NONLINEARITY, IRREVERSIBILITY, AND SURPRISE

MANAGING ATLANTIC COD UNDER CLIMATE CHANGE

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IF EVER THERE WAS A FISH MADE TO ENDURE, IT IS THE ATLANTIC COD—THE COMMON FISH. BUT IT HAS AMONG ITS PREDATORS MAN, AN OPENMOUTHED SPECIES GREEDIER THAN COD.

Mark Kurlansky, 1999
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I would like to thank my family, without whom I would not have accomplished this. My PhD was a long personal and professional journey, which was only possible with the endless support and love from my family. I am nothing without you. Thank you!

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Climate change is at the forefront of today’s global challenges with its potential to turn into a runaway process. Fishing pressure acts in concert and exacerbates the impacts of climate change. The North Atlantic Ocean is no exemption of the increasing anthropogenic stress with Atlantic cod, *Gadus Morhua*, one of its most prominent fish species, displaying the ocean’s state. Most Atlantic cod stocks have experienced high rates of fishing and biomass declines, leading to renovation of fishing regulations and the implementation of rebuilding strategies. Today, the cod stocks differ considerably in trends and commercial status with 8 stocks considered collapsed and 57 % of today’s landings supplied by one single stock, the North East Arctic cod.

What drives the collapse and what drives the recovery of a stock? Elucidating drivers of Atlantic cod productivity at low abundance is inevitable for sustainably managing the species in its changing habitat. This thesis attempts a comprehensive study on climate change impacts by addressing rising ocean temperature (paper I-III), temperature variability (paper II), acidification (paper III) and uncertainty (of the biology and as risk in management under the precautionary approach [paper IV]). Individual and synergistic impacts of climate change are discussed with a particular focus on nonlinear dynamics, including the potential for Allee effects (paper I-III). Allee effects describe the decrease in per capita growth rate at small population size, which can hinder population recovery by reinforcing degradation. Such a shift in the underlying biology can be irreversible and demands proactive and precautionary management measures.

Application of precautionary measures to protect the environment and manage risks in situations of high uncertainty is a central tenet of the “precautionary approach”, a guiding principle in fisheries management. The poor state of various commercial fish stocks worldwide stands in contrast to the precautionary approach and suggests a subordinate role of science in fisheries management. In paper IV, Canada’s fisheries policy and advisory process is contrasted with the EU’s Common Fisheries Policy in regard to the precautionary approach and the role of science, in order to identify policy and institutional constraints that have hindered sustainable, precautionary management practices.

Drawing from insights on climate change driven productivity changes (paper I-III) and the importance of a policy and institutional framework that acknowledges these (paper IV), this thesis ends with suggestions for scientifically informed, precautionary and sustainable fisheries management practices that can speed up recovery and allow for a vital fishery in the future.
LIST OF PAPERS

**Paper I:** Implications of Allee effects for fisheries management in a changing climate: evidence from Atlantic cod
Anna-Marie Winter, Andries P. Richter, Anne Maria Eikeset
Published in *Ecological Applications* in August 2019.

**Paper II:** Spawner weight and ocean temperature drive Allee effect dynamics in Atlantic cod, *Gadus Morhua*: inherent and emergent density regulation
Anna-Marie Winter, Nadezda Vasilyeva, Artem Vladimirov
Submitted to *Biogeosciences* in May 2021.

**Paper III:** End-century projections of Atlantic cod (*Gadus Morhua*) under simultaneous ocean acidification and ocean warming from experimental data and time series
Martina Stiasny, Anna-Marie Winter
Manuscript.

**Paper IV:** Impediments to Fisheries Recovery in Canada: Policy and Institutional Constraints on Developing Management Practices Compliant with the Precautionary Approach
Anna-Marie Winter, Jeffrey A. Hutchings

OTHER PAPERS PUBLISHED DURING PHD:

The downward spiral: eco-evolutionary feedback loops lead to the emergence of ‘elastic’ ranges
Alexander Kubisch, Anna-Marie Winter, Emanuel A. Fronhofer
Published in *Ecography* in April 2015.

The mechanics of blue growth: Management of oceanic natural resource use with multiple, interacting sectors
Dane H. Klinger, Anne Maria Eikeset, Brynhildur Davíðsdóttir, Anna-Marie Winter, James R. Watson
Published in *Marine Policy* in October 2017.
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<th>Abbreviation</th>
<th>Explanation</th>
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<tbody>
<tr>
<td>$\mu$</td>
<td>Probability of maturation</td>
</tr>
<tr>
<td>$\text{age}_{\text{max}}$</td>
<td>Age of oldest age class</td>
</tr>
<tr>
<td>$\text{age}_{\text{rec}}$</td>
<td>Age of youngest age class (recruitment)</td>
</tr>
<tr>
<td>BOFFFF</td>
<td>Big Old Fat Fecund Female Fish</td>
</tr>
<tr>
<td>cod</td>
<td>Atlantic cod, <em>Gadus Morhua</em></td>
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<tr>
<td>DFO</td>
<td>Department Fisheries Oceans (Canada)</td>
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<tr>
<td>EU</td>
<td>European Union</td>
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<tr>
<td>$F$</td>
<td>Fishing rate</td>
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<tr>
<td>FAO</td>
<td>Food and Agriculture Organization of the United Nations</td>
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<td>ICES</td>
<td>International Council for the Exploration of the Sea</td>
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<tr>
<td>$M$</td>
<td>Natural mortality rate</td>
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<tr>
<td>MSY</td>
<td>Maximum sustainable yield</td>
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<tr>
<td>$N$</td>
<td>Population size</td>
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<tr>
<td>$R$</td>
<td>Recruitment</td>
</tr>
<tr>
<td>SSB</td>
<td>Spawning stock biomass</td>
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<td>SST</td>
<td>Sea surface temperature</td>
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<tr>
<td>$t$</td>
<td>Time</td>
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<tr>
<td>TAC</td>
<td>Total allowable catch</td>
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<tr>
<td>UN</td>
<td>United Nations</td>
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<tr>
<td>$w$</td>
<td>Weight</td>
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1 INTRODUCTION

The majority of ecosystems are affected by rising anthropogenic pressure. Climate change, fishing and pollution put the ocean under an increasing level of stress and, on their own or in conjunction, decrease significantly the ocean's potential to produce food, support livelihood, buffer the world's climate and provide other ecosystem services. Only 13 % of the ocean has been identified as devoid of intense human impact (Jones et al. 2018). Reconciling economic growth and food security in the oceans with the conservation of its aquatic resources is a goal of “blue growth” and sustainable development, which is challenged by improved access to, utilization of, and production efficiency from the ocean’s natural resources (Eikeset et al. 2018; Klinger et al. 2018). Independent of the constant change in semantics of global natural resource goals (i.e., sustainability, green growth, blue growth, blue sustainable growth), they all require the same: an understanding of the ecological resource dynamics, which determine (future) resource availability.

