded realized catch (b). Yellow line: mid-century projection period (2030-2049); blue line: late-century projection period (2050-2099).

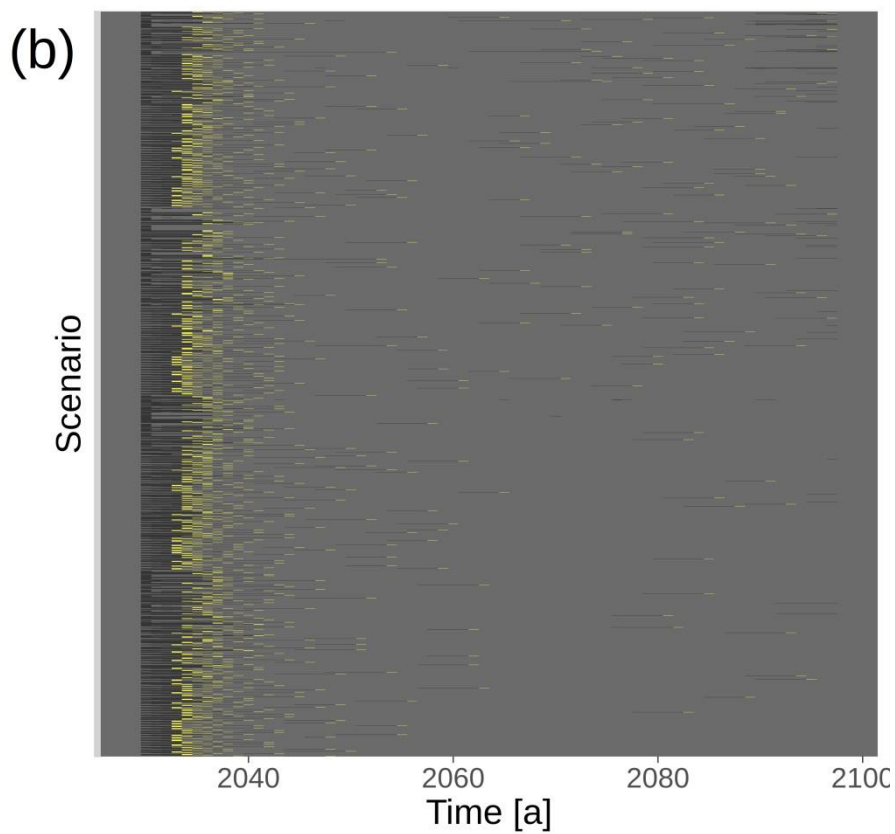
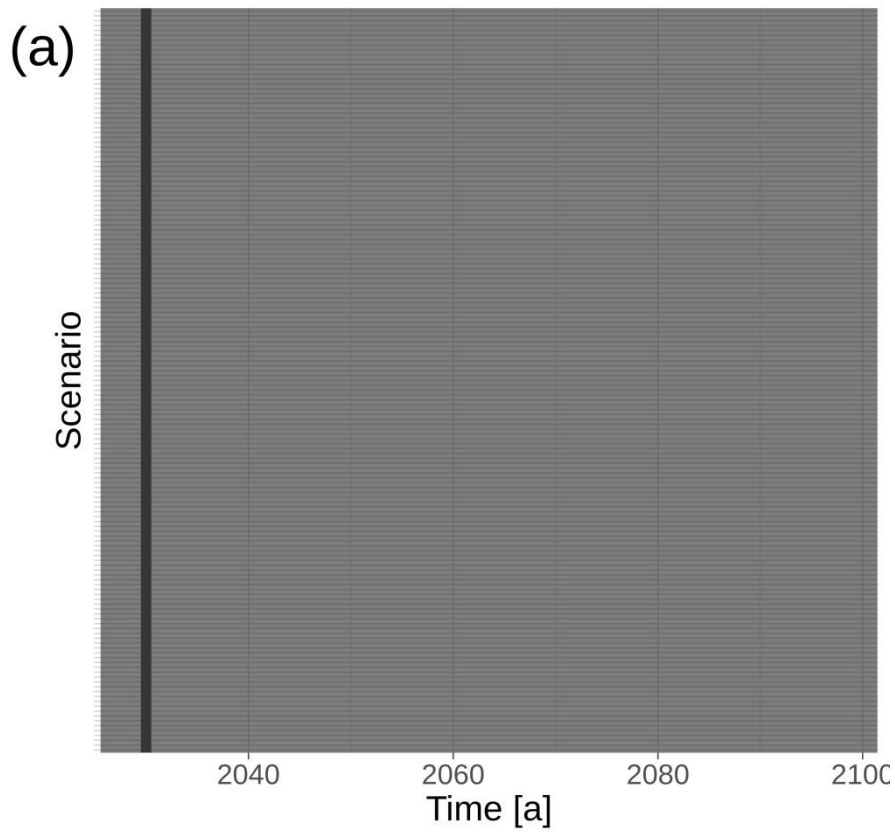


Figure SI CI.11 / 2: Trajectories of realized catch (a) and realized harvest rate (b) that resulted in a deviation of realized catch from intended catch or a deviation of realized harvest rate from intended harvest rate, respectively. Black shading indicates that realized exploitation is lower than intended exploitation but is not zero. In (a), yellow shading highlights initial year in which catch is zero. In (b), there are no occurrences of realized harvest rate being zero, as realized harvest rate recovers to the intended level in every case

### **7.12 SI CI.12: Determining exploitation at best risk trade-off**

Levels of catch and harvest rate corresponding to the best trade-offs were determined based on two criteria: i) additive risk and ii) absolute difference between 1 and the ratio of profitability- to sustainability risk. The exploitation levels corresponding to the lowest sum of the two criteria were selected as those levels corresponding to best trade-off between sustainability- and profitability risk.



## 8. Supplementary material for Chapter II “Safe Operating Space reveals climate-adaptation thresholds for sustainable management of Atlantic cod (*Gadus morhua* L.)”

Jan Conradt<sup>1\*</sup>, Steffen Funk<sup>1</sup>, Thorsten Blenckner<sup>2</sup>, Christian Möllmann<sup>1</sup>

<sup>1</sup>Institute of Marine Ecosystem and Fishery Science, Universität Hamburg, Germany

<sup>2</sup>Stockholm Resilience Center, Stockholm University, Stockholm, Sweden

\*Principal author

### 8.1 SI CII.1: Detailed description of the population model

Our population model followed the design described by Allen (1975).

#### 1.1 Calculation of population numbers and SSB

Population numbers for all age classes except the recruitment age class in a given projection year were calculated via the mortality equation (eq. SI CII.1 / 1). Pre-recruitment age classes were not modeled in this way; i.e. the process of recruitment (survival from being spawned to recruiting to the fished stock) was assumed to be entirely described by the SR model (see SI CII.2). The final age class includes individuals from all higher age classes, which are not considered separately in stock assessments, since they are usually only comprised of few individuals. Population numbers of this age class result from adding the survivors of the second-to-final age class and the survivors from the final age class from the previous year (survival of these two age classes is modeled with two distinct values of fishing- and natural mortality).

$$N_{t+1,a+1} = N_{t,a} e^{-(F_{t,a} + M_{t,a})} \text{ for } a \in [a_r, \dots, A - 1]$$

$$N_{t+1,a+1} = N_{t,a} e^{-(F_{t,a} + M_{t,a})} + N_{t,a+1} e^{-(F_{t,a+1} + M_{t,a+1})} \text{ for } a = A - 1$$

Equation SI CII.1 / 1: Mortality equation. N = population number, F = fishing mortality, M = natural mortality, a = age class, a<sub>r</sub> = age of recruitment, A = number of age classes / highest age class, t = time (1 year)

SSB is the product of age-specific population numbers, weight and maturity rate, summed over all age classes (eq. SI CII.1 / 2).

$$SSB = \sum_{a=1}^A N_a w_a^s m_a$$

Equation SI CII.1 / 2: Calculation of SSB. N = stock numbers,  $w^s$  = weight in the stock, m = maturity rate, a = age class, A = number of age classes

## 1.2 Determination of exploitation pattern

The distribution of a total catch among the age classes (see SI CII.1.3) requires the application of an exploitation pattern. We determined an exploitation pattern in each projection year in the following way:

We determined a reference catch in numbers based on age-class sizes after half a year of natural mortality only and age-specific catchability (eq. SI CII.1 / 4), as given by the ratio of fishing mortality (F) to the maximum F over age classes (eq. SI CII.1 / 3). The latter was calculated as the median over the last five used assessment years (see SI CII.7.7).

$$\gamma_a = \frac{F_a}{\max_{1 \rightarrow A} F}$$

Equation SI CII.1 / 3: Calculation of age-specific catchability.  $\gamma$  = catchability, F = fishing mortality, median over assessment years 2014-2018, a = age class, A = number of age classes

$$C_{ref,a,t}^N = \gamma_a N_{a,t} e^{-0.5M_a}$$

Equation SI CII.1 / 4: Calculation of reference catch.  $C_{ref}^N$  = potential catch in numbers,  $\gamma$  = catchability, N = size of the age class at the beginning of the year, M = natural mortality, a = age class, t = time in years

Age-specific reference catch in kilo-tonnes was calculated by multiplication with weight in the catch (median over the last five used assessment years) (eq. SI CII.1 / 5).

$$C_{ref,a,t}^W = C_{ref,a,t}^N w_a^c$$

Equation SI CII.1 / 5: Calculation of reference catch in weight.  $C_{ref}^W$  = reference catch in weight,  $C_{ref}^N$  = reference catch in numbers,  $w^c$  = weight in the catch, median over assessment years 2014-2018, a = age class, t = time in years

Reference catch in weight was then used to calculate an exploitation pattern that allows spreading a total catch over age classes (eq. SI CII.1 / 6).

$$E_{a,t} = \frac{C_{refa,t}^W}{\sum_{a=1}^A C_{refa,t}^W}$$

Equation SI CII.1 / 6: Calculation of exploitation pattern for generating age-specific catch in weight. E = exploitation pattern (relative value),  $C_{pot}^W$  = reference catch in weight, a = age class, t = time in years, A = number of age classes

It was verified that this approach, when calculating F from age-specific catches (see SI CII.1.5) recreates the current F pattern in the projections when age class strengths support the intended level of catch.

When the intended catch level could not be achieved by applying the exploitation pattern derived from current catchabilities (eq. SI CII.1 / 3), but the population still featured survivors at the end of the year, catchabilities were artificially increased to 1 in a step-wise manner over age classes, until one or both of either conditions were resolved. This procedure was invoked in order to ensure that a lower-than-intended level of catch would not yield a sufficient number of survivors that might generate a level of SSB higher than  $B_P$ , and to thus avoid drawing false conclusions about the effects of intended catch levels. The sequence of age classes for which catchability was set to 1 followed the reverse order of current catchability, in order to limit the deviation from the current catchability pattern. Increasing catchabilities for certain age classes in the model can result in a lack of realism of fishing activity, but may be interpreted as increased effort (e.g. more time spent at sea, usage of nets with lower mesh size) as a means of maintaining a stable level of landings.

### 1.3 Calculation of age-specific catch in numbers

Catch in tonnes was translated into F by solving the catch equation, which predicts catch from stock size, for F. This required a transformation of the total catch into age-specific catches in numbers, which requires knowledge about the ratio between biomass and numbers, and about the exploitation pattern over age classes. The exploitation pattern was determined as the ratio of the products of age-specific catches in numbers and age-specific weight in the stock, both derived from stock assessment files, to the sum of these products over all age classes. The median numbers and weights over the last five assessment years were used in the calculation, and the exploitation pattern was assumed to be constant in all projection years. Catch in numbers was then derived from multiplying the exploitation pattern with total catch in weight and dividing the product by age-specific weight in the catch (here again, the median weight over the last five assessment years was used) (eq. SI CII.1 / 7).

$$C_{a,t}^N = \frac{E_a C_t^W}{w_a^c}$$

Equation SI CII.1 / 7: Calculation of age-specific catch in numbers.  $C^W$  = catch in weight (tonnes),  $C^N$  = catch in numbers (thousands),  $E$  = exploitation pattern,  $a$  = age class,  $w^c$  = weight in the catch,  $t$  = time (1 year)

#### 1.4 Calculation of realized catch

Calculation of realized catch was necessary when the intended age-specific catch in numbers was larger than or equal to the number of individuals in a specific age class in a specific year. In that case, age-specific catch was reset to the size of the age class after half a year of being exposed to natural mortality only (this specification was necessary due to the application of Pope's approximation (Pope, 1972) of determining  $F$ , which assumes that all catch is removed exactly at mid-year; see details below). Total realized catch was then realized catch in numbers multiplied by age-specific weight in the catch, summed over all age classes (eq. SI CII.1 / 8).

$$C_{a,t}^N = \min(C_{a,t}^N, N_{a,t} e^{-0.5M_{a,t}})$$

$$C_t^W = \sum_{a=1}^A C_{a,t}^N w_a^c \text{ for } a \in [a_r, \dots, A]$$

Equation SI CII.1 / 8: Calculation of realized age-specific (top) and total catches (bottom).  $C^W$  = catch in weight,  $C^N$  = catch in numbers,  $N$  = population number,  $a$  = age class,  $a_r$  = age of recruitment,  $w^c$  = weight in the catch,  $M$  = natural mortality,  $t$  = time (1 year)

#### 1.5 Estimation of fishing mortality

An approximation of population numbers of a specific age class that does not require knowledge about  $F$  can be obtained by assuming that the entire catch of one year is removed at once after half a year without fishing, and that this event is followed by another half year of no fishing (Pope's approximation [Pope, 1972]). This process is formulated via a "nested" mortality equation, where natural mortality is multiplied by 0.5 to calculate a reduction in numbers in the course of one half year (eq. SI CII.1 / 9). Using the population numbers thus approximated, as well as those of the previous age class in the previous year, and the corresponding level of natural mortality (a constant) and inserting both into the mortality equation solved for  $F$  (eq. SI CII.1 / 10) yields an approximation of  $F$ .

$$N_{a+1,t+1} \approx ((N_{a,t}e^{-0.5M_{a,t}}) - C_{a,t}^N)e^{-0.5M_{a,t}}$$

Equation SI CII.1 / 9: Pope's (1972) approximation of the mortality equation.  $C^N$  = catch in numbers,  $N$  = population number,  $F$  = fishing mortality,  $M$  = natural mortality,  $a$  = age class,  $t$  = time (1 year)

$$F_{a,t} \approx - \left( (\log N_{a+1,t+1} - \log N_{a,t}) + M_{a,t} \right)$$

Equation SI CII.1 / 10: Mortality equation solved for fishing mortality.  $N$  = population number,  $F$  = fishing mortality,  $M$  = natural mortality,  $a$  = age class,  $t$  = time (1 year)

### 1.6 Determination of model constants

Age-specific weights in the stock, weights in the catch, maturity rates and natural mortalities were used as constants in the population model. For each metric and age class, the median value over the last seven years in the assessment, minus the final two assessment years due to the potential for large retrospective patterns in late assessment years (Mohn, 1999) and associated potential uncertainty about biological parameters in those years, was calculated and used as a constant.

### 1.7 Determination of model constants

The initial population size depended on the level of initial SSB tested. Initial age-specific SSB corresponding to a set initial level of total SSB (i.e. one out of the 20 levels tested [see *Methods – Simulation strategy*]) was calculated by multiplying the latter value with the ratio of age-specific SSB values given by the stock assessment to total SSB (eq. SI CII.1 / 11).

$$SSB_{s,a,t}^{ini} = SSB_s \frac{SSB_{o,a,t}^{ini}}{\sum_{a=1}^A SSB_{o,a,t}^{ini}}$$

Equation SI CII.1 / 11: Calculation of initial age-specific SSB corresponding to a set total SSB (indexed with "s").  $SSB_o$  = observed SSB (final year(s) from stock assessment),  $a$  = age class,  $A$  = number of age classes,  $t$  = time index (one year)

Age-specific SSB was used to calculate age-specific initial population numbers, by dividing the former by the age-specific product of weight and maturity (eq. SI CII.1 / 12).

$$N_{a,t}^{ini} = \frac{SSB_{a,t}^{ini}}{w_a^s m_a}$$

Equation SI CII.1 / 12: Calculation of initial age-specific population size when projecting with a set total SSB.  $N^{ini}$  = initial population size,  $SSB^{ini}$  = initial SSB,  $w^s$  = weight in the stock ((median over final used assessment years),  $m$  = maturity (median over final used assessment years),  $a$  = age class,  $t$  = time index (one year)

In case the lag between SSB and recruitment was larger than one year, the initial population consisted of stock numbers for several years, and both above procedures were conducted for the data for each of those initial years as taken from the stock assessment.

Age-specific population numbers may be undefined for age classes with a maturity rate of zero %, i.e. mostly the first or the first two age classes (in the majority of stocks, maturity of these age classes is larger than zero %, however). In these cases, age-specific initial population number was set to that of the middle age class, multiplied by the ratio of the target age class to the middle age class observed in the initial population size derived from the stock assessment (eq. SI CII.1 / 13).

$$N_a^{ini} = N_{0.5 A}^{ini} \frac{N_a^o}{N_{0.5 A}^o}$$

Equation SI CII.1 / 13: Estimation of initial population number for age classes with zero-% maturity.  $N^{ini}$  = initial population numbers for final stock projection,  $N^o$  = population numbers from stock assessment,  $a$  = age class,  $A$  = number of age classes. For stocks with uneven number of age classes,  $0.5 A$  is replaced by the age classes closest to  $0.5 A$

### 1.8 Modifications for stocks experiencing mortality before spawning

For several stocks, the assessment model assumes that spawning occurs later than January 1<sup>st</sup> (see respective assessment reports and / or annexes for details). Consequently, the stock is decreased by a fraction of the total fishing- and natural mortality before SSB is calculated. We implemented this modification in our population model by modifying the SSB equation (eq. SI CII.1 / 14).

$$SSB = \sum_{a=1}^A N_a e^{-(x_a F_a + y_a M_a)} w_a^s m_a$$

Equation SI CII.1 / 14: Calculation of SSB for stocks with pre-spawning mortality.  $N$  = population numbers,  $F$  = fishing mortality,  $M$  = natural mortality,  $w^s$  = weight in the stock,  $m$  = maturity,  $a$  = age class,  $A$  = number of age classes,  $x$  = fraction of fishing mortality before spawning,  $y$  = fraction of natural mortality before spawning

### 1.9 Modifications for stocks with age-zero recruitment

Irish cod recruitment occurs at age zero (ICES, 2022n). Consequently, numbers of age-zero fish were estimated via the SR relationship only *after* the survivors to age classes 1+ (at January 1st) were calculated via the mortality equation, as SSB depends on the numbers of these survivors. In stocks with SSB-recruitment lags  $> 0$ , recruitment is independent of the survivors to a given year, and was calculated simultaneously with calculation of survivors.