The temperate Northern Atlantic Ocean is one of the highest impacted Ocean realms (Jones et al. 2018), because of increasing sea surface water temperatures, SST, shipping activity and commercial fishing (Halpern et al. 2015). Arctic ice melting further accelerates the human impact by opening new economic growth opportunities and reinforces the ongoing climate change by releasing permafrost carbon to the atmosphere and increasing solar absorption by the Earth’s surface (Yumashev et al. 2019). The Arctic region is and will continue to be one of the regions globally most affected by climate change. While fish species may escape to the Arctic from warming, ocean acidification, changing ocean currents and nutrient inflow may also constrain the northern migration
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(Steiner et al. 2019; Sandø et al. 2020). Especially in the international waters of the Arctic, climate change alters access to fishing grounds and increases risk of fisheries conflict (Mendenhall et al. 2020), which requires multi-lateral cooperation and transboundary governance (Stokke 2011; Østhagen 2020) that keeps pace with changing migration patterns, displacement of fish to new areas and changing stock shares between countries (Blomeyer & Stobberup 2015; Palacios-Abrantes et al. 2020a; Palacios-Abrantes et al. 2020b). For Arctic communities with a longstanding dependence on fish for livelihood and countries fishing in Arctic waters, climate change can impose a particular risk and fishers are challenged with risk management strategies (e.g., Gokhale et al. 2021 in press).

Figure 1: Geographical and size distribution of the 17 Atlantic cod stocks investigated in this PhD research. Coloration of the map is according to ambient sea surface temperatures, which range for Atlantic cod between 3 °C in the Barents Sea (a) and 15 °C at the Flemish Cap (l). Spawning stock biomass (SSB) is highest from the North East Arctic (a) and Icelandic stock (b). Circle colors indicate the driver of recruitment dynamics found in this PhD research (fishing, temperature, ocean acidification, Allee effect). The bar plot shows the change in SSB since monitoring of the stock. Black bars
indicate that the stock is considered collapsed (< 20 % of its maximum SSB). The stocks and the respective investigating PhD papers are: a) North East Arctic cod (II+III), b) Icelandic cod (II), c) (Norwegian) Coastal cod (II), d) Faroe Plateau cod (II), e) Kattegat cod (II), f) Western Baltic cod (II+III), g) North Sea cod (I-III), h) West of Scotland cod (II), i) Irish Sea cod (II), j) Celtic Sea cod (II), k) Northern cod (II+IV), l) Flemish Cap cod (II), m) Southern Grand Bank cod (II), n) Southern Gulf of St. Lawrence cod (II), o) Northern Gulf of St. Lawrence cod (II), p) Gulf of Maine cod (II), q) Georges Bank cod (II).

Approximately 31 % of the fish stocks in the North Atlantic Ocean are fished at unsustainable levels (status 2016; FAO 2018). Atlantic cod, *Gadus Morhua*, (hereafter also just “cod”) is one of the 10 globally most landed species (1.2 mil tons in 2018; FAO 2020) and residues in the North Atlantic Ocean (Figure 1). The species sustains a remarkably long-standing fishery, which is today mainly comprised by the North East Arctic Cod stock (57 % of total Atlantic cod catch in 2018). The different identified Atlantic cod stocks display an extraordinary high diversity in life-history traits, geographical range, fishing practices, institutional framework and socio-economic impact, posing different socio-economic, management and geopolitical challenges. Each stock has experienced high rates of exploitation followed by strong biomass declines, with trajectories remarkably coherent among the different stocks (Lilly *et al.* 2008; Frank *et al.* 2016). Following an increase in biomass in the 1980’s, stocks declined again in the 1990’s. Between the early 1960s and the early 1990s, the total spawning stock biomass of Northwest Atlantic cod stocks is estimated to have declined by more than two million tons, a reduction of more than 90 % (Hutchings & Rangeley 2011) and many of these stocks remain at unsustainable levels since (Figure 1).

Fishing has been identified as the primary driver for stock decline (Hilborn & Litzinger 2009; Brander 2018b). Residual fishing pressure during rebuilding remains challenging (Kraak *et al.* 2013), because of, for example, a high industry demand, poor incentives for fishers to avoid Atlantic cod, control and enforcement issues, overcapacity of the fishery, distrust in fisheries science and management and path dependency of the policy framework (Hegland & Raakjær 2008; Tekwa *et al.* 2019). The temporal and spatial scale of fishing could be sufficient to explain this large-scale coherence in Atlantic cod variability (Frank *et al.* 2016). However, in several stocks, recovery has not or only slowly been promoted by the reduction of directed fishing (e.g., Hutchings 2000; Hutchings &
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Reynolds 2004). Thus, the question “What drives population change, collapse and recovery of Atlantic cod?” has been the subject of numerous papers, which have invoked a range of complex mechanisms, some of which are addressed in this thesis. These include mechanisms related to environmental change (e.g., climate variability and habitat change, paper I-III; changes in species interactions), mechanisms related to population dynamics (e.g., Allee effects, paper I+II), mechanisms related to fishing (e.g., recruitment overfishing, age-size truncation, paper II; vulnerability to by-catch, high-grading, genetic and evolutionary responses) and mechanisms related to the society (e.g., the institutional framework and policies in place, paper IV, societal involvement, the socio-economic context in which the fishery operates).

A major observation emerging from this PhD thesis is that usually not one factor alone, but the cumulative effect of several drivers defines population trajectory. Further, drivers of recovery are not always congruent with drivers of collapse, because of changing system (environmental and population) conditions. This poses challenges from a modeling and also from a fisheries management perspective, because most projection models focus on selected factors and assume stable parameters and functional forms, while these actually may shift (Figure 2). In the extreme case, this alters the conditions for reversing the system shift: while the fish population was still thriving under conditions $a$, after a population collapse, re-establishment of conditions $a$ may not be possible or sufficient anymore to recover the population. The reasons behind could be the triggering of a feedback loop which stabilizes the collapsed population state (e.g., an Allee effect causing hysteresis; symbolized by the deep valley of the red ball in Figure 2) and/or the conditions themselves are simply not reversible (e.g., irreversible change in climate which lowers productivity of the population; symbolized by the change of the landscape in Figure 2 c).