## 8.2 SI CII.2: Detailed description of the stock-recruitment model

We fitted the environmental Ricker (Ricker, 1975) model on the SSB-, SST- and recruitment data. Cod shows cannibalistic behavior at young stages (e.g. Folkvord, 1991; Bogstad et al., 1994), hence we selected the Ricker function, which accounts for negative density-dependent processes (Ricker, 1954). The Ricker function describes a positive linear relationship of recruitment with SSB and a negative exponential relationship of recruitment with SSB, as well as a negative or positive exponential relationship of recruitment with SST. The two SSB-related relationships are described with one parameter each, while the SST-related relationship is described with one parameter. We introduced an additional offset parameter in the exponential term that is not part of the original environmental Ricker function, but aided in the fitting process (see SI CII.3) (eq. SI CII.2 / 1)

$$R_t = N_{t,1} = \alpha SSB_{t-l_s} e^{-\beta SSB_{t-l_s} + \gamma E_{t-l_e} + \delta}$$

Equation SI CII.2 / 1: Environmental Ricker (1975) stock-recruitment-model equation. R = recruitment, N = population number, SSB = spawning-stock biomass, E = environmental variable,  $l_s$  = SSB-recruitment lag,  $l_e$  = lag between environmental effect and recruitment

The functional equations of the Ricker model was re-arranged (eq. SI CII.2 / 2) to allow i) for a formulation closer to that of a linear equation, which can alleviate the fitting procedure, and ii) for fitting the logarithms of the SSB-related parameters ( $\alpha$  and  $\beta$ ). These parameters have no biological meaning when being negative.

The relationships between SSB and recruitment and SST and recruitment are usually subject to a lag of one or several years. While the SSB-recruitment lag is pre-defined by stock assessment, the SST-recruitment relationship is not. In our model simulations, we tested both SR models fitted on data with a SST-R lag equaling the SSB-R lag, and such fitted on data with a SST-R lag extended by an additional year. This extension implies an effect of SST on the spawners (i.e. spawner-habitat selection and –condition, indications of which were found

in distribution- and condition observations on western-Baltic cod [Funk, 2020; Funk et al., 2021; Receveur et al., 2022]) rather than on the pre-recruits themselves.

Parameter fitting was conducted with the nlsLM solver in R (package “minpack.lm” [Elzhov et al., 2016]).

$$\log\left(\frac{R_t}{SSB_{t-l_s}}\right) = \lg\alpha - e^{\lg\beta}SSB_{t-l_s} + \gamma SST_{t-l_e} + \delta$$

Equation SI CII.2 / 2: Environmental Ricker SR function, re-arranged equation. For details see eq. SI CII.2 / 1. Note that “lg $\alpha$ ” and “lg $\beta$ ” are technically the logarithms of  $\alpha$  and  $\beta$  (from eq. SI CII.2 / 1), but are treated as proper optimizable parameters here

### 8.3 SI CII.3: Fitting the stock-recruitment model

#### 3.1 Sequential incorporation of predictor variables

We noted that when fitting recruitment simultaneously against SSB and SST, the partial effects of predictor variables in the model would occasionally reflect the observed correlation of recruitment with one variable well, but the correlation with the other variable poorly. As this behavior might indicate an inaccurate reflection of the predictor effects, especially when a correlation of recruitment with both predictor variables was clearly visible in the data, we instead implemented a sequential fitting procedure:

We first fitted recruitment separately against SSB and SST in two models that each contained the respective parameter-specific terms of the full Ricker equation (eq. SI CII.2 / 1).

$$\log\left(\frac{R_t}{SSB_{t-l_s}}\right) = \lg\alpha - e^{\lg\beta}SSB_{t-l_s}$$

$$\log(R_t) = \gamma SST_{t-l_e} + \delta$$

Equation SI CII.3 / 1: Separate SR functions describing recruitment as a function purely of SSB (top) and purely of SST (bottom). Functions are derived from eq. SI CII.2 / 2. For details see eq. SI CII.2 / 2

We then checked the normality of distribution of the residuals of these univariate models with the Shapiro-Wilk test (Shapiro & Wilk, 1965). We selected the model with more normally distributed residuals and then fitted the recruitment residuals of that model against the respective other predictor variable (eq. SI CII.3 / 2).



$$\log(P_{m_{SSB}}) = \gamma SST_{t-l_e} + \delta$$

$$\log(P_{m_{SST}}) = lg\alpha - e^{lg\beta} SSB_{t-l_s}$$

Equation SI CII.3 / 2: Functions predicting the residuals yielded by the fitted univariate SR functions (eq. SI CII.3 / 1).  $P$  = residuals,  $m_{SSB}$  denotes SR model fitted only on SSB,  $m_{SST}$  denotes SR model fitted only on SST

We then combined predicted log-recruitment from the first model with predicted log-residuals from the second model to obtain the final recruitment prediction. We observed that this procedure mitigated the tendency of the SR model to fit primarily to one predictor variable described above.

### 3.2 Accounting for uncertainty and temporal variability in the SR relationship

In order to account for the large uncertainty inherent to the relationship between spawning biomass (SSB), environmental drivers and recruitment, and for potential temporal variability in the shape of the relationship (Myers et al., 1998; Tirronen et al., 2022), we considered a large range of potential future SR relationships by fitting SR models to subsets of various lengths of the recruitment time series (similar to the analytical approach employed by Szuwalksi et al. [2019] on forage fish). We set the minimum number of data points to be included in these subsets to 10. Also, we set the constraint that all data points in a subset should be of sequential years to reflect the potential shifting of the SR relationship through time. We only retained a model fitted on a given subset if its predictive loss (mean squared error on the recruitment) was lower than that of a model fitted on the entire time series of data, in order to avoid including overly unrealistic models in our analysis.

We collected the parameters from all fitted models and created a separate set for each of the two time lags tested and for each of the two different fitting sequences, in case both occurred (see SI CII.3.1). We used these parameter sets to generate different parameterizations of the SR model for usage within the population model: In order to avoid an over-weighting of SR parameters from models fitted on short time series, we treated the minimum and maximum value of each parameter as the limits of a range for uniform sampling. However, we did not sample the parameters fully independently of each other, as some, especially  $lg\alpha$  and  $\gamma$ , showed a clear correlation. Instead, when sampling a value for a specific parameter  $i$ , the three other parameters were set to the corresponding elements of the empirical parameter vector closest (absolute Euclidean distance) to the sample in terms of parameter  $i$ .

We sampled ten values for each of the four parameters, and assigned the corresponding values for the other three parameters as described, which resulted in 40 different parameterizations of the SR model for a specific combination of SST-recruitment lag and fitting sequence. The total number of SR model set-ups for a given stock was thus 160.

#### **8.4 SI CII.4: Stock-recruitment – partial effects of fitted models**

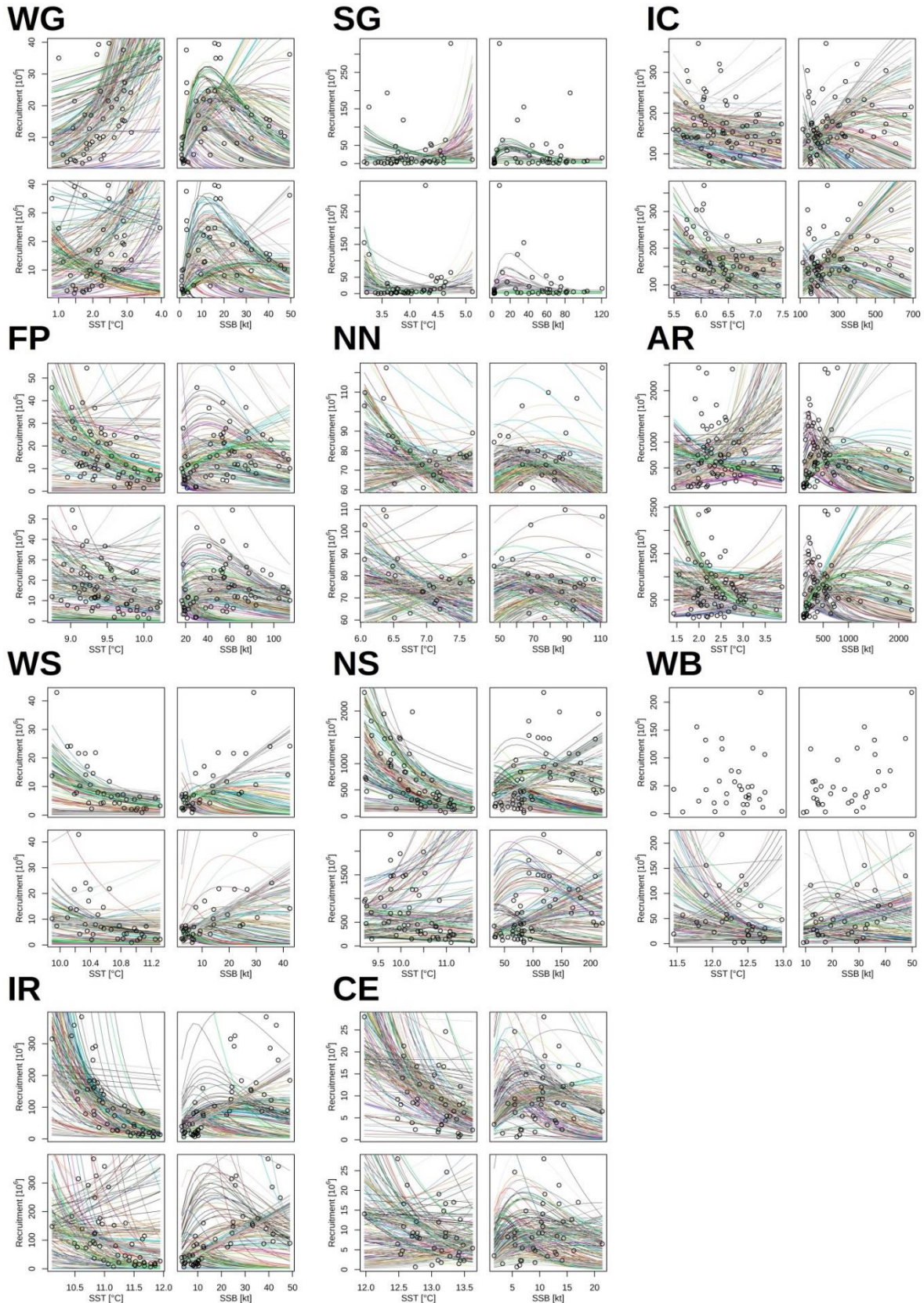


Figure SI CII.4 / 1: Partial effects of SST (left panels in each plot) and SSB (right panels) on recruitment in European and high-latitude stocks, as predicted by the fitted SR models. Shown are SR models fitted with a SST-R lag equaling the SSB-R lag (top panels in each plot) and a SST-R lag equaling the SSB-R lag plus one year (bottom panels). Points represent the recruitment estimates from the stock assessments. For stock abbreviations see fig. CII.1 in the main text

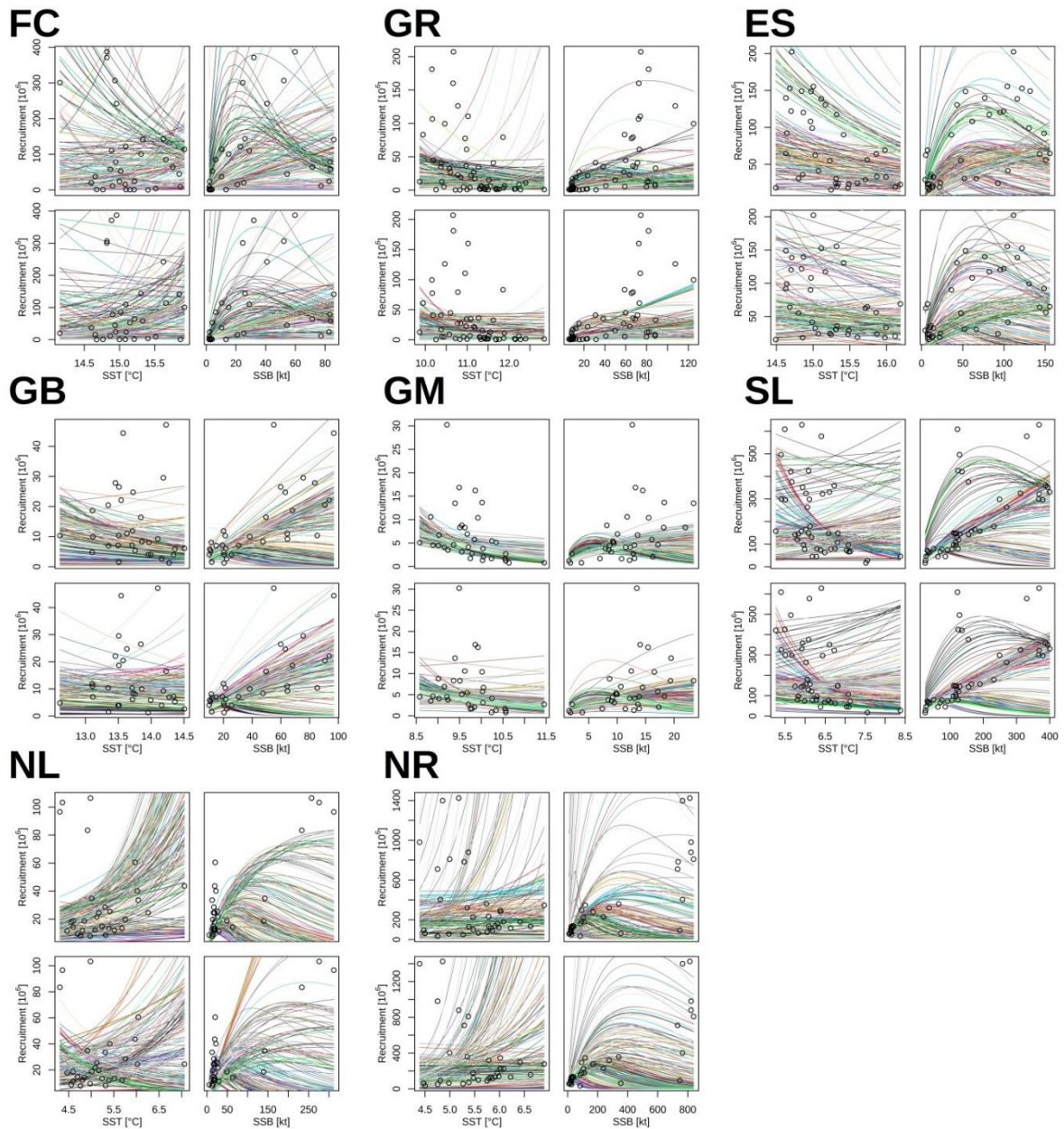


Figure SI CII.4 / 2: Partial effects of SST (left panels in each plot) and SSB (right panels) on recruitment in North-American stocks, as predicted by the fitted SR models. Shown are SR models fitted with a SST-R lag equaling the SSB-R lag (top panels in each plot) and a SST-R lag equaling the SSB-R lag plus one year (bottom panels). Points represent the recruitment estimates from the stock assessments. For stock abbreviations see fig. CII.1 in the main text

## **8.5 SI CII.5: Forcing catch levels by altering the selectivity pattern**

Forcing a population model with fixed levels of catch and a fixed selectivity pattern can result in a lower-than-intended realized total catch when catch in numbers exceeds cohort size for certain age classes. Up to some limit, the stock may be able to generate the intended catch by adjusting the selectivity pattern, such that more fish of other age classes are caught to compensate the limitation posed by cohort size of certain age classes. As we were interested in the sustainability of fixed catch levels (i.e. try to reduce deviations of realized- from intended catch), and assume that fishers would change fishing strategies to generate a different selectivity pattern in order to maximize catch, we invoked a routine in our model projections that checks for deviations between total intended and total realized catch and alters the selectivity pattern to reduce that deviation:

The routine is started by setting selectivity for the second highest selectivity (the highest selectivity is always 1.0) to 1.0, so that selectivity is 1.0 for two age classes. We repeat the calculation of cohort-specific realized catch,  $F$  and survivors, as well as total realized catch (in kilo-tonnes), as described in SI CII.1. Total realized catch is then again compared to intended catch, and it is checked whether the total number of survivors is larger than zero. If the former still results in a deviation, and the latter is true, then selectivity for the next-strongest-selected class is set to 1.0. The procedure is repeated until either the deviation between intended and realized catch is reduced to zero, or the total number of survivors is zero, or selectivity of all age classes has been set to 1.0.

The routine does not prevent deviations between realized and intended catch in every case, however – catch levels that exceed total stock size are not possible to realize as the required stock size (biomass of fish) is simply not available.

## **8.6 SI CII.6: Calculation of risk of unsustainable management**

Risk of unsustainable management was determined by counting, for each combination of catch level, SST increase and initial SSB, the number of instances, i.e. SR parameterizations and simulation time steps, in which SSB was below  $B_P$ , and dividing that number by the total number of instances (eq. SI CII.6 / 1).



$$R_{c,s,b} = \frac{N_{SSB_{c,s,b} \leq B_P}}{F * I} * 100$$

Equation SI CII.6 / 1: Calculation of risk of unsustainable management. R = risk, F = number of SR parameterizations, I = number of model iterations, N = number of valid instances (count), c = catch level, s = level of SST increase, b = level of initial SSB

## 8.7 SI CII.7: Biological constants and reference points

Biological constants (tab. SI CII.7 / 2-3) and reference points (tab. SI CII.7 / 1) were taken from the assessment reports by ICES, DFO, NOAA, NAFO and the Joint Russian-Norwegian Working Group on Arctic Fisheries. Biological constants (natural mortality, maturity rates, weight in the stock, weight in the catch, selectivity pattern) were set to the median over the last five assessment years after removing the final two assessment years to account for potential retrospective patterns in future assessments (Mohn, 1999). Where an estimate of the limit reference point ( $B_{lim}$ ) was available but none of  $B_P$ , a custom estimate was calculated using the functional relationship between  $B_{lim}$  and MSY  $B_{trigger}$  given by ICES (2021c) (see SI CII.8).

Table SI CII.7 / 1: Estimates of  $B_P$

Stock	Estimate of $B_P$ [t]
South-East Greenland	18146 (ICES, 2022f)
West Greenland	5983 (ICES, 2022g)
Iceland	265000 (ICES, 2022h)
Faroe Plateau	24739 (ICES, 2022i)
Northern Norwegian Coast	67743 (ICES, 2022j)
North-East Arctic	460000 (Joint Russian-Norwegian Working Group on Arctic Fisheries [JRN-AFWG], 2022)
West of Scotland	20126 (ICES, 2022k)
North Sea	97777 (ICES, 2022l)
Western Baltic	23492 (ICES, 2022m)
Irish	11538 (ICES, 2022n)

Celtic	5800 (ICES, 2022o)
Flemish Cap	20895* (González-Troncoso et al., 2022 )
Georges Bank	93309* (Northeast Fisheries Science Center, 2013)
Grand Banks	83375* (Rideout et al., 2021 )
Eastern Scotian Shelf	69479* (Mohn & Rowe, 2011)
Gulf of Maine	24981* <sup>X</sup> (NOAA, 2021)
Southern Gulf of St. Lawrence	111166* (DFO, 2019a)
Northern Gulf of St. Lawrence	188000 (DFO, 2019b)
Northern	1097762* (Bratley et al., 2018); P. Regular (pers. comm.)

\*Custom estimate of  $B_P$  calculated via ICES rule. Reference refers to  $B_{lim}$

<sup>X</sup>Mean of two values corresponding to two different assumptions about natural mortality in the assessment model

Table SI CII.7 / 2: Additional information on stocks. “Biological constants” refers to natural mortality, maturity, weight in the stock and weight in the catch

Stock	Age-classes contributing to $F_{bar}$	SSB-recruitment lag [years]	Mortality before spawning [%]	Period for averaging biological constants
South-East Greenland	5-10	1	0	2015-2019
West Greenland	4-8	1	0	2015-2019
Iceland	5-10	3	25 (F), [9, 18, 25, 30, 38, 44, 48, 48, 48, 48, 48, 48] (M, for the respective age classes)	2016-2020
Faroe Plateau	3-7	1	0	2016-2020
Northern Norwegian Coast	4-8	2	80	2015-2019

North-East Arctic	5-10	3	0	2015-2019
West of Scotland	2-5	1	0	2015-2019
North Sea	2-4	1	0	2015-2019
Western Baltic	3-5	1	0	2015-2019
Irish	2-4	0	0	2015-2019
Celtic	2-5	1	0	2015-2019
Flemish Cap	3-5	1	0*	2015-2019
Georges Bank	5-8	1	0*	2005-2009
Grand Banks	4-6	3	0*	2013-2017
Eastern Scotian Shelf	5-15	1	0*	2004-2008
Gulf of Maine	8	1	25	2012-2016
Southern Gulf of St. Lawrence	5-8	2	0*	2012-2016
Northern Gulf of St. Lawrence	7-9	3	0*	2012-2016
Northern	5-14	2	0*	2014-2018

\*Mortality fraction before spawning not found in the literature, assumed to be zero

Table SI CII.7 / 3: Further comments on usage of stock data

Stock	Metric	Comment
Northern Norwegian Coast	SSB-recruitment lag	official recruitment is at age 3 (ICES, 2023), but age classes contributing to the fished stock include age class 2, hence age-2 recruitment was used
Gulf of Maine	natural mortality	average from two different assumptions (NOAA, 2019) used



Gulf of Maine	stock numbers	average from assessment models conditioned with two different assumptions on natural mortality (NOAA, 2019) used
Gulf of Maine	fishing mortality	average from assessment models conditioned with two different assumptions on natural mortality (NOAA, 2019) used
Northern	weight in the catch (2014-2018)	no data available; instead, age-specific medians of 2009-2013 data from 2018 assessment report (Brattay et al., 2018) were used

### 8.8 SI CII.8: Estimating biomass reference points

Estimates of  $B_P$  were not available from the literature for a number of stocks from the Atlantic west coast. In these cases we calculated a custom  $B_P$  reference point using a common rule describing the relationship between  $B_{lim}$  and  $MSY B_{trigger}$  as employed in ICES benchmark assessments (ICES, 2021d) (eq. SI CII.8 / 1).

$$MSY B_{trigger} \approx B_{lim} e^{1.645\sigma}$$

Equation SI CII.8 / 1: Estimation of  $B_P$  from  $B_{lim}$  using the ICES rule (ICES, 2021d).  $\sigma$  was set to the ICES default of 0.2

Our estimates of  $B_P$  are listed in tab. SI CII.7 / 1.

## 8.9 SI CII.9: Historical trajectories of SSB

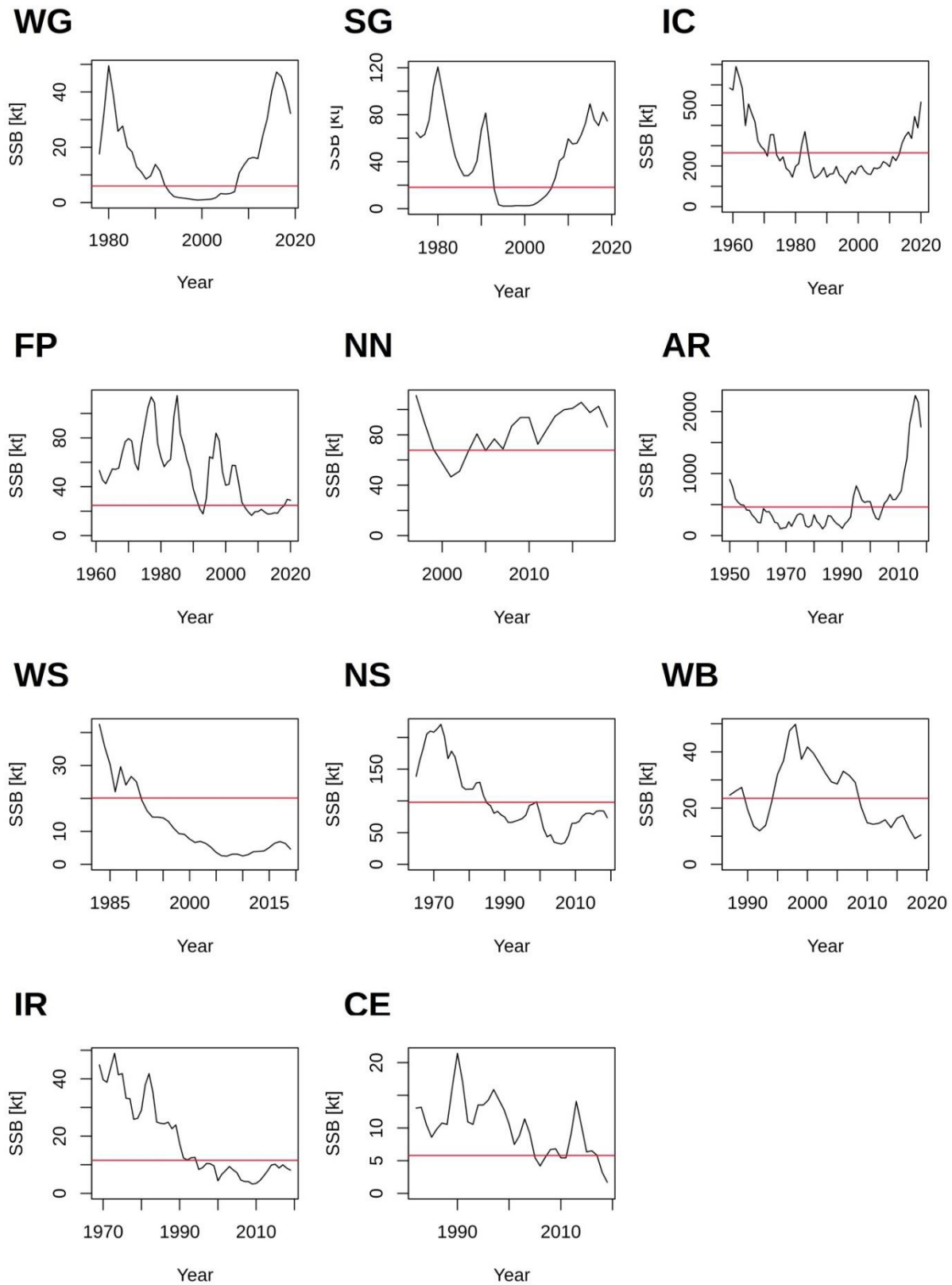


Figure SI CII.9 / 1: Historical trajectories of SSB of eastern-Atlantic and high-latitude cod stocks. Red line indicates  $B_P$  (or an approximation thereof). For stock abbreviations see fig. CII.1 in the main text

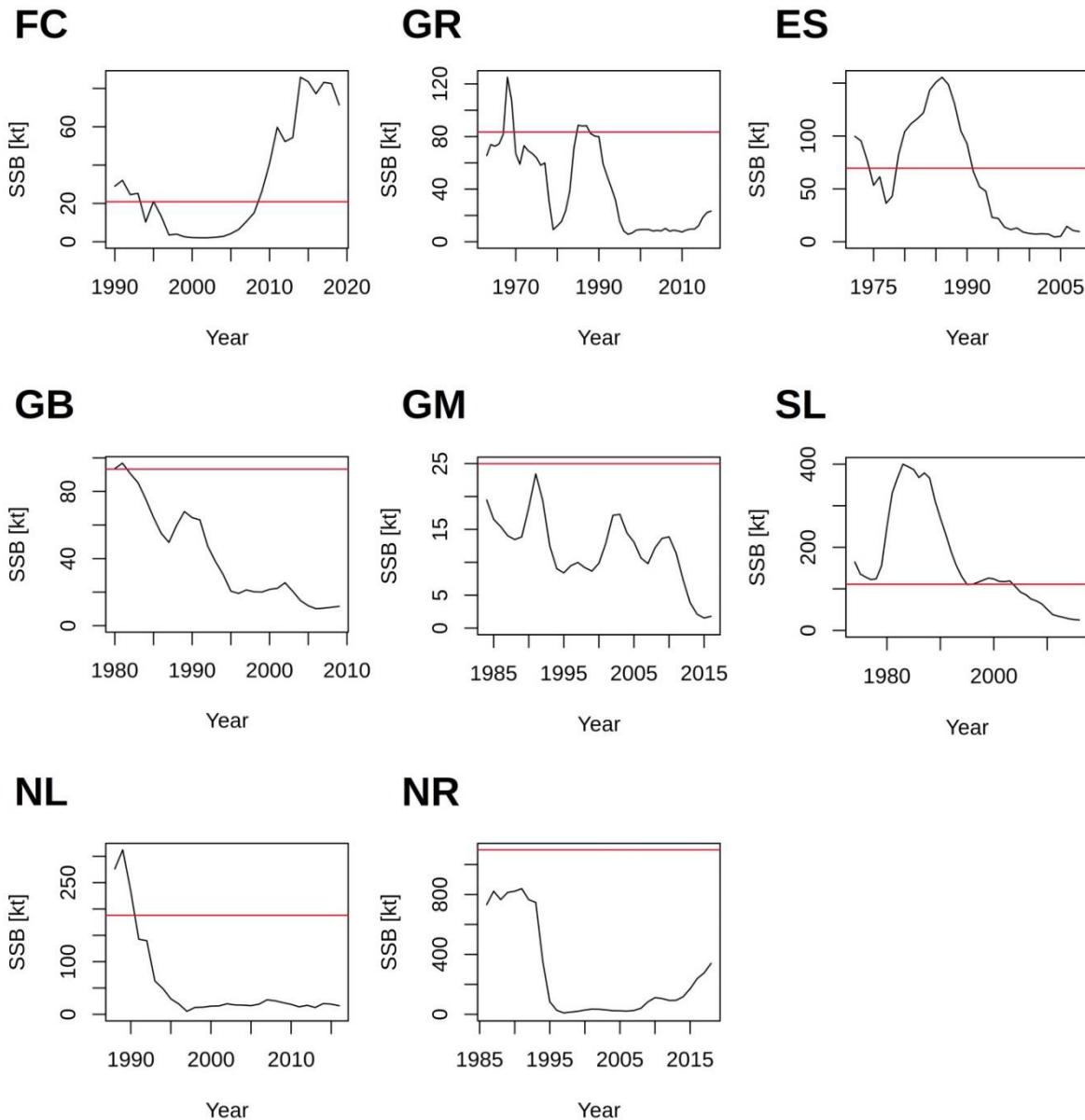


Figure SI CII.9 / 2: Historical trajectories of SSB of western-Atlantic cod stocks. Red line indicates  $B_p$  (or an approximation thereof). For stock abbreviations see fig. CII.1 in the main text

### 8.10 SI CII.10: Sources of stock data

Stock-specific biological- and catch data were obtained from recent quantitative assessments as reported by ICES, DFO, NOAA and NAFO, with the exception of Eastern Scotian Shelf cod, where outputs from an assessment model presented in a research publication were used (tab. SI CII.10 / 1). In some specific cases, additional information was obtained from the respective stock assessor. For some stocks, quantitative assessment was stopped at some point in the past. In these cases, we used the latest available quantitative assessment and projected the stock from the end of the assessment time series onward.

Table SI CII.10 / 2: Sources of stock-specific data

Stock	Source(s)
South-East Greenland	ICES NWWG assessment report 2022 (ICES, 2022a)
West Greenland	ICES NWWG assessment report 2022 (ICES, 2022a); ICES IBPGCod Report 2018 (ICES, 2018a); ICES stock annex (ICES, 2018b)
Iceland	ICES NWWG assessment report 2022 (ICES, 2022a), ICES stock annex (ICES, 2021b)
Faroe Plateau	ICES NWWG assessment report 2022 (ICES, 2022a), ICES Interbenchmark Protocol on Faroese demersal stocks (IBPFAR) (ICES, 2022b)
Northern Norwegian Coast	ICES AFWG report 2022 (ICES 2023)
North-East Arctic	Joint Russian-Norwegian Working Group on Arctic Fisheries Assessment Report 2022 (Howell et al., 2022)
West of Scotland	ICES WGCSE report 2022 (ICES 2022c)
North Sea	ICES WGNSSK assessment report 2022 (ICES, 2022d); ICES Benchmark Workshop on North Sea Stocks (WKNSEA) (ICES, 2021c)
Western Baltic	ICES WGBFAS assessment report 2022 (ICES, 2022e)
Irish	ICES WGCSE assessment report 2022 (ICES, 2022c), P. Schuchert (pers. comm.)
Celtic	ICES WGCSE assessment report 2022 (ICES, 2022c); ICES Benchmark Workshop on Celtic Sea stocks (WKCELTIC) (ICES, 2020a); ICES stock annex (ICES, 2020b)
Flemish Cap	NAFO assessment report 2022 (González-

	Troncoso et al., 2022); Diana González-Troncoso (Instituto Espanol de Oceanografia) (pers. comm.)
Georges Bank	NOAA Assessment report 2013 (Northeast Fisheries Science Center, 2013); Gary Shepherd (NOAA Fisheries) (pers. comm.)
Grand Banks	NAFO assessment report 2021 (Rideout et al., 2021)
Eastern Scotian Shelf	Swain & Mohn, 2012 (supplementary materials)
Gulf of Maine	NOAA Assessment update report 2019 (NOAA, 2019); NOAA Assessment report 2013 (NOAA, 2013); Charles Perretti (NOAA Fisheries) (pers. Comm.)
Southern Gulf of St. Lawrence	DFO assessment report 2019 (Swain et al., 2019)
Northern Gulf of St. Lawrence	DFO assessment report 2019 (Brassard et al., 2019)
Northern	DFO assessment report 2018 (Bratney et al., 2018); DFO advisory report 2022 (DFO, 2022); Paul Regular (DFO) (pers. comm.)

### 8.11 SI CII.11: Estimating range for future SST increase

We estimated the maximum level of SST increase to be implemented in our stock projections by determining the area-specific maximum SST increase (annual average over stock area) from CMIP6-climate-model output for scenarios SSP1-2.6 and SSP5-8.5 (Eyring et al., 2016; Riahi et al., 2017) relative to the historical maximum (within the temporal range of stock-assessment data) given by SST reconstructions (Huang et al., 2017). Climate models were selected for each area and emission scenario (tab. SI CII.11 / 1) according to lowest squared difference between CMIP6-model data and SST reconstructions. SST projections were bias-corrected (Maraun et al., 2016) by adding the median difference between CMIP6-model data and SST reconstructions for the period of overlap to the SST-projection data. Maximum SST

increase over all areas and emissions scenarios was estimated to be appx. 7 °C (fig. SI CII.11 / 1).