In both cases, the recovery pathway of the system differs from its pathway of degradation and it is questionable whether a full recovery to pre-collapse conditions is actually possible. Drivers can affect both system state variable (Figure 2 b) and the system parameter (Figure 2 c) (Beisner et al. 2003), depending on the mechanism. Thus, in order to understand and anticipate such a shift, it is necessary to elaborate on the potential mechanisms through which the system is affected.
Figure 2: Conceptual (ball-in-cup) figure of a regime shift. The ball represents the system (a fish population) at different states (regimes), which is depicted by the two valleys (cups). Each state is stabilized by different feedback effects. Compensatory recruitment production, for example, adjusts for biomass loss in the conserved state and in the degraded state an Allee effect counteracts population replenishment. The fish population can shift from a conserved to a degraded state by, for example, overfishing (a change in the system state variables, b)) or by climate change reducing recruitment production (a change in the system parameters, c)). As becomes apparent, the ball cannot easily be pushed back into its original valley, because the current valley is very deep and/or the original valley might have disappeared (c). Figure inspired by Beisner et al. (2003).

Besides ecological and environmental constraints on recovery, there are essential governance and management mechanisms that might be required to achieve sustainability (Cardinale & Svedäng 2008; Gezelius 2008; Bailey et al. 2016), in particular under climate change (Pinnegar & Engelhard 2008; Klein & Thurstan 2016). The present-day is characterized by high uncertainty and risk regarding the future, brought by global issues such as climate change and the covid-19 pandemic, bringing attention to the “precautionary approach”. With the 1995 UN Agreement on Straddling and Highly Migratory Fish Stocks (UN Fish Stocks Agreement; United Nations 1995) and the FAO Code of Conduct for Responsible Fisheries; FAO 1995), the precautionary approach was introduced to fisheries management. The purpose of the precautionary approach is the protection of the environment (e.g., a fish stock) and limitation of risks (e.g., a fish stock
collapse) by taking early preventive action in response to threats of environmental harm, including situations of scientific uncertainty. The precautionary approach recognizes that the absence of full scientific certainty shall not motivate the postponing of decisions where there is a chance of serious or irreversible harm (Article 6.2; United Nations 1995). Thus, the precautionary approach tries to improve the society’s ability to identify environmental risks and act responsibly by bridging scientific uncertainty and decision-making (Kriebel et al. 2001). In paper IV we examine compliance to the precautionary approach in the role of science in Canada’s fisheries management practices and compare the findings with the European Union (EU), which is legally bound to the precautionary approach implementation, but which differs profoundly in its institutional organization and decision-making process (Figure 3). We discuss the importance of scientifically informed fisheries policies which are fully compliant with the precautionary approach (Hilborn et al. 2001; Shelton 2007; VanderZwaag et al. 2012) to promote the recovery of fish stocks, such as the Northern cod.

Figure 3: The decision-making process for determining total allowable catch, TAC, in the European Union (EU) (a) and in Canada (b). In the EU, ICES (International Council for the Exploration of the Sea) provides the science advice to the European Council (DG MARE), which is the starting point for decision-making. Advisory Councils with stakeholders are asked for consultation. DG MARE’s policy advice is then sent for
decision to the Council of the EU. Each step of the linear decision-making process is transparent and thus accountable. Science has a defined role, and is distinct and publicly distinguishable from stakeholder advice. In Canada, the Department of Fisheries Oceans’ in-house Canadian Science Advisory Secretariat facilitates the science. The science advice is less transparent because of the inseparable stakeholder involvement and management considerations that influence the entire advisory process. In some cases (such as harvest control rules), management decisions need not be based on science advice (hatched arrow). The policy advice published by the Canadian Science Advisory Secretariat is presented to the Minister who has discretion to base all, part, or none of her/his TAC decision on science. As a consequence, the role of science is not as central, well-defined and publicly clear in Canada as in the EU, which limits the accountability of the decision-making process and integrity of science. Figure with legend from Winter and Hutchings (2020).

Ultimately, I aimed to investigate in my PhD how fisheries management should be adjusted to allow for a viable fishery in the future under climate change. I did this by focusing on nonlinear and transient recruitment dynamics (e.g., caused by an Allee effect; nonlinearity), which can increase the risk of irreversible productivity changes under persistent climate change (irreversibility). Based on the findings that recruitment and population dynamics under climate change are difficult to predict (surprise), this thesis discusses how management and governance can mitigate the impacts of climate change and can also increase the resilience of fish populations. This thesis is a comprehensive study on climate change by addressing rising ocean temperature (paper I-III), temperature variability (paper II), acidification (paper III) and uncertainty (as environmental variation [paper I-III], regime shifts [paper I+II], and as risk in management under the precautionary approach [paper IV]). While paper I-III study climate change impacts on population dynamics, paper IV discusses how such science could be incorporated for sustainable management. Each thesis chapter draws from results of all 4 PhD papers. Motivation and objectives for each paper are elaborated in chapter 2. Chapter 3 elaborates further on stock choice and methods applied in the different papers. A summary of the findings is given in chapter 4, which further highlights the implications for managing Atlantic cod under a changing climate and how future research could aid in doing so.
1.1 Drivers of growth rate and how they affect recovery

Changes in fish stocks can have many interrelated causes, which may not be separable or reducible to a single factor, because of lacking field data and because they are strongly confounded in time and space. Commercial fish populations and in particular Atlantic cod, a highly commercially valuable fish, are continuously exposed to fishing pressure. On average, 2.0 million tons of Atlantic cod are removed per 0.1 $\text{yr}^{-1}$ (Frank et al. 2016). In addition to fishing, fish stocks are exposed to continuous environmental changes. In my PhD research I was therefore interested in the cumulative stress level and further, which factors synergistically affect the growth rate dynamics and recovery in such a way that the pathways of collapse and recovery are not identical (Figure 2). In other words, stopping the factor responsible for population collapse (e.g., fishing pressure) does not lead to population recovery, because recovery is driven by a different factor. In Figure 2 for example, using the same force to push the ball back, as was used to make it fall (Figure 2 b), does not push the ball back to the first valley, because the current valley is much deeper. Similar, reducing the hill back to its previous size does not push the ball back, because the remaining hill is still too steep to roll over (Figure 2 c). Such synergistic interactions between environmental conditions have been indicated to be more common than additive or antagonistic interactions (Przeslawski et al. 2015).