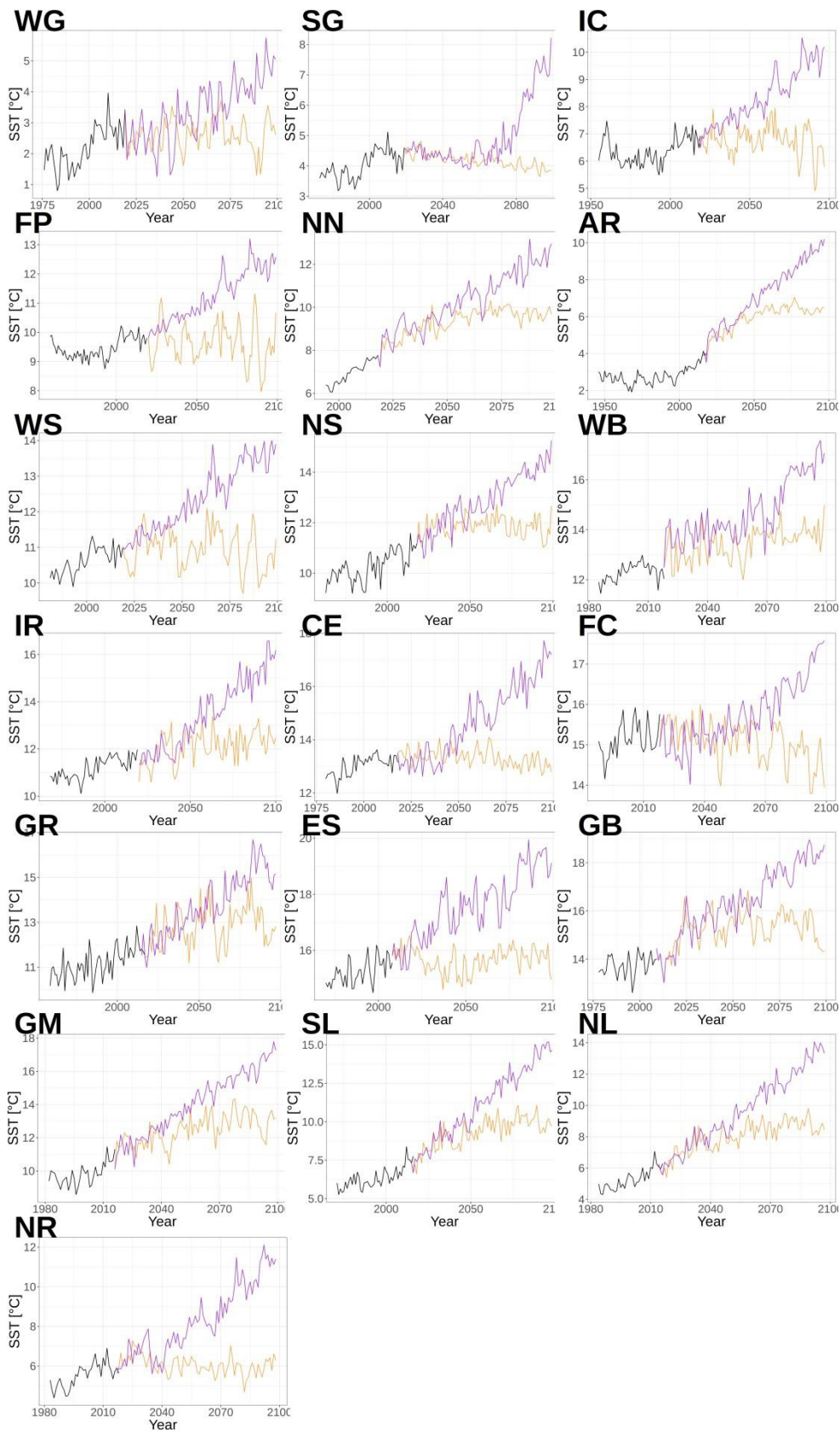


Figure SI CII.11 / 1: Trajectories of past (black) and projected future SST, for emissions scenarios SSP1-2.6 (orange) and SSP5-8.5 (purple). For stock abbreviations see fig. CII.1 in the main text

Table SI CII.11 / 2: Climate models chosen for the stock projections

Stock	Climate scenario	Climate model	Area of model data
West Greenland		MIROC-ES2L (Hajima et al., 2020)	NAFO division 1A-F
West Greenland		MIROC-ES2L (Hajima et al., 2020)	NAFO division 1A-F
South-East Greenland		GFDL-ESM4 (Dunne et al., 2020)	ICES subarea 14 and NAFO division 1F
South-East Greenland		CNRM-ESM2-1 (Séférian et al., 2019)	ICES subarea 14 and NAFO division 1F
Iceland		MIROC-ES2L (Hajima et al., 2020)	Subdivision Va
Iceland		GFDL-ESM4 (Dunne et al., 2020)	Subdivision Va
Faroe Plateau		MIROC-ES2L (Hajima et al., 2020)	Subdivision Vb1
Faroe Plateau		GFDL-ESM4 (Dunne et al., 2020)	Subdivision Vb1
Northern Norway		CanESM5 (Swart et al., 2019)	Coordinates 67-72 °N, 9-33 °E (appx. Norwegian catch reporting areas 0, 3, 4 and 5)
Northern Norway		CanESM5 (Swart et al., 2019)	Coordinates 67-72 °N, 9-33 °E (appx. Norwegian catch reporting areas 0, 3, 4 and 5)
Arctic	SSP1-2.6	CanESM5 (Swart et al., 2019)	ICES subareas 1 & 2; coordinates 67-80 °N, 10-50 °E (



			Sokolova et al., 2021)*
Arctic	SSP5-8.5	CanESM5 (Swart et al., 2019)	ICES subareas 1 & 2; coordinates 67-80 °N, 10-50 °E (Sokolova et al., 2021)*
West of Scotland		MIROC-ES2L (Hajima et al., 2020)	ICES division VIa
West of Scotland		GFDL-ESM4 (Dunne et al., 2020)	ICES division VIa
North Sea	SSP1-2.6	MIROC-ES2L (Hajima et al., 2020)	ICES subarea 4, division 7.d and division IIIa
North Sea	SSP5-8.5	MIROC-ES2L (Hajima et al., 2020)	ICES subarea 4, division 7.d and division IIIa
Western Baltic	SSP1-2.6	CNRM-ESM2-1 (Séférian et al., 2019)	ICES subdivisions 22-24
Western Baltic	SSP5-8.5	CNRM-ESM2-1 (Séférian et al., 2019)	ICES subdivisions 22-24
Irish		IPSL-CM6A-LR (Boucher et al., 2020)	ICES division VIIa
Irish		IPSL-CM6A-LR (Boucher et al., 2020)	ICES division VIIa
Celtic	SSP1-2.6	GFDL-ESM4 (Dunne et al., 2020)	ICES divisions 7.e-7.k
Celtic	SSP5-8.5	IPSL-CM6A-LR (Boucher et al., 2020)	ICES divisions 7.e-7.k
Flemish Cap	SSP1-2.6	GFDL-ESM4 (Dunne et al., 2020)	NAFO division 3M
Flemish Cap	SSP5-8.5	GFDL-ESM4 (Dunne et al., 2020)	NAFO division 3M
Grand Banks		MIROC-ES2L (Haji-	NAFO division

		ma et al., 2020)	3NO
Grand Banks		MIROC-ES2L (Hajima et al., 2020)	NAFO division 3NO
Eastern Scotian Shelf		GFDL-ESM4 (Dunne et al., 2020)	NAFO division 4VsW
Eastern Scotian Shelf		CNRM-ESM2-1 (Séférian et al., 2019)	NAFO division 4VsW
Georges Bank	SSP1-2.6	MIROC-ES2L (Hajima et al., 2020)	NAFO division 5Z
Georges Bank	SSP5-8.5	MIROC-ES2L (Hajima et al., 2020)	NAFO division 5Z
Gulf of Maine	SSP1-2.6	UKESM1-0-LL (Sel-lar et al., 2019)	NAFO division 5Y
Gulf of Maine	SSP5-8.5	GFDL-ESM4 (Dunne et al., 2020)	NAFO division 5Y
Southern Gulf of St. Lawrence		UKESM1-0-LL (Sel-lar et al., 2019)	NAFO division 4TVn
Southern Gulf of St. Lawrence		UKESM1-0-LL (Sel-lar et al., 2019)	NAFO division 4TVn
Northern Gulf of St. Lawrence		UKESM1-0-LL (Sel-lar et al., 2019)	NAFO divisions 3Pn and 4RS
Northern Gulf of St. Lawrence		UKESM1-0-LL (Sel-lar et al., 2019)	NAFO divisions 3Pn and 4RS
Northern	SSP1-2.6	MPI-ESM1.2-HR (Mauritsen et al., 2019)	NAFO divisions 2J and 3KL
Northern	SSP5-8.5	IPSL-CM6A-LR (Boucher et al., 2020)	NAFO division 2J3KL

\*Arctic cod inhabits a limited portion of ICES subareas 1 and 2 (F. Dahlke, pers. comm.), hence we limited the geographical area over which SST averages were computed

## 9. Supplementary material for the manuscript “Designing sustainable management strategies for Atlantic cod (*Gadus morhua* L.) under deep uncertainty via multi-objective optimization”

Jan Conradt<sup>1\*</sup>, Steffen Funk<sup>1</sup>, Christian Möllmann<sup>1</sup>

<sup>1</sup>Institute of Marine Ecosystem and Fishery Science, Universität Hamburg, Hamburg, Germany

\*Principal author

### 9.1 SI CIII.1: Population model

The population model used to project the stock is a classical numerical age-based population model as commonly used in fish stock assessments (Allen, 1975): Cohorts of equal-aged fish are projected through time, with the fish advancing through consecutive age classes and calendar years. Their numbers are reduced by natural- and fishing mortality (F), with the latter being the rate of instantaneous mortality caused by fisheries removals of individuals from the stock (eq. SI CIII.1 / 1, top). A plus group collects the individuals of maximum age in the model and older, and unlike with the lower age classes, both the pre-plus-group age class and the plus group from a given year supply their survivors to next year’s plus group (eq. SI CIII.1 / 1, middle). The number of age-1 fish, the youngest age class in the model, is predicted from the functional relationship between historical data of spawning biomass (SSB), sea-surface-temperature (SST) and recruitment (“recruitment” is an equal term for the number of fish in the youngest age class), the so-called stock-recruitment- (SR-) relationship (eq. SI CIII.1 / 1, bottom) (for more details on the SR relationship, see SI CIII.2). Predicted recruitment was capped at the maximum recruitment estimated by the assessment in order to avoid unrealistically high predictions.

$$\begin{aligned}N_{t+1,a+1} &= N_{t,a} e^{-(F_{t,a}+M_{t,a})} \text{ for } a \in [a_r, \dots, A-1] \\N_{t+1,a+1} &= N_{t,a} e^{-(F_{t,a}+M_{t,a})} + N_{t,a+1} e^{-(F_{t,a+1}+M_{t,a+1})} \text{ for } a = A-1 \\N_{t+1,a} &= f(SSB_t, SST_{t-1}) \text{ for } a = a_r\end{aligned}$$

Equation SI CIII.1 / 1: Equations of population dynamics for all age classes except plus group and recruitment age class (mortality equation, top), for the plus group (modified mortality equation, middle) and for the recruitment age class (stock-recruitment function, bottom). N = population number, F = fishing mortality, M = natural mortality, a = age class,  $a_r$  = age of recruitment, A = number of age classes / highest age class, SST = third-quarter sea-surface temperature, t = time (1 year)

SSB is the product of cohort abundance, individual weight and maturity rate, summed over all age classes for a given year (i.e. over all differently-aged cohorts existing in that year) (eq. SI CIII.1 / 2). In our projections, we assumed age-specific individual weights and maturity rates to be constant (equaling the estimates of the 2021 stock assessment [ICES, 2021e ]) throughout all projection years.

$$SSB_t = \sum_{a=1}^A N_{t,a} w_a^s m_a$$

Equation SI CIII.1 / 2: Calculation of spawning-stock biomass (SSB). N = stock numbers,  $w^s$  = weight in the stock, m = maturity rate, a = age class, A = number of age classes

Age-specific catch in numbers is the number of fish in a given age class in a given year, reduced by the number of survivors to the next year (i.e. the number of dead fish), multiplied with the ratio of fishing mortality to total (natural- and fishing-) mortality (eq. SI CIII.1 / 3). Total catch in weight (also termed yield) is the product of age-specific catch in numbers multiplied with individual weight, summed over all age classes (eq. SI CIII.1 / 4). Note that specific individual weights-in-the-catch are used, which were also taken from stock-assessment data (ICES, 2021e ) and assumed to be constant through time.

$$C_{t,a}^N = \frac{F_{t,a}}{F_{t,a} + M_{t,a}} N_{t,a} (1 - e^{-(F_{t,a} + M_{t,a})})$$

Equation SI CIII.1 / 3: Catch equation.  $C^N$  = catch in numbers, N = stock numbers, F = fishing mortality, M = natural mortality, a = age class, t = time (1 year)

$$C_t^W = \sum_{a=1}^A C_{t,a}^N w_a^c$$

Equation SI CIII.1 / 4: Calculation of total catch in weight.  $C^W$  = total catch in weight,  $C^N$  = catch in numbers,  $W^C$  = weight in the catch, a = age class, A = number of age classes, t = time (in years)

The population model was initialized with start-of-the-year population numbers and SSB of 2021 (ICES, 2021e), and with age-specific weights in the stock, weights in the catch, maturity rates and natural mortalities set to the 2021 estimates (ICES, 2021e). The first predicted population numbers are thus the 2022 population numbers.

## 9.2 SI CIII.2: Stock-recruitment relationship

A classical environmental Beverton-Holt function (Beverton & Holt, 1957; Hilborn & Walters, 1992) was used to model the relationship between SSB, SST and recruitment (eq. SI CIII.2 / 1). The Beverton-Holt function assumes that recruitment increases linearly with SSB, but that density-related limitations lead to the approach of an asymptotic approach of maximum recruitment (this is expressed through a second parameterized effect of SSB). SST either limits or promotes recruitment through an exponential effect, with the direction depending on the data to which the function is fitted.

$$R_{t+1} = N_{t+1,1} = e^{\gamma SST_{t-1}} \frac{\alpha SSB_t}{1 + \beta SSB_t}$$

Equation SI CIII.2 / 1: Environmental Beverton-and-Holt (Hilborn & Walters, 1992) stock-recruitment-model equation. R = recruitment, N = population number, SSB = spawning-stock biomass, SST = third-quarter sea-surface temperature

The Beverton-Holt function was re-arranged to a linearized and logarithmized form (eq. SI CIII.2 / 2), which eases the numerical fitting process and prevents an estimation of negative SSB-related parameters, which are biologically meaningless (eq. SI CIII.2 / 2). The “nlminb” optimizer from the R (R Core Team, 2020) package “minpack.lm” (Elzhov et al., 2016) was used to fit the SR function to the SSB- and recruitment data from the ICES stock assessment (ICES, 2021e ), and to a time series of reconstructed SST in the western Baltic Sea (Lehmann & Hinrichsen, 2000; Lehmann et al., 2002; Lehmann et al., 2014). We here used SST (temperature of the uppermost three meters) reconstructions from the third quarter of the year, averaged over the entire western Baltic Sea, and imposed a two-year lag between SST and recruitment. SST thus affects adult individuals, i.e. spawners, rather than the pre-recruits directly. In warm summers (i.e. quarter-three months), Western Baltic cod limit their distributions to deep waters that are deficient of food, which negatively affects their condition and likely their reproductive capacity (Funk, 2020; Funk et al., 2020, 2021; Receveur et al., 2022).

$$\log(R_{t+1}) = -\gamma SST_{t-1} + \alpha' + \log(SSB_t) - \log(1 + e^{\beta' + \log(SSB_t)})$$

where  $\alpha' = \log(\alpha)$  and  $\beta' = \log(\beta)$

Equation SI CIII.2 / 2: linearized environmental Beverton-and-Holt stock-recruitment-model equation. R = recruitment, SSB = spawning-stock biomass, SST = third-quarter sea-surface temperature

SR relationships usually have only a weak fit on the data, as is the case for Western Baltic cod; furthermore, the relationship can change through time, reflective of different regimes of productivity (Sguotti et al., 2019), and especially environment-recruitment relationships are highly spurious (Myers et al. 1998) and can lead to undesirable management outcomes (Free et al., 2022). These characteristics likely disable reliable projections using single assumptions about the SR relationship, and to address this constraint, we fitted several SR relationships on segments of the historical time series of various lengths (while imposing a lower limit of ten years to ensure a minimum level of predictive robustness). We then pooled the parameter values estimated for all SR relationships, and, in order to avoid weighing the parameterizations for the more frequent shorter time segments, sampled evenly from the minimum to the maximum estimate over all relationships, for each of the three SR parameters. As parameter values of the three parameters, especially of the linear SSB-related parameter and of the SST-related parameter, were found to be strongly correlated, we generated a set of SR parameterizations where for each sampled value for one of the three parameters we assigned those “observed” parameter values to the other two parameters that corresponded to the SR relationship closest to the sample in Euclidean distance in terms of the sampled parameter (i.e., for a given sample of  $\log(\alpha)$ , we set  $\log(\beta)$  and  $\gamma$  to the values corresponding to the SR relationship whose  $\log(\alpha)$  value was closest to the sampled  $\log(\alpha)$ ). In total, we thus obtained 90 different SR parameterizations (based on 30 samples per parameter) that strongly differed in recruitment strength per kg SSB and recruitment strength per °C SST (fig. SI CIII.8 / 1).

### **9.3 SI CIII.3: Recurrent neural network**

The recurrent neural network (RNN) followed the design of the classic “long short-term memory” (LSTM) cell (Hochreiter & Schmidhuber, 1997). We employed a relatively simple design with a single LSTM cell predicting  $F$  from standardized input data (SSB and catch in the previous year, standardized with respect to the historical time series data [from the 2021 stock assessment {ICES, 2021e}]) and the hidden state of the LSTM cell at the previous time step (initialized to a value of 1.0 at the first time step) (eq. SI CIII.3 / 1). Different from the original LSTM conception, we utilized only sigmoid activation functions instead of a mixture of sigmoid and tanh activation functions, as we noticed a better optimization performance with the former set-up.

$$\begin{aligned}
f_{t,s} &= \frac{1}{1 + e^{-(\alpha_t^f + \beta_t^f SSB_{t,s}^* + \gamma_t^f C_{t-1,s}^* + \delta_t^f + \varepsilon_t^f h_{t-1,s})}} \\
i_{t,s} &= \frac{1}{1 + e^{-(\alpha_t^i + \beta_t^i SSB_{t,s}^* + \gamma_t^i C_{t-1,s}^* + \delta_t^i + \varepsilon_t^i h_{t-1,s})}} \\
o_{t,s} &= \frac{1}{1 + e^{-(\alpha_t^o + \beta_t^o SSB_{t,s}^* + \gamma_t^o C_{t-1,s}^* + \delta_t^o + \varepsilon_t^o h_{t-1,s})}} \\
\hat{c}_{t,s} &= \frac{1}{1 + e^{-(\alpha_t^{\hat{c}} + \beta_t^{\hat{c}} SSB_{t,s}^* + \gamma_t^{\hat{c}} C_{t-1,s}^* + \delta_t^{\hat{c}} + \varepsilon_t^{\hat{c}} h_{t-1,s})}} \\
c_{t,s} &= f_{t,s} c_{t-1,s} + i_{t,s} \hat{c}_{t,s} \\
h_{t,s} &= o_{t,s} \frac{1}{1 + e^{-c_{t,s}}}
\end{aligned}$$

where  $SSB_{t,s}^* = \frac{SSB_{t,s} - \mu_{SSB[1985, \dots, 2020]}}{\sigma_{SSB[1985, \dots, 2020]}}$

and  $C_{t,s}^* = \frac{C_{t,s} - \mu_{C[1985, \dots, 2020]}}{\sigma_{C[1985, \dots, 2020]}}$

Equation SI CIII.3 / 1: Mathematical graph of the RNN.  $\alpha$ ,  $\beta$ ,  $\gamma$ ,  $\delta$  and  $\varepsilon$  are optimizable parameters.  $f$ ,  $i$ ,  $o$ ,  $\hat{c}$ ,  $c$  and  $h$  are intermediate calculations, whereby  $c$  and  $h$  represent “hidden states” of the RNN that also represent inputs at the subsequent time step.  $SSB$  = spawning-stock biomass,  $SSB^*$  =  $SSB$  standardized by mean ( $\mu_{SSB}$ ) and standard deviation ( $\sigma_{SSB}$ ) of  $SSB$  over the period 1985-2020.  $C$  = catch (total, in weight),  $C^*$  = catch standardized by mean ( $\mu_C$ ) and standard deviation ( $\sigma_C$ ) of catch over the period 1985-2020.  $s$  = replicate for one SR parameterization,  $t$  = time (1 year)

The RNN predicted a value between zero and one ( $h_{t,s}$  in eq. SI CIII.3 / 1). An average over the predictions for all SR parameterizations (i.e. for the varying  $SSB$ - and catch inputs resulting from these parameterizations) was calculated and multiplied with the maximum  $F$  (set to  $F_{MSY} = 0.26$ ) in order to yield an  $F$  prediction between zero and 0.26 (eq. SI CIII.3 / 2).

$$F_{t,bar} = F_{MSY} \frac{1}{S} \sum_{s=1}^S h_{t,s}$$

Equation SI CIII.3 / 2: Calculation of  $F_{bar}$ .  $h$  = output of the RNN,  $s$  = replicate for one SR parameterization,  $S$  = number of SR parameterizations,  $t$  = time (1 year)

#### 9.4 SI CIII.4: Calculating age-specific $F$ from $F_{bar}$

$F_{bar}$  is the average  $F$  over the most strongly fished age classes, in the case of Western Baltic cod these are age classes 3-5 (ICES, 2021e). The population model requires age-specific  $F$  values. We multiplied the predicted  $F_{bar}$  with the ratio of the 2021  $F$  values for age classes 3-

5 to the 2021 F<sub>bar</sub> to obtain predicted age-specific F values for these age classes (eq. SI CIII.4 / 1, top). For the remaining age classes, we calculated age-specific F predictions as the product of the F prediction for age class 4 and the ratio of the age-specific 2021 F values to the 2021 F of age class 4 (eq. SI CIII.4 / 1, bottom).

$$F_{t,a} = F_{t,bar} \frac{F_{2021,a}}{F_{2021,bar}} \text{ for } a \in [3,4,5]$$

$$F_{t,a} = F_{t,4} \frac{F_{2021,a}}{F_{2021,4}} \text{ for } a \in [1,2,6,7+]$$

Equation SI CIII.4 / 1: Calculation of age-specific F from F<sub>bar</sub>. a = age class, t = time (1 year)

### 9.5 SI CIII.5: Adam optimizer

We invoked the Adam optimization algorithm (Kingma & Ba, 2014), the state-of-the art optimizer for neural networks, to implement the gradient-decent-based parameter updates between consecutive optimization steps (eq. SI CIII.5 / 1).

$$\mathbf{m}_i = \beta_1 \mathbf{m}_{i-1} + (1 - \beta_1) \nabla f_i$$

$$\mathbf{v}_i = \beta_2 \mathbf{v}_{i-1} + (1 - \beta_2) \nabla f_i^2$$

$$\hat{\mathbf{m}}_i = \frac{\mathbf{m}_i}{1 - \beta_1^i}$$

$$\hat{\mathbf{v}}_i = \frac{\mathbf{v}_i}{1 - \beta_2^i}$$

$$\mathbf{P}_{i+1} = \mathbf{P}_i - \frac{\lambda \hat{\mathbf{m}}_i}{\sqrt{\hat{\mathbf{v}}_i + \varepsilon}}$$

where  $\mathbf{P} = \begin{bmatrix} p_{1,1} & \dots & p_{1,T} \\ \vdots & \ddots & \vdots \\ p_{N,1} & \dots & p_{N,T} \end{bmatrix}$

Equation SI CIII.5 / 1: Adam optimizer implemented after Kingma & Ba (2014).  $\nabla f$  = RNN gradients,  $\mathbf{P}$  = RNN parameters, i = iteration,  $\lambda$  = learning rate,  $\mathbf{m}$ ,  $\mathbf{v}$ ,  $\beta_1$ ,  $\beta_2$ ,  $\hat{\mathbf{m}}$ ,  $\hat{\mathbf{v}}$  and  $\varepsilon$  = optimizer hyper-parameters.  $\mathbf{m}$  and  $\mathbf{v}$  were initialized to zeros,  $\beta_1$  and  $\beta_2$  were set to  $10^{-3}$ ,  $\lambda$  was set to 0.05,  $\varepsilon$  was set to  $10^{-10}$ . N = number of parameters within one LSTM cell. t = time step (1 year), T = number of time steps

We used an independent set of RNN parameters for each time step in order to allow full flexibility for the optimization F for each time step.



We did not formally check for convergence of the optimization (e.g. via analysis of the Hessian matrix), as our aim was not a mathematically exact optimization but rather an investigation into the potential for machine-based design of a management pathway towards management objectives. We did check for reduction and stabilization of the loss over iterations (fig. CIII.6 in the main text).

## 9.6 SI CIII.6: Optimization rule

We invoked a rule describing the contribution of the two objective metrics (SSB and catch) to the model loss, in order to guide the parameter optimization: The ratio of SSB(t) to  $B_P$  for a time step t was added to the loss whenever it was less than 1. The ratio of catch(t-1) to the target catch level was added to the loss whenever it was less than 1 and SSB was larger than  $B_P$  (eq. SI CIII.6 / 1).

$$\begin{aligned}
 l_{t,s}^{sust} &= \frac{1}{S} \frac{B_P}{SSB_{t,s}} |SSB_{t,s} \leq B_P \\
 l_{t,s}^{sust} &= 0 |SSB_{t,s} > B_P \\
 l_{t,s}^{catch} &= \frac{1}{S} \frac{C_{target}^w}{C_{t-1,s}^w} | (C_{t-1,s}^w < C_{target}^w \ \& \ SSB_{t,s} > B_P) \\
 l_{t,s}^{catch} &= 0 | (C_{t-1,s}^w \geq C_{target}^w | (C_{t-1,s}^w < C_{target}^w \ \& \ SSB_{t,s} \leq B_P)) \\
 l &= \sum_{s=1}^S \sum_{t=1}^T l_{t,s}^{sust} + l_{t,s}^{catch}
 \end{aligned}$$

Equation SI CIII.6 / 1: Calculation of sustainability loss ( $l^{sust}$ ), catch loss ( $l^{catch}$ ) and total loss ( $l$ ).  $c_{target}^w$  = target catch,  $c^w$  = catch (total over age classes, in weight),  $s$  = one SR parameterization,  $S$  = number of SR parameterizations,  $t$  = time step (1 year),  $T$  = number of time steps

This rule was applied in order to make optimization for catch objectives conditional on a stock in biologically safe levels, and to avoid optimization to excessively large SSB levels at cost of reaching target catch.

## 9.7 SI CIII.7: Risk calculation

For the analysis of the performance of the optimized F time series towards the two management objectives, we calculated both the risk of SSB being equal to or less than  $B_P$  (risk of missing the precautionary threshold / of unsustainable management; “sustainability risk”) and the risk of catch being less than target catch (risk of not achieving harvest aims;

“catch risk”). This was achieved by calculating the ratio between the number of SR parameterizations yielding unwanted outcomes and the total number of SR parameterizations for each time step (eq. SI CIII.7 / 1).

$$\begin{aligned}
 o_{t,s}^{sust} &= 1 | SSB_{t,s} \leq B_P \\
 o_{t,s}^{sust} &= 0 | SSB_{t,s} > B_P \\
 o_{t,s}^{catch} &= 1 | C_{t-1,s}^w < C_{target}^w \\
 o_{t,s}^{catch} &= 0 | C_{t-1,s}^w \geq C_{target}^w \\
 r_t^{sust} &= \frac{1}{S} \sum_{s=1}^S o_{t,s}^{sust} \\
 r_t^{catch} &= \frac{1}{S} \sum_{s=1}^S o_{t,s}^{catch}
 \end{aligned}$$

Equation SI CIII.7 / 1: Calculation of sustainability risks (rsust) and catch risk (rcatch).  $o^{sust}$  = binary sustainability outcome (SSB exceeding  $B_P$  or not),  $o^{catch}$  = binary catch outcome (catch equaling or exceeding target catch or not),  $c_{target}^w$  = target catch,  $c^w$  = catch (total over age classes, in weight),  $s$  = one SR parameterization,  $S$  = number of SR parameterizations,  $t$  = time step (1 year)

### 9.8 SI CIII.8: Partial effects of fitted SR models

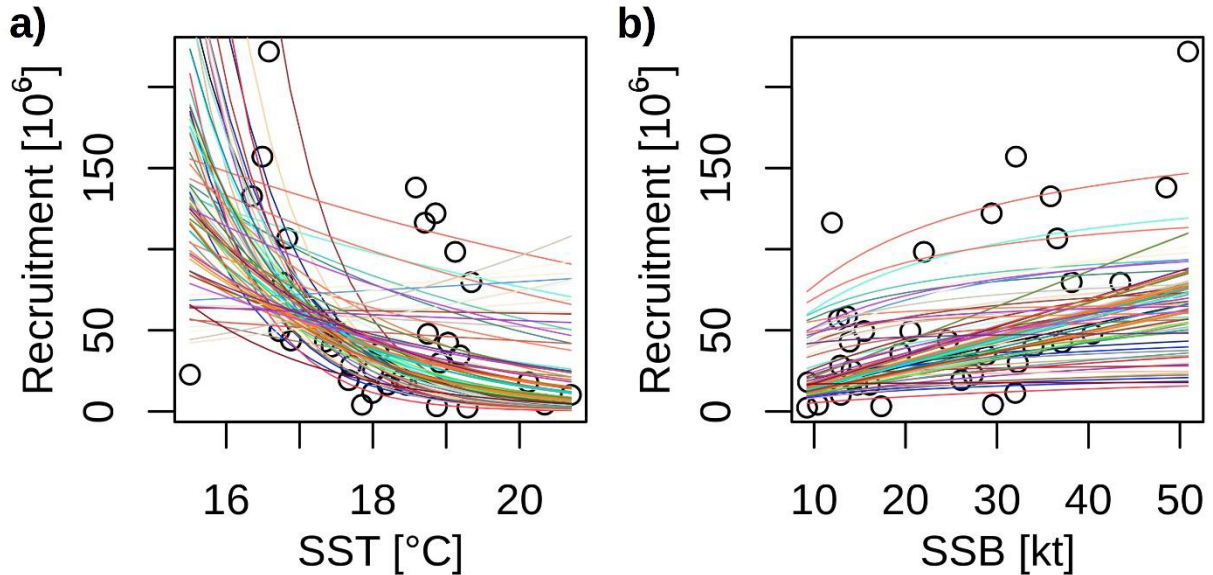


Figure SI CIII.8 / 1: Partial effects of SST (a) and SSB (b) on recruitment in the various SR relationships fitted on subsets of the historical time series of data

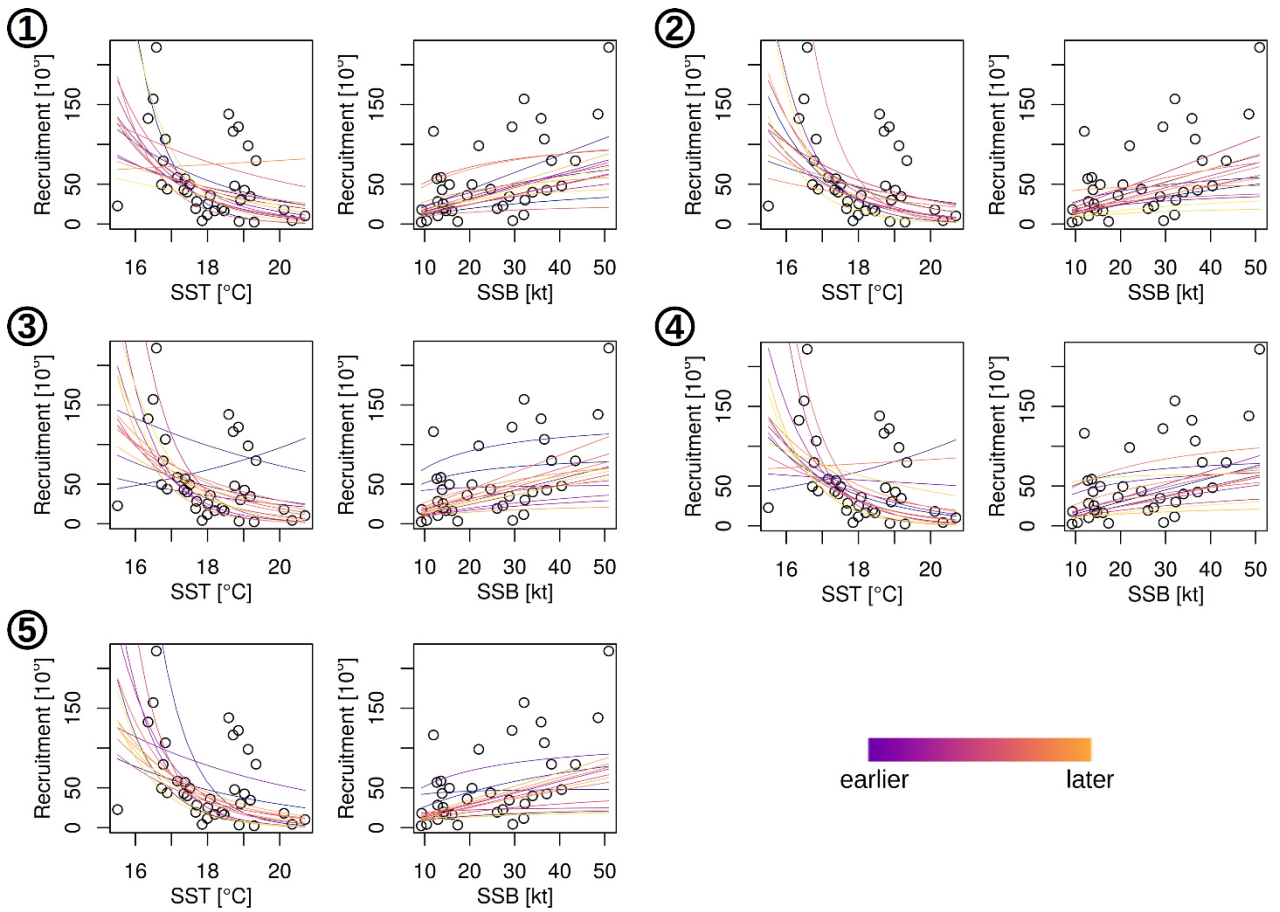


Figure SI CIII.8 / 2: Partial effects of SST (a) and SSB (b) on recruitment in the random SR relationships forming the “ground truth” time series in the management-application test of the optimization methodology. Color denotes appearance within the time series. Numbers indicate replicate