In contrast to a large population, the dynamics of a small, in particular exploited, fish population are mainly driven by stochastic events (Rouyer et al. 2012), demographic variability (Anderson et al. 2008), environmental variability (Ottersen et al. 2006; Shelton & Mangel 2011) and recruitment variability (Hsieh et al. 2006; Kuparinen et al. 2014b). Overfished populations are in particular vulnerable because of their reduced age and size-diversity (Longhurst 2002; Hsieh et al. 2006; Anderson et al. 2008; Rouyer et al. 2012) leading to reduced reproduction and resilience (Marteinsdottir & Steinarsson 1998; Murawski et al. 2001; Birkeland & Dayton 2005; Hixon et al. 2013; van Overzee & Rijnsdorp 2015), low genetic diversity (Caughley 1994; Lande 1994) and often a decline in geographical range (Swain & Wade 1993).

Several hypotheses have been proposed to explain recruitment variability, most of which derive from insights and hypotheses proposed by Johan Hjort in the last century (Hjort 1914; Hjort 1926; Houde 2016). Most mechanisms and processes focus on the early life stages when high and variable mortality rates occur: For example, the “Critical Period” hypothesis in which the fate of year classes depends on the ability of first-feeding larvae to find suitable prey in sufficient quantity, the basis for Cushing’s “Match-Mismatch”
hypothesis (Cushing 1990), where the timing of larval fish production is critically dependent on schedules and levels of zooplankton production; “Aberrant drift” describing the favorable or unfavorable transport of eggs and larvae with wind and ocean currents; the “Optimum Environmental Window” (Cury & Roy 1989) describing an optimal oceanographic window where the encounter rates between fish larvae and prey is optimal; or the “Member-Vagrant” hypothesis (Sinclair & Iles 1989) proposing that recruitment success rests on the retention and the physical oceanographic features of spawning areas that restrict dispersal of eggs and early stage larvae.

Recruitment places a firm constraint on the number of individuals that can potentially grow to maturity and contribute to population growth (Payne et al. 2009). Understanding recruitment dynamics is important to predict future resource availability and adapt management accordingly. Because recruitment is not only crucial for collapse and recovery dynamics of a population, but has also been shown to be more susceptible to environmental changes (Anderson et al. 2008; Pankhurst & Munday 2011), I focused on drivers influencing the stock-recruitment function.

1.1.1 The Allee effect

The Allee effect is one of the few population ecological mechanisms leading to a mismatch of the pathway for collapse and recovery. In several depleted fish populations, the Allee effect has been suggested to explain the observed lack of recovery despite substantial fishing reductions (Myers et al. 1995; Rose 2004; Hilborn et al. 2014; Hutchings 2015 and Figure 1). A demographic Allee effect is a functional description of the positive density-dependence (or abundance-dependence) of the per capita (individual) growth rate at low population size (Courchamp et al. 1999; Hutchings 2015). It emerges, when the per capita growth rate reduces contemporaneously with declines in population size and is thus the opposite of the widely assumed compensatory growth of fish populations. In my thesis, I refer to demographic Allee effects in contrast to component Allee effects. A component Allee effect describes the positive affect of population size on a single (or multiple) fitness component, but without leading to an overall reduction of population fitness (i.e., the per capita growth rate) at low abundance (Stephens et al. 1999; Fauvergue 2013). At a demographic Allee effect, there is a positive density-dependence of the overall realized individual fitness and per capita growth rate declines at low abundance (Stephens et al. 1999; Fauvergue 2013).

Because the Allee effects becomes effective at small population size, it is often associated with a population’s risk of extinction (Stephens et al. 1999; Dennis 2002) and how
probable a population will successfully expand its range (Taylor & Hastings 2005; Kubisch et al. 2016). However, only if the demographic Allee effect is strong, there is a critical threshold in population size (the Allee threshold), below which the per capita growth rate drops below zero. In a deterministic setting, this causes bistability and the population can go extinct below the Allee threshold (Berec et al. 2007; Courchamp et al. 2008). This is, because extinction is a stable equilibrium, which is reinforced by a negative population growth rate: Once collapsed, there are no or very few individuals left to produce recruitment, even in the event of successful restoration of the pre-collapse conditions. To recover the population, it is not sufficient to reduce the fishing pressure to pre-collapse levels but instead, negative fishing pressure, i.e., re-stocking (paper I), or a re-establishment of the demographic structure (paper II) may be necessary.

Figure 4: The interaction between an Allee effect and ocean warming reinforces hysteresis (introduction of an inflection point) and a regime shift. The green lines indicate the growth rate without an Allee effect and without ocean warming, the orange lines indicate the growth rate in presence of an Allee effect and ocean warming of +1°C, and the red lines show the growth rate in presence of an Allee effect and ocean warming of +2°C. (a) The simulated net per capita growth rate (recruitment per SSB) as a function of log population size. The strong Allee effect (orange and red lines) introduces an unstable equilibrium point and, in presence of fishing, the population suddenly collapses at unprecedented high biomass levels (broken arrow). At +1°C and in the presence of an Allee effect, the population can withstand a fishing pressure of \( \leq 0.5 \, yr^{-1} \), at +2°C of \( \leq 0.3 \, yr^{-1} \). Without an Allee effect, the population declines, but does not suddenly collapse. (b) The simulated log population size as a function of fishing rate. Temperature strengthens
the Allee effect by strengthening hysteresis (orange and red lines) and, as a result, the pathways of collapse and recovery differ. A reduction of the fishing rate to pre-collapse conditions is not sufficient to recover the population. Increasing temperature shifts the last point before collapse (called “tipping point” in case of a hysteresis) to higher biomasses and requires higher rebuilding effort. In contrast, the path of collapse and recovery is the same if no Allee effect is present (green line). Figure with legend from Winter et al. (2020).

A shift to the lower biomass equilibrium can occur as a result of a shock event (e.g., fishing) and/or slow changes in the underlying variables (e.g., fishing, climate change) and internal feedbacks that define the ecological system (Beisner et al. 2003). Allee effects have been mainly seen as a static population characteristic with suggested mechanisms in marine fish mainly related to reduced antipredator vigilance due to a smaller school size (Clark 1974; Saether et al. 1996), difficulties in finding mates (Rowe et al. 2004), lowered egg fertilization rate and decreased genetic variation among offspring (Rowe & Hutchings 2003; Courchamp et al. 2008). Empirical evidence is strongest for Atlantic cod (Rowe et al. 2004; Keith & Hutchings 2012a, b), with possible Allee effect mechanisms including increased predation on adult fish (Swain & Chouinard 2008; Kuparinen & Hutchings 2014; Swain & Benoit 2015) and altered food webs (Walters & Kitchell 2001; Frank et al. 2011). In this thesis, we find that the presence of Allee effects is dynamic. In paper I and paper II, for example, we show that an Allee effect can be strengthened by warming of the sea (Figure 4) and by fishing and/or climate induced changes in the demographic structure towards smaller, lighter spawners, because of their reduced recruitment potential (Marteinsdottir & Thorarinsson 1998; Murawski et al. 2001; Hutchings 2005).

These are examples of the cumulative effects of fishing and climate change and show that many drivers of population change can be synergistic, with the total response much greater than the sum of individual disturbances (Myers 1995), because self-feeding processes may kick in that defeat any attempts of sustainable management.

1.1.2 Fishing
The main factor governing stock decline and recovery is fishing pressure (Jackson et al. 2001; Frank et al. 2016; Brander 2018b). Fishing is the oldest, longest-standing anthropogenic stressor (Jackson et al. 2001). For population recovery, the long-term and often irreversible effects of fishing on population growth are especially relevant. Such
effects can be induced by fishing altering the food web, the demographic composition and influencing life history traits (Enberg et al. 2009). Fishing can make populations vulnerable to climate change and Allee effects, which are both difficult to reverse and manage.

Because Atlantic cod is often the apex predator of the food web, fishing pressure on Atlantic cod can cascade down the trophic chain, affecting multiple trophic levels and ultimately leading to a restructuring of the community. This can lead to a persistent new regime characterized by low abundance of Atlantic cod and high abundance of its forage fish (e.g., Sand lace, Atlantic herring, capelin, sprat, mackerel) released from predation (Swain & Sinclair 2000; De Roos et al. 2003; Bundy & Fanning 2005; Frank et al. 2005; Möllmann et al. 2008; Van Leeuwen et al. 2008; Fauchald 2010). In the new regime, forage fish are competing with small Atlantic cod for food, while preying on early life stages of Atlantic cod, thus reducing its reproductive success and inducing an Allee effect (a demographic Allee effect also called “cultivation Allee effect”; Walters & Kitchell 2001). Modeling studies have further shown that releasing the prey population from high predation pressure could lead to higher intraspecific competition within the prey population. This could cause a reduction in the prey’s population and individual body size, which could mean less food of less quality for Atlantic cod (De Roos & Persson 2002; Van Leeuwen et al. 2008; Gårdmark et al. 2015). In this scenario, restricting fishing pressure on Atlantic cod does not recover the population, because the new regime is stabilized by predation pressure on the juveniles and less available food. The pathways of collapse and recovery differ and diminishing the driver of collapse (fishing out Atlantic cod) will not lead to recovery.

The age- and size-selectivity of most fishing gear can influence population growth by changing the demographic structure. Fishing out the largest and oldest individuals can reduce recruitment production by decreasing the number of most fertile and experienced spawners (Big Old Fat Fecund Female Fish, “BOFFFFS” (Marteinsdottir & Thorarinsson 1998; Murawski et al. 2001; Hutchings 2005). As the demographic change occurs because of high fishing pressure, it is often accompanied by a reduction in the overall population size, thus potentially leading to an Allee effect (paper II). In particular for Atlantic cod, there is strong evidence for an age-size truncation (Law 2000; Ottersen 2008; Shelton et al. 2015; Svedäng & Hornborg 2017) with repercussions for productivity (Sharpe & Hendry 2009; Ottersen et al. 2014; Dunlop et al. 2015; Heino et al. 2015; Svedäng & Hornborg 2017).
Life history changes can be induced when fishing reduces the intraspecific competition, thereby promoting phenotypic plasticity, or when fishing targets specific phenotypic traits (Trippel 1995; Enberg et al. 2009). Strong selective harvesting pressure can also lead to an evolutionary pressure towards the adaption to the new high mortality regime. For slow life history species such as Atlantic cod, there is strong evidence that targeting the largest and oldest individuals exerts a selective pressure towards faster life histories, which can become genetically manifested (“Fisheries induced evolution”; Sharpe & Hendry 2009; Dunlop et al. 2015; Heino et al. 2015). Even a uniform rise in fishing mortality across all body size can cause evolution of life history traits, because an overall increased mortality favors faster life histories (Heino et al. 2015). Faster life histories are realized through earlier maturation, reduced post-maturation growth and increased reproductive investment, thus reducing the risk of collapse and accelerating recovery (Dunlop et al. 2015; Nussle et al. 2016). On the other hand, species with faster life histories tend to devote more of their resources to annual reproductive output, thus having an increased survival cost of reproduction, resulting in higher natural mortality and a shorter life span and reduced population growth (Swain 2011; Kuparinen et al. 2012). This illustrates the potential long-term effects of fishing, which can make rebuilding efforts, such as a limited fishing quota, void by stabilizing the small population size. The small population size is a new regime (illustrated as a second valley in Figure 2), governed by different factors and drivers of collapse and recovery differ.

Because of lower genetic diversity, smaller bet-hedging capacity, reduced spatial heterogeneity and higher demographic variability (Hutchings & Myers 1993; Marteinsdottir & Steinarsson 1998; Anderson et al. 2008; Hsieh et al. 2008; Shelton & Mangel 2011; Rouyer et al. 2012), a small population is more susceptible to stochastic events and environmental fluctuations (Ottersen et al. 2006; Hsieh et al. 2008), thus emphasizing timely and decisive rebuilding measures (Brown et al. 2012; Neubauer et al. 2013). If a population shows an Allee effect, for example, gradual reduction of the population size through fishing reduces the interval between the two equilibrium population sizes (Figure 4, paper I) with the result that additional pressure from climate change will be more likely to reduce the population to critical numbers (i.e., proximity of a tipping point) and the population will be more vulnerable to extinction (Stephens & Sutherland 1999). Fishing thus increases the population’s vulnerability to climate change.
1.1.3 Increasing sea temperature

Climate change is an advancing, persistent stressor, which, different to fishing, cannot be stopped locally (though species may be able to migrate and/or adapt). Temperature has a direct, thermodynamic effect on biochemical reaction rates (e.g., ATP production, metabolic rate, mitochondrial respiration) and influences a number of physiological processes in fish (Gillooly et al. 2001; Pörtner et al. 2008; Drinkwater et al. 2010; Little et al. 2020), which are therefore predicted to change in response to ocean warming and alter population dynamics (Pörtner & Farrell 2008; Pörtner & Peck 2010). Changes in species’ distribution and trophic transfer, a rising growth rate and earlier maturation in response to warming have been found to increase the proportion of smaller sized individuals (Daufresne et al. 2009; Cheung et al. 2013; Tu et al. 2018), with repercussions for the productivity and resilience of the entire population.