### 9.9 SI CIII.9: Optimization trajectories

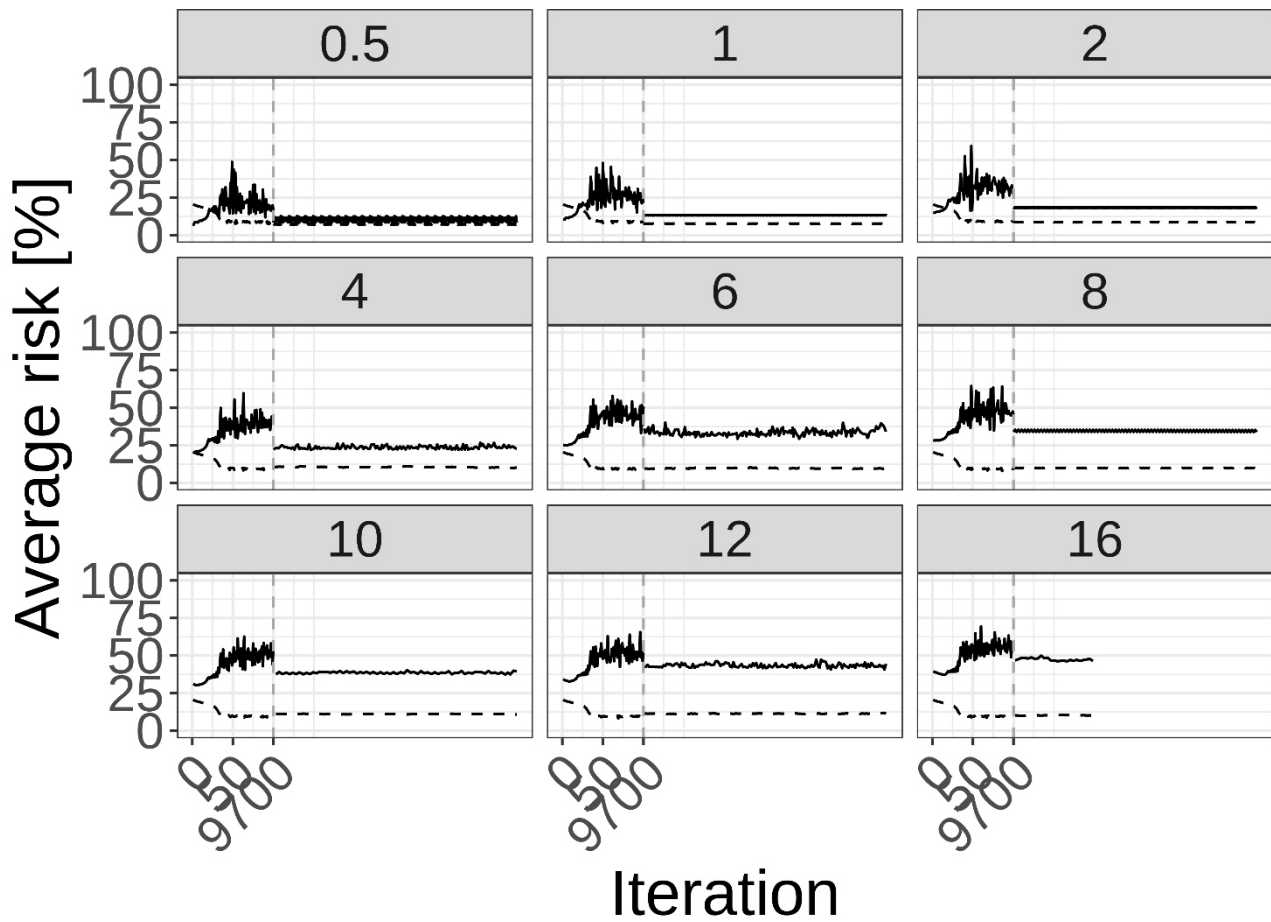


Figure SI CIII.9 / 1: Trajectories of average risk over iterations of optimization for all levels of target catch. Iterations 1-100 and 9700-10000 are shown

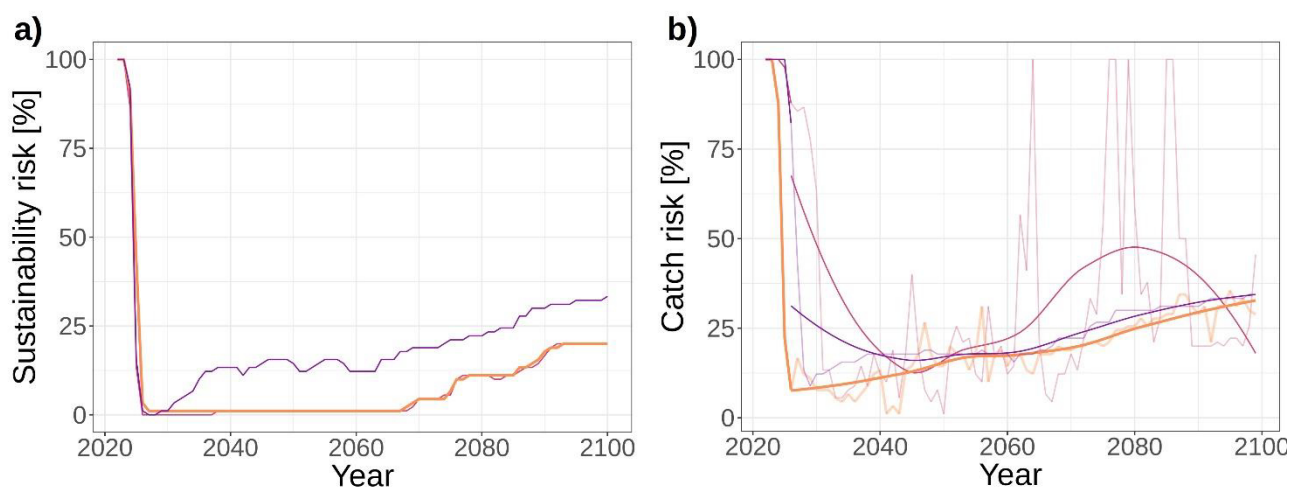


Figure SI CIII.9 / 2: Trajectories of sustainability risk (a) and catch risk (b) resulting from the optimized fishing-mortality trajectories after 1 (purple), 150 (red) and 10000 iterations (orange) of optimization (see also fig. CIII.6 in the main text). Solid lines in (b) show smoothed trajectories, transparent lines show actual trajectories

## 9.10 SI CIII.10: Comparison of optimization approaches

Optimization of the F time series could be conducted in simpler ways than by utilizing an RNN as done here, e.g. by replacing the RNN with a relatively simple logistic model where F is directly predicted from SSB, catch and the prediction for the previous year (eq. SI CIII.10 / 1), or by predicting F directly from an optimizable parameter (eq. SI CIII.10 / 2).

$$h_{t,s} = \frac{1}{1 + e^{-(\alpha_t + \beta_t SSB_{t,s}^* + \gamma_t C_{t-1,s}^* + \delta_t + \varepsilon_t h_{t-1,s})}}$$

$$F_{t,bar} = F_{MSY} \frac{1}{S} \sum_{s=1}^S h_{t,s}$$

Equation SI CIII.10 / 1: Structure of simpler logistic model (top) and prediction of  $F_{bar}$  from the model output  $h$ .  $\alpha$ ,  $\beta$ ,  $\gamma$ ,  $\delta$  and  $\varepsilon$  are optimizable parameters.  $SSB^*$  = standardized spawning-stock biomass,  $C^*$  = standardized catch (total, in weight) (for both see eq. SI CIII.3 / 1 for details).  $s$  = one SR parameterization,  $S$  = number of SR parameterizations

$$F_{t,bar} = F_{MSY} \frac{1}{1 + e^{-\alpha_t}}$$

Equation SI CIII.10 / 2: Direct prediction of  $F_{bar}$  from logistic “activation” of optimizable parameter  $\alpha$ . Note the lack of any state variable in the “model”

We found that the optimized F trajectories were similar between the approaches, but that F was maintained at a higher level until appx. 2060 in the RNN approach (fig. SI CIII.10 / 1). This resulted in markedly reduced catch risk from the mid-2020s until the mid-2040s in that approach. Sustainability risk was highly similar between all three approaches.

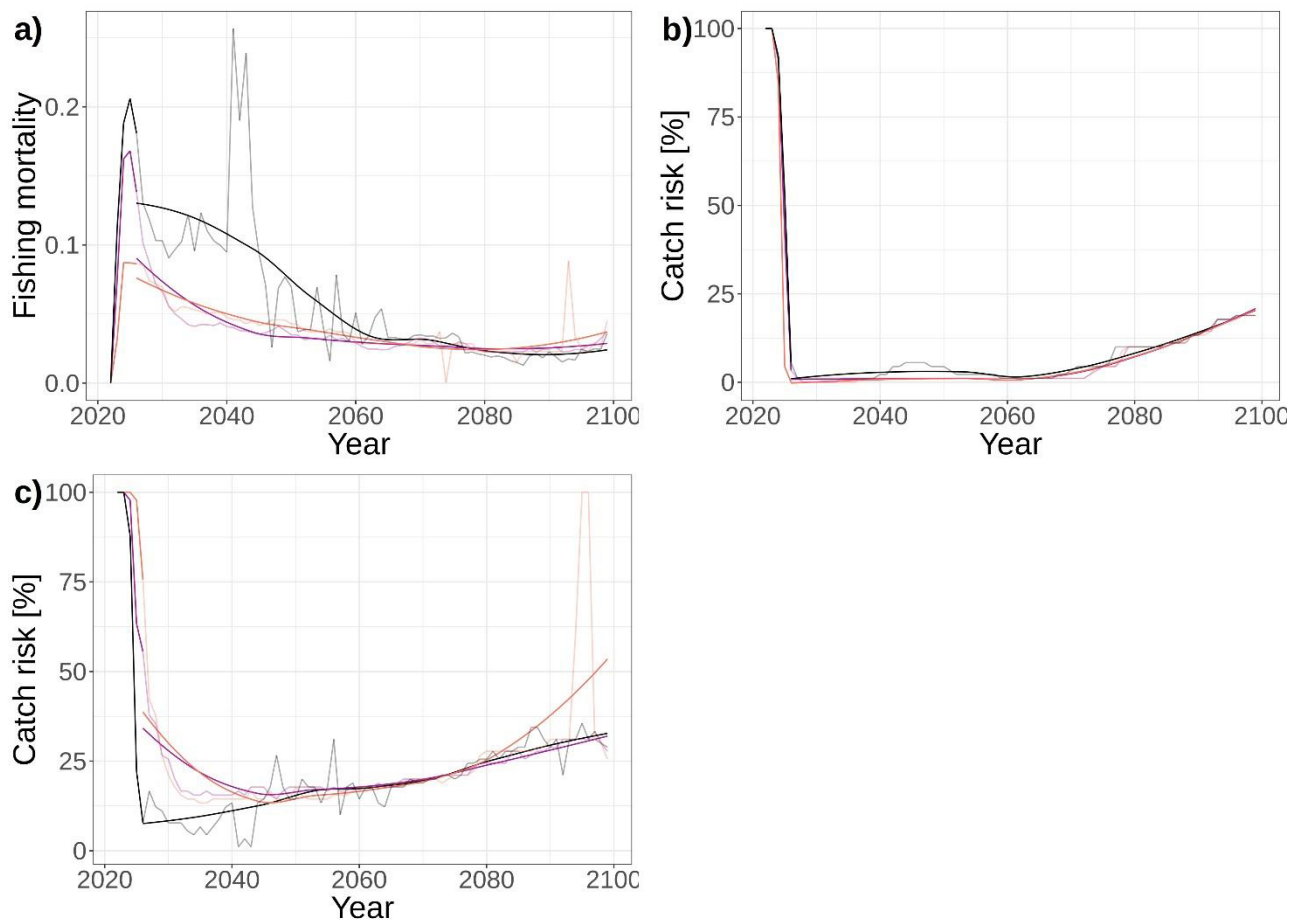


Figure SI CIII.10 / 1: Comparison of optimization procedures in terms of optimized trajectories of  $F$  (a) and resulting trajectories of sustainability risk (b) and catch risk (c). Black line represents optimization via RNN, orange line represents optimization with simpler model, purple line represents direct optimization of  $F$ . Solid lines show smoothed trajectories, transparent lines show actual trajectories

We conclude that utilization of an RNN might be able to generate better trade-offs between sustainability- and harvest objectives, which could possibly be more pronounced in more complex or data-driven models. In our case, the higher number of parameters in the RNN did lead to longer, but not excessively long computing times, suggesting that the selection of the RNN over the simpler approaches is reasonable.

### 9.11 SI CIII.11: Biological constants used in the model

Table SI CIII.11 / 1: biological constants used in the population model

parameter ↓ / age class →	1	2	3	4	5	6	7+
natural mortality	0.598	0.411	0.324	0.274	0.241	0.218	0.201
weight in the stock	0.057	0.379	0.933	2.122	3.112	4.221	6.184
weight in the catch	0.353	0.693	1.277	1.593	2.736	3.946	6.558
maturity ogive	0.06	0.6	0.84	0.86	0.90	0.94	1.00
initial population (for first time step)	18033	5355	1004	193	1756	28	35
fishing mortality (reference for selectivity)	0.054	0.286	0.701	0.882	1.064	1.064	1.064

9.12 SI CIII.12: SST time series projected for RCP8.5 scenario

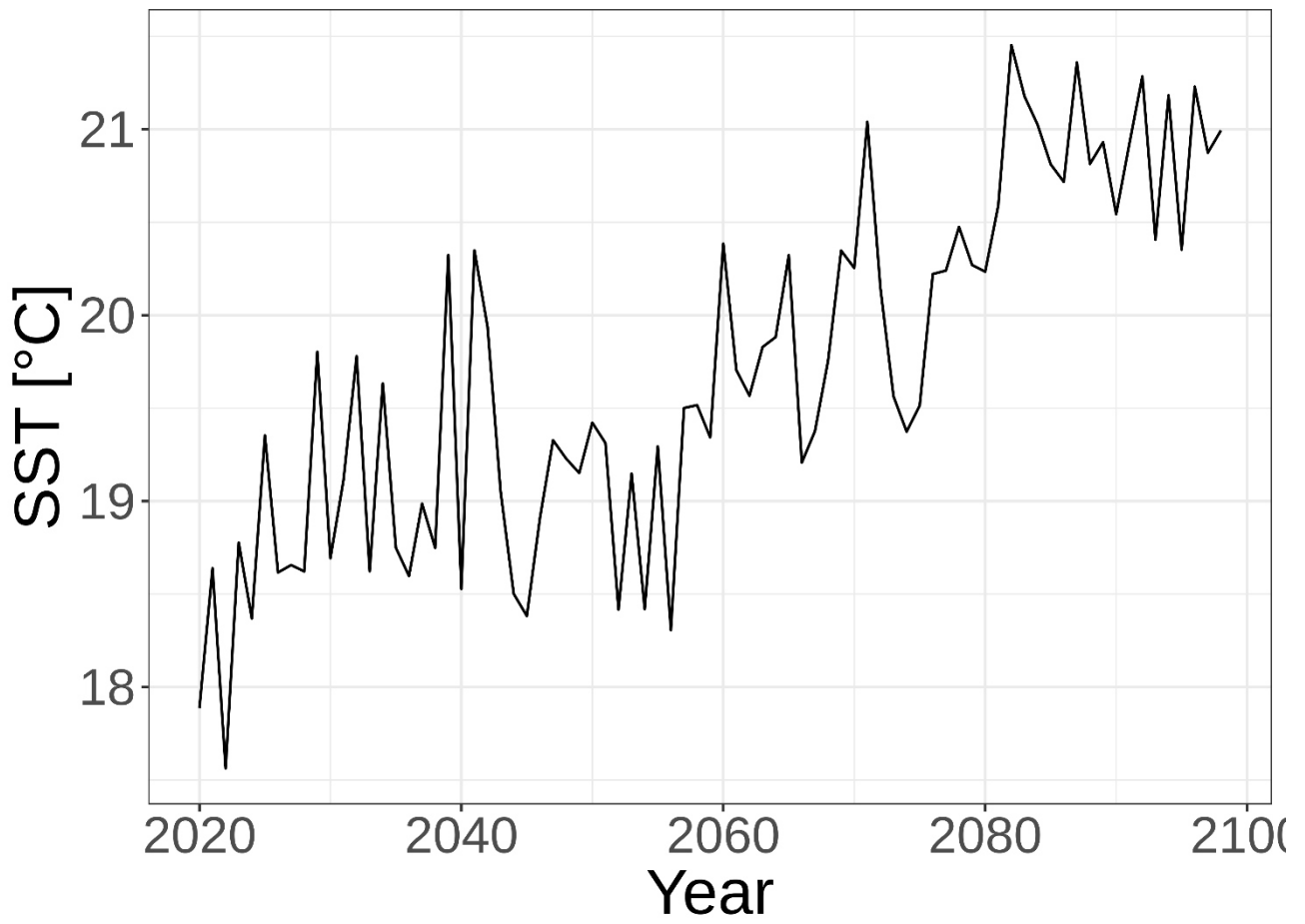


Figure SI CIII.12 / 1: Trajectory of western-Baltic SST projected for the RCP8.5 scenario