On a recruitment level, temperature impacts, among others, spawner fertility, egg numbers and egg quality, hatching success and larval conditions (Brander 2010; Drinkwater et al. 2010), which can often not be distinguished or quantified separately. The net effect of temperature on recruitment success can be incorporated in the stock-recruitment function with one additional parameter (Hilborn & Walters 1992). Temperature is then considered a linear, density-independent factor. Following this approach, we find that an increase of temperature by 2 °C decreases recruitment of the North Sea cod up to 25.7 % (paper I), and increases recruitment of the North East Arctic cod by factor 2.54 (paper III). Thus, while Atlantic cod shows a wide span of temperature tolerance (Figure 1), direction and intensity of the recruitment response depends on its geographical position (Planque & Fredou 1999; Drinkwater 2005; Mantzouni & MacKenzie 2010). At the geographical limits of the species range, recruitment response to environmental factors is strongest (Brunel & Boucher 2006). At the cold, northern limits of the species’ range, recruitment is most strongly and positively related to water temperature (Planque & Fredou 1999; Drinkwater 2005; Mantzouni & MacKenzie 2010), which supported North East Arctic’s cod’s management success in the past (Kjesbu et al. 2014) and positive predictions for its near future (Hänsel et al. 2020 and paper III). It is, however, unlikely that the temperature-recruitment relation remains linear and constant with future temperatures. Especially in northern waters, temperature predictions have been as high as +12 °C, because of ice melting and the albedo effect (Overland et al. 2014; IPCC 2019). A simple linear recruitment model would predict an unrealistically large recruitment increase and would place the stock outside its thermal optimum, by
ignoring future factors such as food and habitat alteration, the physiological tolerance limit as well as the strong density-regulation. The North East Arctic cod recruitment has been shown to have a temperature optimum (Koenigstein et al. 2018; Hänsel et al. 2020).

To consider a non-monotonic temperature dependence, we fit the Lorentz function in paper II to recruitment and sea temperature data of different cod stocks. The model finds a temperature optimum for recruitment production for five stocks (Icelandic, Western Baltic, Kattegat, Celtic Sea, Georges Bank stocks), of which two stocks already passed the optimal temperature and further warming has a negative effect on recruitment. The fitted temperature optima for recruitment production are within the documented range for Atlantic cod (e.g., Planque & Fredou 1999; Pörtner et al. 2001; Drinkwater 2005; Righton et al. 2010), though depending on the different physiological and/or ecological mechanism. A different approach was used in paper I and paper III (appendix), where we used recruitment anomalies (recruitment change with temperature) to fit a nonlinear model. Because we fit non-mechanistic recruitment models, it is still to be clarified which exact mechanism is responsible for the observed temperature impact on recruitment production.

Temperature change has been implicated in various large scale marine regime shifts (Hare & Mantua 2000; Parsons & Lear 2001; Benson & Trites 2002; Beaugrand 2004; Lees et al. 2006; Beaugrand et al. 2008; Möllmann & Diekmann 2012; Conversi et al. 2015; Rocha et al. 2015), leading to cod recruitment failure and a decrease in cod biomass. If recruitment production responds negatively to rising ocean temperatures, it can strengthen an already existing Allee effect, thus increasing collapse risk and restricting recovery (paper I+II; Figure 4).

The impact of increasing sea temperature on collapse and recovery dynamics is bidirectional: It can support rebuilding efforts by boosting recruitment production, but it can also counteract and even squander rebuilding measures by inducing a regime shift such as an Allee effect, where collapse will very likely be irreversible. Because of the nonlinear, time-varying temperature dependence, also the efficiency of recovery measures changes over time and needs to be adapted to the prevailing conditions.

1.1.4 Ocean acidification

Because fishes have a well-developed acid–base regulatory system, ocean acidification has been only in the last 20 years recognized as a serious threat to marine fishes (and not only to corals and calcifiers). Only recently, ocean acidification effects are quantified with experiments and data remains limited especially of both warm and acidic conditions.
Where investigated, acidification effects seem to be more pronounced at higher temperatures (Dahlke et al. 2017; Leo et al. 2017). Further, the pH level of the sea varies with sea temperature, which is why multiple stressors should be looked at simultaneously to consider their interactive effects. Atmospheric carbon dioxide concentrations have been rising from average pre-industrial levels of around 280 μatm to present-day levels of approximately 410 μatm, with end-of-century predictions of 900–1,000 μatm, exceeding what most marine species have experienced in the past 30 million years (Clark et al. 2020). The oceans absorb about a quarter to a third of the excess carbon dioxide, thus buffering global warming, but at the same time resulting in the “other CO2 problem”: ocean acidification (Doney et al. 2009). Projections state that the pH level will further decrease globally between 0.1 and 0.4 by the year 2100, depending on the assumed reaction concentrations pathway (RCP scenario) and the geographical position. Especially high latitudes and coastal areas where some Atlantic cod stocks reside (Figure 1) are expected to experience lower pH values than the global average (AMAP 2018). This is in part due to the higher solubility of carbon dioxide at lower temperatures as well as the positive enforcement due to the melting of sea ice, which uncovers greater areas of the ocean, reducing the Albedo effect and allowing more interaction with the atmosphere.