### 9.13 SI CIII.13: Development of risk trajectories over optimization instances in management simulation

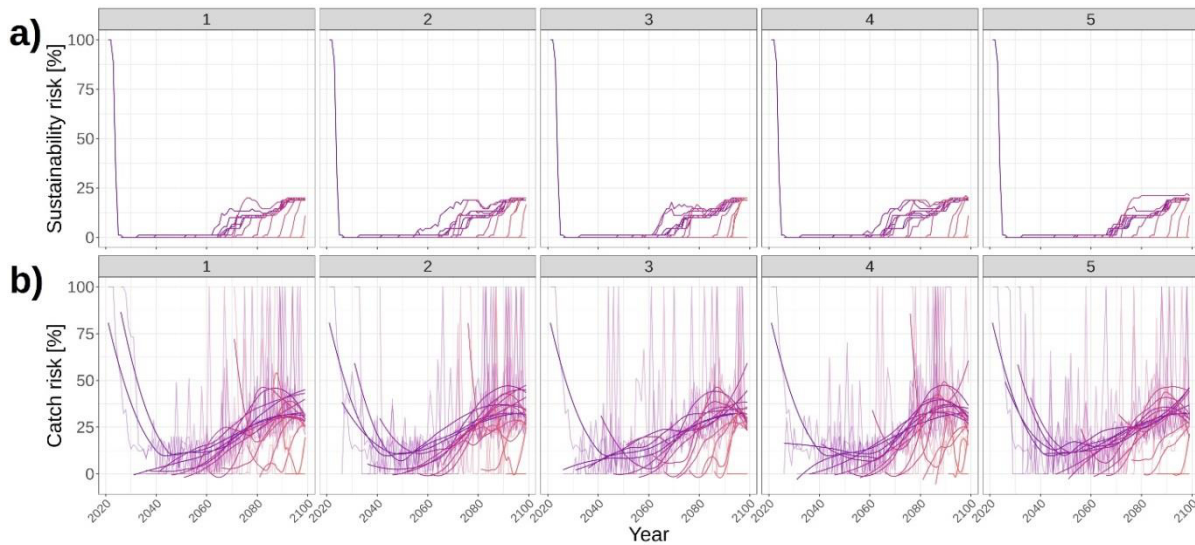


Figure SI CIII.13 / 1: Development of trajectories of sustainability risk (a) and catch risk (b) over optimization instances in management simulation. Color denotes optimization instance, with brighter colors denoting later instances (conducted later within the simulation time series and thus leading to shorter risk time series covering the remaining years yet to be simulated). In (b), bold lines represent smoothed trends, transparent lines show actual trajectories

### 9.14 SI CIII.14: Validation of the effect of smoothed optimized F on SSB and catch

Smoothed trajectories (smoothed via Loess smoother [Cleveland et al., 1992] in base R [R Core Team, 2020]) of optimized F are shown in fig. CIII.7 and discussed in the main text. To validate whether the smoothed trajectories have a comparable effect on the SSB- and catch trajectories as the original (non-smoothed) F trajectories, we ran a population projection with the smoothed F trajectories as input (all other model inputs were left unchanged compared to the optimization runs). We replaced the first smoothed F value with the first actual optimized F value, as the smoothing operation eliminated the distinct first year where F was optimized to be close to zero in order to enable the fast stock rebuilding.

We found that the SSB- and catch trajectories resulting from the use of the smoothed F trajectories in the projection were overall very similar in dynamics and magnitude to the original ones obtained from the actual optimized F trajectories (fig. SI CIII.14 / 1). Especially the smoothed SSB- and catch trajectories showed very marginal differences when comparing the outputs generated with the original and the smoothed F trajectories.

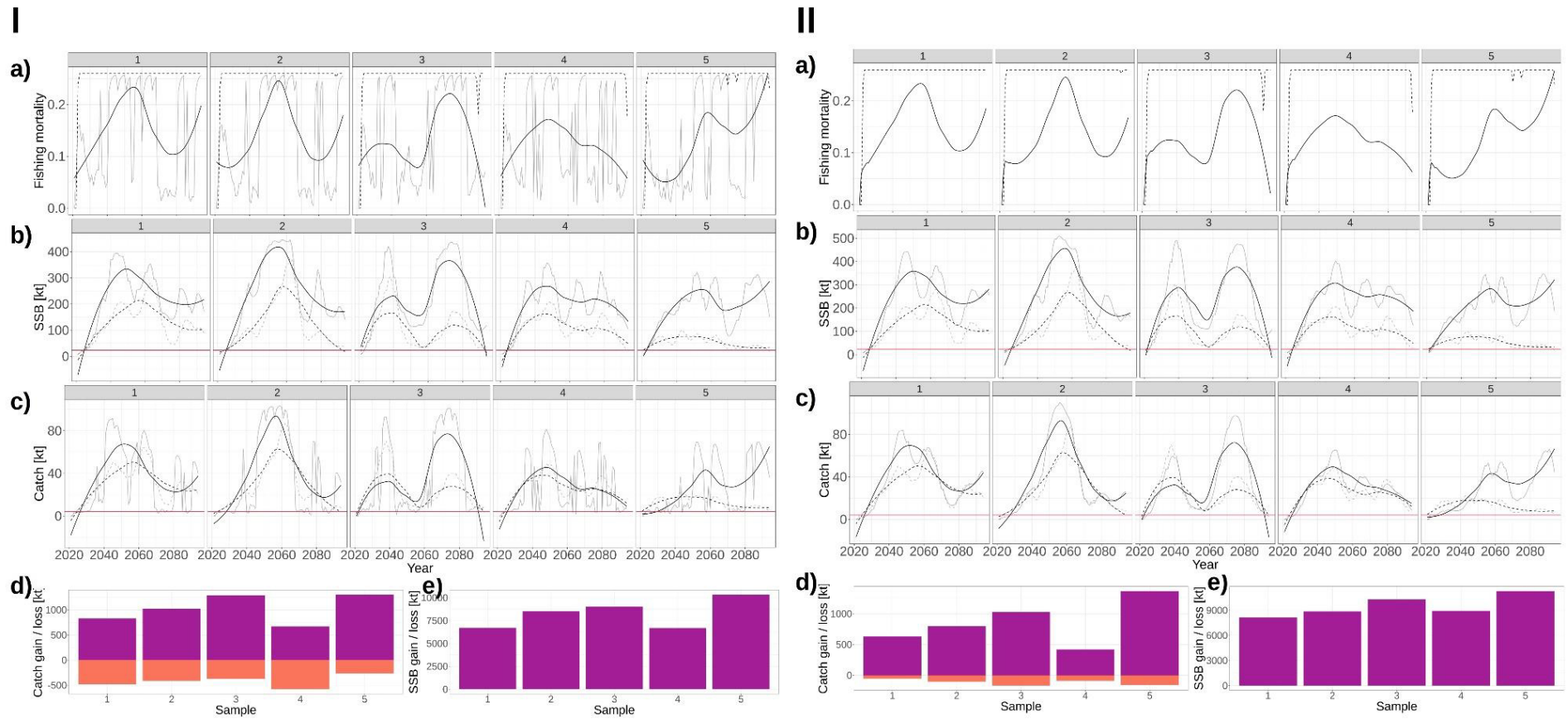


Figure SI CIII.14 / 1: Comparison of model output generated with original optimized F values (I) and smoothed F values (II). Shown are the trajectories of F (a), SSB (b) and catch (c), as well as the gains (purple) and losses (orange) of catch (d) and SSB (e) when compared to model output generated using the MSY-based ICES advice rule (see *Methods* for details). For further details on (I) see identical fig. CIII.7. Solid black line in (b) and (c) of (II) shows smoothed output generated with the smoothed optimized F. Solid grey line shows actual output. Dashed black line shows output (non-smoothed) generated with the ICES advice rule

## 10. Supplementary references

- Allen, R. L. (1975). Models for fish populations: a review. *NZ Operational Research*, 4, 1-20
- Baranov, F. I. (1918). On the question of the biological basis of fisheries. *Nauch. Issledov. Iktiolog. Inst. Izv.*, 1, 81-128
- Beverton, R. J. H. & Holt, S. J. (1957). On the dynamics of exploited fish populations, Chapman & Hall, London / UK, 533 pp. doi: 10.1007/978-94-011-2106-4
- BLE (2020). Monatsbericht 2020. Bericht über die Fischerei und die Marktsituation für Fischereierzeugnisse in der Bundesrepublik Deutschland. German federal office for agriculture and food (BLE), Bonn / DE, 49 pp.
- Bogstad, B., Lilly, G. R., Mehl, S., Pálsson, Ó. K. & Stefánsson, G. (1994). Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents Sea, Iceland, and eastern Newfoundland). *ICES Marine Science Symposia*, 198, 576-599
- Boucher, O., Servonnat, J., Albright, A. L., Aumont, O., Balkanski, Y., Bastrikov, V., Bekki, S. et al. (2020). Presentation and evaluation of the IPSL-CM6A-LR climate model. *Journal of Advances in Modeling Earth Systems*, 12, e2019MS002010. doi: <https://doi.org/10.1029/2019MS002010>
- Brassard, C., Lussier, J.-F., Benoît, H., Way, M. & Collier, F. (2019). The status of northern Gulf of St. Lawrence (3Pn, 4RS) Atlantic Cod (*Gadus morhua*) stock in 2018. DFO Canadian Science Advisory Secretariat Research Document 2019/075, x+117 pp.
- Brattey, J., Cadigan, N., Dwyer, K. S., Healey, B. P., Ings, D. W., Lee, E. M., Maddock Parsons, D. et al. (2018). Assessment of the Northern Cod (*Gadus morhua*) stock in NAFO Divisions 2J3KL in 2016. DFO Canadian Science Advisory Secretariat Research Document 2018/018, v+107 pp.
- Cleveland, W. S., Grosse, E. & Shyu, W. M. (1992). Local regression models. In: Chambers, J. M. & Hastie, T. J. (eds.): *Statistical Models in S*, Routledge, Oxfordshire / UK, Chapter 8
- DFO (2019a). Assessment of the Northern Gulf of St. Lawrence (3PN, 4RS) cod stock in 2018. DFO Canadian Science Advisory Secretariat Science Advisory Report 2019/032, 16 pp.
- DFO (2019b). Assessment of Atlantic cod (*Gadus morhua*) in the Southern Gulf of St. Lawrence (NAFO Div. 4T-4VN (Nov.-April)) to 2018. DFO Canadian Science Advisory Secretariat Science Advisory Report 2019/021, 20 pp.
- Dunne, J. P., Horowitz, L. W., Adcroft, A. J., Ginoux, P., Held, I. M., John, J. G., Krastings, J. P. et al. (2020). The GFDL Earth System Model Version 4.1 (GFDL-ESM 4.1): Overall coupled model description and simulation characteristics. *Journal of Advances in Modeling Earth Systems*, 12, e2019MS002015. doi: <https://doi.org/10.1029/2019MS002015>
- Elzhov, T. V., Mullen, K. M., Spiess, A.-N. & Bolker, B. (2016). minpack.lm: R interface to the Levenberg-Marquardt non-linear least-squares algorithm found in MINPACK, plus support for bounds. <https://CRAN.R-project.org/package=minpack.lm>. Last access 22nd June, 2023

- Eyring, V., Bony, S., Meehl, G. A., Senior, C. A., Stevens, B., Stouffer, R. J. & Taylor, K. E. (2016). Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization. *Geoscientific Model Development*, 9, 1937-1958. doi: 10.5194/gmd-9-1937-2016
- Folkvord, A. (1991). Growth, survival and cannibalism of cod juveniles (*Gadus morhua*): effects of feed type, starvation and fish size. *Aquaculture*, 97, 41-59. doi: 10.1016/0044-8486(91)90278-F
- Free, C. M., Mangin, T., Wiedenmann, J., Smith, C., McVeigh, H. & Gaines, S. D. (2022). Harvest control rules used in US federal fisheries management and implications for climate resilience. *Fish and Fisheries*, 24, 248-262. doi: 10.1111/faf.12724
- Funk, S. (2020). Spatio-temporal distribution, food intake and growth of cod (*Gadus morhua* L.) in the Western Baltic Sea. Dissertation, Universität Hamburg, 215 pp. <https://ediss.sub.uni-hamburg.de/handle/ediss/8379>. Last access: 13<sup>th</sup> June, 2023
- Funk, S., Krumme, U., Temming, A., & Möllmann, C. (2020). Gillnet fishers' knowledge reveals seasonality in depth and habitat use of cod (*Gadus morhua*) in the Western Baltic Sea. *ICES Journal of Marine Science*, 77, 1816-1829. doi: 10.1093/icesjms/fsaa071
- Funk, S., Frelat, R., Möllmann, C., Temming, A. & Krumme, U. (2021). The forgotten feeding ground: patterns in seasonal and depth-specific food intake of adult cod *Gadus morhua* in the western Baltic Sea. *Journal of Fish Biology*, 98, 707-722. doi: 10.1111/jfb.14615
- González-Troncoso, D., González-Costas, F. & Garrido, I. (2022). Assessment of the cod stock in NAFO Division 3M. NAFO Scientific Council Research Document, 22/025, Serial No. N7298, 58 pp.
- Hajima, T., Watanabe, M., Yamamoto, A., Tatebe, H., Noguchi, M. A., Abe, M., Ohgaito, R. et al. (2020). Development of the MIROC-ES2L Earth system model and the evaluation of biogeochemical processes and feedbacks. *Geoscientific Model Development*, 13, 2197-2244. doi: <https://doi.org/10.5194/gmd-13-2197-2020>
- Hilborn, R., & Walters, C. J. (1992). *Quantitative Fisheries Stock Assessment. Choice, Dynamics and Uncertainty*, Chapman and Hall, London / UK, 570 pp. doi: 10.1007/978-1-4615-3598-0
- Hochreiter, S. & Schmidhuber, J. (1997). Long short-term memory. *Neural Computation*, 9, 1735-1780. doi: 10.1162/neco.1997.9.8.1735
- Howell, D., Bogstad, B., Chetyrkin, A., Fall, J., Filin, A., Aanestad-Godiksen, J., Höffle, H. et al. (2022). Report of the Joint Russian-Norwegian Working Group on Arctic Fisheries (JRN-AFWG) 2022. IMR-PINRO, 6 / 2022, 213 pp.
- Huang, B., Thorne, P. W., Banzon, V. F., Boyer, T., Chepurin, G., Lawrimore, J. H., Menne, M. J., Smith, T. M., Vose, R. S. & Zhang, H.-M. (2017). Extended Reconstructed Sea Surface Temperature, Version 5 (ERSSTv5): upgrades, validations, and intercomparisons. *Journal of Climate*, 30, 8179-8205. doi: 10.1175/JCLI-D-16-0836.1
- ICES (2018a). Report of the InterBenchmark Protocol on Greenland Cod (IBPGCod). Report 2018 8-9, January 2018. Copenhagen, Denmark. ICES CM 2018/ACOM:30. 205 pp. doi: 10.17895/ices.pub.5266

- ICES (2018b). Stock Annex: Cod (*Gadus morhua*) in NAFO Subarea 1, inshore (West Greenland cod). ICES Stock Annexes. Report. doi: 10.17895/ices.pub.18622256.v2
- ICES (2020a). Benchmark Workshop on Celtic Sea Stocks (WKCELTIC). ICES Scientific Reports, 2 (97), 166 pp. doi: 10.17895/ices.pub.5983
- ICES (2020b). Stock Annex: Cod (*Gadus morhua*) in Divisions 7.e-k (eastern English Channel and southern Celtic Sea). ICES Stock Annexes. Report. doi: 10.17895/ices.pub.18622229.v1
- ICES (2021a). Cod (*Gadus morhua*) in Subarea 4, Division 7.d, and Subdivision 20 (North Sea, eastern English Channel, Skagerrak). ICES Working Group on the Assessments of Demersal Stocks in the North Sea and Skagerrak, 2 (61), 101-181. doi: 10.17895/ices.pub.6092
- ICES (2021b). Stock Annex: Cod (*Gadus morhua*) in Division 5.a (Iceland grounds). ICES Stock Annexes. 28 pp. doi: 10.17895/ices.pub.18622199
- ICES (2021c). Benchmark Workshop on North Sea Stocks (WKNSEA). ICES Scientific Reports, 3 (25), 756 pp. doi: 10.17895/ices.pub.7922
- ICES (2021d). ICES fisheries management reference points for category 1 and 2 stocks. Technical Guidelines. In: Report of the ICES Advisory Committee, 2021. ICES Advice 2021, Section 16.4.3.1. doi: 10.17895/ices.advice.7891
- ICES (2021e). Baltic Fisheries Assessment Working Group (WGBFAS). ICES Scientific Reports, 3 (53), 717 pp. doi: 10.17895/ices.pub.8187
- ICES (2022a). Northwestern Working Group (NWWG). ICES Scientific Reports, 4 (42), 734 pp. doi: 10.17895/ices.pub.19771381
- ICES (2022b). Interbenchmark protocol on Faroese demersal stocks (IBPFAR). ICES Scientific Reports, 4 (87), 52 pp. doi: 10.17895/ices.pub.21565164
- ICES (2022c). Working Group for the Celtic Seas Ecoregion (WGCSE). ICES Scientific Reports, 4 (45), 1413 pp. doi: 10.17895/ices.pub.19863796
- ICES (2022d). Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK). ICES Scientific Reports, 4 (43), 1367 pp. doi: 10.17895/ices.pub.19786285
- ICES (2022e). Baltic Fisheries Assessment Working Group (WGBFAS). ICES Scientific Reports, 4 (44), 659 pp. doi: 10.17895/ices.pub.19793014
- ICES (2022f). Cod (*Gadus morhua*) in ICES Subarea 14 and NAFO Division 1.F (East Greenland, South Greenland). In: Report of the ICES Advisory Committee, 2022. ICES Advice 2022, cod.21.1. doi: 10.17895/ices.advice.19447838
- ICES (2022g). Cod (*Gadus morhua*) in NAFO Subarea 1, inshore (West Greenland cod). In: Report of the ICES Advisory Committee, 2022. ICES Advice 2022, cod.2127.1f14. doi: 10.17895/ices.advice.19447835
- ICES (2022h). Cod (*Gadus morhua*) in Division 5.a (Iceland grounds). In: Report of the ICES Advisory Committee, 2022. ICES Advice 2022, cod.27.5a. doi: 10.17895/ices.advice.19447886