While for marine fish various acidification effects on physiology, behavior and vital rates have been reported (Clements & Hunt 2015; AMAP 2018; Esbaugh 2018), rarely these have been projected to population level to discuss collapse and recovery dynamics. General evidence of acidification effects for commercially exploited fish species is still sparse (AMAP 2018). Because of the juvenile’s lower competence in regulating their internal acid–base balance due to e.g., lacking gills, juvenile fish are potentially more susceptible to the effects of ocean acidification and thus research focus is increasingly being placed on the reproductive stages and juveniles (AMAP 2018). In Atlantic cod recruitment, a wide range of physiological effects e.g., on sperm mobility (Frommel et al. 2010), hatching (Frommel et al. 2013), larval tissue (Frommel et al. 2012), mitochondrial functioning and oxygen consumption of embryos (Dahlke et al. 2017), otolith physiology (Frommel et al. 2013; Maneja et al. 2013b), acid-base physiology and morphometrics of larvae (Dahlke et al. 2017), as well as behavioral effects e.g., on larval swimming behavior (Maneja et al. 2013a; Jutfelt & Hedgärde 2015), predator and CO2 avoidance (Jutfelt & Hedgärde 2013) and the emergence from shelter and lateralization (Jutfelt & Hedgärde 2015) have been documented. Some effects are ambiguous, possibly due to
experimental artefacts (Pimentel et al. 2016; Clark et al. 2020), but there is a general consensus that ocean acidification impairs Atlantic cod larval survival (Frommel et al. 2012; Stiasny et al. 2016; AMAP 2018). In paper III, we find ocean acidification to reduce recruitment of the North East Arctic and the Western Baltic cod stock to 17 % and 4 %, respectively, by the end of the century. The Western Baltic cod stock is projected to fall below its biomass limit reference point, even without ocean warming reducing the stock’s recruitment, and a viable fishery cannot be sustained (paper III and Voss et al. 2019). Ocean acidification has less impact on the North East Arctic stock as long as recruitment responds positively to ocean warming (paper III and Hänsel et al. 2020). Beyond the recruitment’s temperature optimum, ocean acidification rapidly reduces recruitment and catch and increases the risk of stock collapse (Koenigstein et al. 2018; Hänsel et al. 2020).

Because ocean acidification impairs various life stages of marine fish and increases recruitment mortality, it worsens impacts of other stressors, increasing the risk of population collapse and hampering recovery. On a broader level, ocean acidification can lead to shifts in the fish population’s community and habitat (e.g., loss of habitat complexity, decline in species biodiversity [Sunday et al. 2017; Cattano et al. 2020], and alterations in resource and predator relations [Nagelkerken et al. 2016]), which are likely to hinder recovery.

While fish populations might adapt and migrate to survive the growing stressors, it remains unclear whether the process can occur rapidly enough to keep ecosystem functions and services unchanged in the face of the forecasted rapid ocean warming and acidification. Populations may be able to relocate to maintain current environmental (temperature) ranges, but then other (a)biotic constraints may apply and interactions between stressors may be different. Spawning sites of the North East Arctic cod, for example, may move northwards due to warming (Langangen et al. 2019; Sandø et al. 2020), but the stock will also be then exposed to increased ocean acidification (Steiner et al. 2019). The adaptive potential will be proportional to the population’s size and generation time, with populations that have large population sizes (greater genetic variation) and short generation times having the highest adaptation rates (Riebesell & Gattuso 2015). Thus, highly depleted stocks, which may even be “locked” in a low abundance stable state due to an Allee effect, are especially vulnerable to extinction. The risk is further increased for many commercially important fish such as Atlantic cod, which have long generation times and thus low adaption rates.
2 MOTIVATION AND OBJECTIVES

There is increasing human stress imposed on the oceans, because of a rising anthropogenic impact on the physical environment and because of a growing demand for food from the ocean (Costello et al. 2020). A high proportion of fish stocks is outside biologically sustainable levels (e.g., 25 % in the EU [STECF 2019], 30 % in Canada [OCEANA Canada 2019]) and, even though Atlantic cod is within the top 10 of globally most landed species (FAO 2020), many of its stocks are collapsed (47 % of the stocks investigated here have a biomass < 20 % of their maximum; all of Canada’s stocks are considered collapsed [Castañeda et al. 2020]). Because today commercial fish populations are not only exposed to fishing but also to a rapidly changing climate, I looked at the cumulative and interactive effects between fishing pressure and environmental change that alter the status quo of recruitment production and thus change collapse and recovery dynamics of Atlantic cod.

Even though overfishing is recognized and an increasing effort is directed towards rebuilding depleted stocks and reducing fishing pressure, many stocks only slowly recover or remain depleted (Hutchings 2000; Hutchings & Reynolds 2004; Hutchings 2015). In paper I+II, we therefore looked at the Allee effect as a mechanism for a regime shift that could stabilize the degraded population state and thus hinder recovery. The Allee effect is often depicted in a theoretical framework, which is why the objective here was to illustrate an Allee effect empirically. And even further, to empirically demonstrate a potential interaction between the Allee effect and ocean warming (i.e., Figure 4 is based on data). Besides exploring how the Allee effect impacts collapse and recovery under SST rise and different fishing regimes, in paper I we quantified the effect of each on the probability of collapse and recovery and identified under which conditions the Allee
Chapter 2: Motivation and Objectives

effect matters most. Given that fishing may be easier to manage than ocean warming, we were in particular interested in defining the sustainable level of fishing pressure and investigated to what extend restricting fishing can prevent and revert population collapse in presence of an Allee effect and ocean warming. In paper I, we focused on North Sea cod, where recruitment productivity is negatively affected by increasing SST (Planque & Fredou 1999; O’Brien et al. 2000; Clark et al. 2003; Pörtner et al. 2008), biomass continues to oscillate around the limit reference point despite fishing restrictions (ICES 2019b) and for which Allee effects has been discussed (Cabral et al. 2013).

Because the first paper omitted analyzing potential mechanisms leading to an Allee effect, paper II had the objective to focus on identifying factors facilitating the Allee effect. In particular, we were interested in testing whether, apart from spawner abundance, also changes in spawner weight can influence Allee effect presence. Younger, smaller fish do not have the same productivity per unit biomass as older, bigger fish (“BOFFFFs”), because smaller and younger fish are less fertile and less experienced spawners (Marteinsdottir & Steinarsson 1998; Murawski et al. 2001; Birkeland & Dayton 2005; Hixon et al. 2013; van Overzee & Rijnsdorp 2015). Thus, if the population is age-size truncated, for instance caused by heavy fishing, recruitment production shifts (Beamish et al. 2006) and could show an Allee effect. In contrast, heavy fishing could also increase recruitment production when imposing an evolutionary pressure towards faster life histories, such as earlier maturation and increased reproductive output (Dunlop et al. 2015; Nussle et al. 2016). As ocean temperature too influences recruitment production and success (Anderson et al. 2008; Brander 2010; Drinkwater et al. 2010; Pankhurst & Munday 2011; Hixon et al. 2013; Stige et al. 2017; Färber et al. 2020), we also considered SST to affect Allee effect presence. We hypothesized that if strong stock depletion is accompanied by changes in spawner weight and sea temperature changes, patterns of an Allee effect could emerge, be strengthened or masked. Besides, emergence and time-variance of Allee effects, we further elaborated on Allee effect variability by distinguishing between Allee effect strength (how much does the per capita growth rate decline) and position of the Allee effect threshold (when does the per capita growth rate decline). With this Allee effect characterization we hoped to gain further insight about when Allee effects matter for population trajectories. In paper II we used data from 17 Atlantic cod stocks and simulated trajectories for each stock individually. Therefore, from a modeling perspective, paper II had also the objective to develop population functions
and a data standardization procedure that allowed to capture the large diversity of all cod stocks by a single population model.