- ICES (2022i). Cod (*Gadus morhua*) in Subdivision 5.b.1 (Faroe Plateau). In: Report of the ICES Advisory Committee, 2022. ICES Advice 2022, cod.27.5b1. doi: 10.17895/ices.advice.19772368
- ICES (2022j). Cod (*Gadus morhua*) in subareas 1 and 2 north of 67 °N (Norwegian Sea and Barents Sea), northern Norwegian coastal cod. In: Report of the ICES Advisory Committee, 2022. ICES Advice 2022, cod.27.1-2coastN. doi: 10.17895/ices.advice.20071997
- ICES (2022k). Cod (*Gadus morhua*) in Division 6.a (West of Scotland). In: Report of the ICES Advisory Committee, 2022. ICES Advice 2022, cod.27.6a. doi: 10.17895/ices.advice.19447889
- ICES (2022l). Cod (*Gadus morhua*) in Subarea 4, Division 7.d, and Subdivision 20 (North Sea, eastern English Channel, Skagerrak). In: Report of the ICES Advisory Committee, 2022. ICES Advice 2022, cod.27.47d20. doi: 10.17895/ices.advice.19447880
- ICES (2022m). Cod (*Gadus morhua*) in subdivisions 22-24, western Baltic stock (western Baltic Sea). In: Report of the ICES Advisory Committee, 2022. ICES Advice 2022, cod.27.22-24. doi: 10.17895/ices.advice.19447868
- ICES (2022n). Cod (*Gadus morhua*) in Division 7.a (Irish Sea). In: Report of the ICES Advisory Committee, 2022. ICES Advice 2022, cod.27.7a. doi: 10.17895/ices.advice.19447895
- ICES (2022o). Cod (*Gadus morhua*) in divisions 7.e-k. In: Report of the ICES Advisory Committee, 2022. ICES Advice 2022, cod.27.7e-k. doi: 10.17895/ices.advice.19447898
- ICES (2023). Arctic Fisheries Working Group (AFWG; outputs from 2022 meeting). ICES Scientific Reports, 5 (18), 507 pp. doi: 10.17895/ices.pub.20012675
- Joint Russian-Norwegian Working Group on Arctic Fisheries (JRN-AFWG). Advice on fishing opportunities for Northeast Arctic cod in 2023 in ICES subareas 1 and 2. IMR-PINRO, 3 / 2022, 15 pp.
- Kingma, D. P. & Ba, J. (2014). Adam: a method for stochastic optimization. arXiv:1412.6980. doi: 10.48550/arXiv.1412.6980
- Lehmann, A. & Hinrichsen, H.-H. (2000). On the thermohaline variability of the Baltic Sea. *Journal of Marine Systems*, 25, 233-357. doi: 10.1016/S0924-7963(00)00026-9
- Lehmann, A., Krauss, W. & Hinrichsen, H.-H. (2002). Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. *Tellus A*, 54, 299-316
- Lehmann, A., Hinrichsen, H.-H. & Getzlaff, K. (2014). Identifying potentially high risk areas for environmental pollution in the Baltic Sea. *Boreal Environment Research*, 19, 140-152
- Lindegren, M., Checkley Jr., D. M., Rouyer, T., MacDall, A. D. & Stenseth, N. C. (2013). Climate, fishing, and fluctuations of sardine and anchovy in the California Current. *PNAS*, 110, 13672-13677. doi: 10.1073/pnas.1305733110
- Maraun, D. (2016). Bias correcting climate change simulations – a critical review. *Current Climate Change Reports*, 2, 211-220. doi: 10.1007/s40641-016-0050-x
- Mauritsen, T., Bader, J., Becker, T., Behrens, J., Bittner, M., Brokopf, R., Brovkin, V. et al. (2019). Developments in the MPI-M Earth system model version 1.2 (MPI-ESM1.2) and its

response to increasing CO<sub>2</sub>. *Journal of Advances in Modeling Earth Systems*, 11, 998-1038. doi: <https://doi.org/10.1029/2018MS001400>

- Mohn, R. (1999). The retrospective problem in sequential population analysis: An investigation using cod fishery and simulated data. *ICES Journal of Marine Science*, 56, 473-488. doi: 10.1006/jmsc.1999.0481

- Mohn, R. K. & Rowe, S. (2011). Recovery potential assessment for the Laurentian South designatable unit of Atlantic cod (*Gadus morhua*): The Eastern Scotian Shelf cod stock (NAFO Div. 4VsW). DFO Canadian Science Advisory Secretariat Research Document 2011/138, viii+71 pp.

- Myers, R. A. (1998). When do environment–recruitment correlations work? *Reviews in Fish Biology and Fisheries*, 8, 285-305. doi: 10.1023/A:1008828730759

- NOAA (2019). 2019 Assessment update of Gulf of Maine Atlantic cod. <https://apps-nefsc.fisheries.noaa.gov/saw/sasi.php>. Last access 13<sup>th</sup> June, 2023

- NOAA (2021). 2019 Update assessment of Gulf of Maine Atlantic cod. <https://apps-nefsc.fisheries.noaa.gov/saw/sasi.php>. Last access 13<sup>th</sup> June, 2023

- Northeast Fisheries Science Center (2013). 55<sup>th</sup> Northeast Regional Stock Assessment Workshop (55<sup>th</sup> SAW) Assessment Report. US Department of Commerce, Northeast Fisheries Science Center Reference Document 13-11, 845 pp.

- Peck, M. A., Catalán, I. A., Damalas, D., Elliott, M., Ferreira, J. G., Hamon, K. G., Kamer-mans, P. et al. (2020). Climate change and European fisheries and aquaculture. CERES Project Synthesis Report, Universität Hamburg, Hamburg / DE, 110 pp. doi: 10.25592/uhhfdm.804

- Pope, J. G. (1972). An investigation of the accuracy of virtual population analysis using cohort analysis. *ICNAF Research Bulletin*, 9, 65-74

- R Core Team (2020). R: an environment for statistical computing. R Foundation for Statistical Computing, Vienna. [www.r-project.org](http://www.r-project.org). Last access 29th August, 2023

- Receveur, A., Bleil, M., Funk, S., Stötera, S., Gräwe, U., Naumann, M., Duthheil, C. & Krumme, U. (2022). Western Baltic cod in distress: decline in energy reserves since 1977. *ICES Journal of Marine Science*, 79, 1187-1201. doi: 10.1093/icesjms/fsac042

- Riahi, K., van Vuuren, D. P., Kriegler, E., Edmonds, J., O'Neill, B., Fujimori, S., Bauer, N. et al. (2017). The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. *Global Environmental Change*, 42, 153-168. doi: 10.1016/j.gloenvcha.2016.05.009

- Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, 11, 559-623. doi: 10.1139/f54-039

- Rideout, R. M., Rogers, R. & Ings, D. W. (2021). An updated assessment of the cod stock in NAFO Divisions 3NO. NAFO Scientific Council Research Document, 21/031, Serial No. N7199, 57 pp.

- Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada*, 191, Department of the Environment, Fisheries and Marine Service, Ottawa / CA, 382 pp. doi: 10.2307/3800109



- Schenk, H., Zimmermann, F. & Quaas, M. (2023). The economics of reversing fisheries-induced evolution. *Nature Sustainability*, 6, 706-711. doi: 10.1038/s41893-023-01078-9
- Séférian, R., Nabat, P., Michou, M., Saint-Martin, D., Voldoire, A., Colin, J., Decharme, B. et al. (2019). Evaluation of the CNRM Earth system model, CNRM-ESM2-1: Role of Earth system processes in present-day and future climate. *Journal of Advances in Modeling Earth Systems*, 11, 4182-4227. doi: <https://doi.org/10.1029/2019MS001791>
- Sguotti, C., Otto, S. A., Frelat, R., Langbehn, T. J., Plambech Ryberg, M., Lindegren, M., Durant, J. M., Stenseth, N. C. & Möllmann, C. (2019). Catastrophic dynamics limit Atlantic cod recovery. *Proceedings of the Royal Society B*, 286, 1898. doi: 10.1098/rspb.2018.2877
- Shapiro, S. S. & Wilk, M. B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, 52, 591-611. doi: 10.1093/biomet/52.3-4.591
- Sokolova, N., Butzin, M., Dahlke, F., Werner, K. M., Balting, D., Lohmann, G. & Pörtner, H.-O. (2021). Exploring the role of temperature in observed inter-population differences of Atlantic cod (*Gadus morhua*) with a 4-dimensional modelling approach. *ICES Journal of Marine Science*, 78, 1519-1529. doi: 10.1093/icesjms/fsab043
- Swain, D. P. & Mohn, R. K. (2012). Forage fish and the factors governing recovery of Atlantic cod (*Gadus morhua*) on the eastern Scotian Shelf. *Canadian Journal of Fisheries and Aquatic Sciences*, 69, 997-1001. doi: 10.1139/F2012-045
- Swain, D. P., Ricard, D., Rolland, N. & Aubry, É. (2019). Assessment of the southern Gulf of St. Lawrence Cod (*Gadus morhua*) stock of NAFO Div. 4T and 4Vn (November to April), March 2019. DFO Canadian Science Advisory Secretariat Research Document 2019/038, iv+105 pp.
- Swart, N. C., Cole, J. N. S., Kharin, V. V., Lazare, M., Scinocca, J. F., Gillett, N. P., Anstey, J. et al. (2019). The Canadian Earth System Model version 5 (CanESM5.03). *Geoscientific Model Devevelopment*, 12, 4823-4873. doi: <https://doi.org/10.5194/gmd-12-4823-2019>
- Szuwalski, C. S., Britten, G. L., Licandeo, R., Amoroso, R. O., Hilborn, R. & Walters, C. (2019). Global forage fish recruitment dynamics: A comparison of methods, time-variation, and reverse causality. *Fisheries Research*, 214, 56-64. doi: 10.1016/j.fishres.2019.01.007
- Tirronen, M., Perälä, T. & Kuparinen, A. (2022). Temporary Allee effects among non-stationary recruitment dynamics in depleted gadid and flatfish populations. *Fish and Fisheries*, 23, 392-406. doi: 10.1111/faf.12623



## List of abbreviations

B <sub>P</sub>	precautionary biomass level (refers to spawning stock biomass)
DMDU	decision-making under deep uncertainty
F	fishing mortality
FMSY	fishing mortality generating maximum sustainable yield
HCR	harvest-control rule
MSE	management-strategy evaluation
MSY	maximum sustainable yield
RDM	robust decision-making
RNN	recurrent neural network
SOS	safe operating space
SSB	spawning stock biomass
SST	sea-surface temperature
TAC	total allowable catch

## List of publications

### Papers

Conradt, J., Funk, S., Sguotti, C., Voss, R., Blenckner, T. & Möllmann, C. Robust fisheries management strategies under deep uncertainty. In preparation

Conradt, J., Funk, S., Blenckner, T. & Möllmann, C. Safe Operating Space reveals climate-adaptation thresholds for sustainable management of Atlantic cod (*Gadus morhua* L.). In preparation

Conradt, J., Funk, S. & Möllmann, C. Designing sustainable management strategies for Atlantic cod (*Gadus morhua* L.) under deep uncertainty via multi-objective optimization. In preparation

### Oral presentations

Conradt, J., Funk, S., Sguotti, C., Voss, R., Blenckner, T. & Möllmann, C. (2022). Climate-proof management of North Sea cod (*Gadus morhua* L.) in a deeply-uncertain future. ICES Annual Science Conference 2022, 19-22 September, 2022, Dublin, Ireland

Conradt, J., Funk, S., Sguotti, C., Voss, R., Blenckner, T. & Möllmann, C. (2022). Climate-proof management of North Sea cod (*Gadus morhua* L.) in a deeply-uncertain future. 5th International Symposium on Effects of Climate Change on the World's Oceans (ECCWO 5), 17-21 April, 2023, Bergen, Norway

## Acknowledgements

First and foremost, my thanks to my supervisor Christian Möllmann, who, despite an often busy schedule, took the time to discuss and debate methods, results and presentations, and who I could always count on in urgent and important issues. From him, I did not merely learn about the technical subject matter, but also a lot about the skill of designing and writing a paper and communicating results. Thanks also for your patience in face of i.a. an ever-changing population model and too-complex-to-understand figures, and for giving me the opportunity to pursue my own research ideas.

My second big thanks go to Steffen Funk, who was always available for answering questions about cod, marine ecosystems and research in general and making suggestions on how to improve my research. Thanks for reading many of my manuscripts in admirably short time (even one that I later completely scrapped and rewrote – sorry for that!), and for your critical but never offensive feedback.

Thanks to my further collaborators, advisors, dear colleagues: Camilla Sguotti, who introduced me to my research topic and gave advice especially in the first year of my PhD; Thorsten Blenckner, who introduced me to the SOS concept and to my funding project COMFORT; Rudi Voss, who introduced me to bioeconomic theory and acquainted me with the iDiv institute; and Flemming Dahlke for his insights into Northeast Arctic cod, and for valuable comments on my research work.

I would not have been able to perform the kind of modeling work presented here were it not for the efforts of several people from IMF who taught me and fueled interest into programming and modeling during my Bachelor and Master studies: Jens Floeter, Saskia Otto, Inga Hense and Axel Temming – thank you!

My special thanks to my dear colleagues Alexandra Blöcker and Gregor Börner for your help and advice; Alex especially for reading and commenting on my “General...” manuscripts in no time; Greg especially for doing the plankton-classifier study with me (not part of the PhD but anyway...); and both for your camaraderie, your encouragement and the good times!

Many thanks also to all my other dear colleagues from AG Möllmann, from the IMF and from the “Baltic projects”. Special thanks to Silke Janssen, Nicole Funk, Rene Plonus, Frane Madiraca, Leonie Färber, Giannina Passuni, Elvis Kamberi, Rolf Koppelman, Bettina Martin and Stefanie Schnell, and *very* special thanks to Guilherme Pinto, Helene Gutte, Johanna

Biederbick, Elena Hauten, Raquel Marques, and Heike Schwermer, for the good times and all your support!

Laura Schmidt and Patricia Gorre deserve an extra entry for your tremendous help in managing all the administrative challenges!

It can be surprisingly hard to obtain and understand complete sets of stock-assessment data, and so for their aid in doing that my thanks go to the following stock-assessment experts: Diana González-Troncoso from the Instituto Español de Oceanografía, Paul Regular from Fisheries and Oceans Canada, Charles Perretti and Gary Shepherd from the Northeast Fisheries Science Center and Pia Schuchert from afbi Agri-Food & Biosciences Institute.

For their help in obtaining and extracting data, I thank Eleanore Campbell from Stockholm Resilience Center and my student assistant Hanna Robitschko – your work has saved me some valuable hours for modeling, plotting and writing. Thanks to Hanna Schenk from iDiv for explaining your economic model to me, and thanks to Nicole Funk for creating the nice icons for Chapter I.

Last but certainly not least thank you to my parents Sebastian and Karin Conradt and my brother Nils Conradt for all your support!

## Funding acknowledgements



I am grateful for the funding of this dissertation by the EU Horizon 2020 project COMFORT – Our Common Future Ocean in the Earth System, and by the Universität Hamburg.

This project has received funding from the European Union’s Horizon 2020 research and innovation programme under grant agreement No 820989 (project COMFORT, Our common future ocean in the Earth system – quantifying coupled cycles of carbon, oxygen, and nutrients for determining and achieving safe operating spaces with respect to tipping points).

The work reflects only the authors’ view; the European Commission and their executive agency are not responsible for any use that may be made of the information the work contains.

## **Author contributions**

Abbreviations: JC – Jan Conradt, CM – Prof. Dr. Christian Möllmann, SF – Dr. Steffen Funk, RV – Dr. Rüdiger Voss, TB – Dr. Thorsten Blenckner, CS – Dr. Camilla Sguotti

### **Chapter 1: Robust fisheries management strategies under deep uncertainty**

JC and CM wrote the manuscript. CM, JC, SF, CS, RV and TB conceived the study (main conceptualization by CM and JC, additional contributions by SF, CS, RV and TB). JC, CM and SF did the modeling and the analysis of model output (coding done by JC). CS, RV and TB provided additional input and comments on the manuscript. All authors reviewed and commented on the manuscript.

### **Chapter 2: Safe Operating Space reveals climate-adaptation thresholds for sustainable management of Atlantic cod (*Gadus morhua* L.)**

JC wrote the manuscript. CM reviewed and edited the manuscript. JC, CM, SF and TB conceived the study (main conceptualization by JC and CM). JC, CM and SF did the modeling (baseline SOS design and coding done by JC).

### **Chapter 3: Designing sustainable management strategies for Atlantic cod (*Gadus morhua* L.) under deep uncertainty via multi-objective optimization**

JC wrote the manuscript. SF and CM reviewed and edited the manuscript. JC, CM and SF conceived the study (main conceptualization by JC). JC, CM and SF did the modeling (baseline algorithm design and coding done by JC).

## **Supervisors' signature**

Hamburg, 18.10.2023

Prof. Dr. Christian Möllmann (supervisor)

## **Eidesstattliche Versicherung – declaration on oath**

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

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

Hamburg, den 18.10.2023

Jan Conradt

## **Erklärung zur Identität der gedruckten Dissertation**

Ich versichere, dass dieses gebundene Exemplar der Dissertation und das in elektronischer Form eingereichte Dissertationsexemplar (über den Docata-Upload) und das bei der Fakultät (Studienbüro des Fachbereichs Biologie der Universität Hamburg) zur Archivierung eingereichte gedruckte gebundene Exemplar der Dissertationsschrift identisch sind.

Hamburg, 18.10.2023

Jan Conradt