In paper III ocean acidification was considered as another climate change component affecting recruitment production. Ocean acidification had long been neglected as part of climate change, but has been demonstrated to affect performance and survival of various marine fish species (Clements & Hunt 2015; AMAP 2018; Esbaugh 2018). Thus, when studying climate change effects as a whole, ocean acidification effects need to be considered as well. Especially in recruitment, where regulation pathways are not yet fully developed, exposure to both warming and acidification could invoke a trade-off between investing in thermal acclimation and in the acid–base regulation. Exposure to elevated CO$_2$ levels have been found to increase the thermal sensitivity of marine fish (e.g., by constraining oxygen consumption and decreasing hatching success [Dahlke et al. 2017; Leo et al. 2017] and by decreasing food intake and digestion [Cominassi et al. 2020]), indicating a synergistic interaction between ocean acidification and ocean warming. The objective of paper III was therefore to investigate their combined effects on Atlantic cod. We compared the North East Arctic and Western Baltic cod stock, because they are particularly exposed to ocean warming in the North Atlantic and to ocean acidification due to their coastal proximity (Hüssy 2011; Ottersen et al. 2014), where input of terrestrial organic carbon increases water CO$_2$. In contrast to the Western Baltic cod, which is relatively constrained to the semi-enclosed Baltic Sea, the North East Arctic cod can move poleward, though its migration northward might be constrained by higher exposure to CO$_2$ (Steiner et al. 2019). The two stocks are so far the only Atlantic cod stocks, for which acidification induced larval mortality has been experimentally validated and quantified and can be incorporated into population models. While a few population modeling studies consider the combined effect of ocean warming and ocean temperature (e.g., Koenigstein et al. 2018; Voss et al. 2019), the impacts are not discussed in regard to differences in state of exploitation (the North East Arctic stock is above the biomass level sustaining maximum sustainable yield, MSY [ICES 2018], the Western Baltic cod stock is considered overfished [ICES 2019a]), life history traits (North East Arctic cod individuals are heavier and later mature than of the Western Baltic cod) and the recruitment-temperature dependence (negative for Western Baltic cod, positive or nonlinear for North East Arctic cod [Planque & Fredou 1999; Drinkwater 2005; Hänsel et al. 2020]), which was an objective of paper III. By upscaling recruitment effects to the population level under different climate change scenarios, we investigated whether
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and how fisheries management can adapt in order to allow for a sustainable fishery at the end of the century. We thereby also elaborated on the general conception that marine fishes located in the north are more resilient to the effect of climate change (Lam et al. 2016a; Lam et al. 2016b).

**Paper IV** was motivated by the general poor state of Canada’s fish stocks (OCEANA Canada 2019) and by the recent re-opening (and frequent re-opening in the past) of the Northern cod fishery (DFO 2019), even though the stock’s biomass is well in the critical zone. The federal department Fisheries and Oceans Canada permitted a 30 % increase in directed catch, despite the science advice that removals from all sources should be at the lowest possible level (DFO 2018a) and recent strengthening of the Canada’s Fisheries Act to rebuild depleted fish stocks (Government of Canada 2019). This apparent subordinate role of science in decision-making, we further analyzed in **paper IV** by looking at the policy framework and institutional structure in regard to Canada’s Sustainable Fisheries Framework. Because the state of Canada’s fish stocks stands in contrast to the precautionary approach which aids in protecting the environment and limit risks (Hilborn et al. 2001; Hanson 2018), we analyzed compliance with the precautionary approach in the role of science. We compared the findings to fisheries management practices in the EU, which is also bound to the precautionary approach, but which differs in its institutional organization and decision-making process (Figure 3). In particular, we looked at the role of science in setting reference points, harvest control rules and total allowable catches, the role of science in handling uncertainty and data limitations, the peer-review process of scientific evidence and the transparency of the science advisory process. We intended to locate weaknesses in application of the precautionary approach and suggest ways of improvement towards a scientifically informed fisheries policy that is fully compliant with the precautionary approach.
3 METHODS

The first three research articles are based on population models of different Atlantic cod stocks, focusing on different drivers of recruitment production that impact collapse and recovery dynamics. In the final paper, an analytical framework was established to elaborate on the precautionary principle in fisheries management.

3.1 Modeling recruitment response to a changing climate

Following Occam's razor's principle (Law of parsimony), I aimed for the simplest model describing the data. Fish stock assessment-models and in particular, those applied to Atlantic cod, are age-structured models (ICES and DFO webpages and Shertzer et al. 2014) that aggregate individuals of the same age assuming same life history properties within each age class. Such a structured modeling approach is effective as it significantly reduces complexity, data demand and thus sources of uncertainty (ICES 2003), but still allows to explore individual-level processes (e.g., survival and reproduction) and population dynamics (e.g., population growth, collapse and recovery) by upscaling these processes (Caswell 2001). Because most cold water fish show an annual reproductive cycle that culminates each year, most traditional fisheries models are also time-discrete (Hilborn & Walters 1992; Quinn & Deriso 1999). In this PhD research, a time-discrete, age-structured model was used, utilizing stock-assessment data for parametrization and proceeding on a number of assumptions: 1) As the dynamics of recruitment are considered the primary determinant of population change and entry of environmental changes, I focused only on the functional response of recruitment (e.g., no consideration of other functions such as body growth) and limited environmental factors and stochasticity to the
recruitment function. 2) I assumed age-specific, constant and non-evolutionary life-history parameters and 3) assumed that the behavior of the fishery remains constant (e.g., its selectivity and objectives). 4) I disregarded migration, spatial factors as well as 5) species interactions for population dynamics. This way, I could trace back all changes in the population trajectory and attribute them to recruitment.

In general, the model can be summarized as a time-discrete, age-structured population model linked with a stock-recruitment function that accounts for an Allee effect (paper I+II), for SST change (paper I-III) and/or rising acidification (paper III). Recruitment reproduction and fishing happen annually at the beginning and end of the year, respectively.

\[
N_{age,t} = \begin{cases} 
N_{age-1,1} * e^{-(M_{age-1,1} + F_{age-1,1})} & \text{if age}_{rec} < age < age_{max} \\
R_t & \text{if age}=age_{rec}
\end{cases} \quad \text{Equation 1}
\]

where age\(_{rec}\) defines the age of the first age class, recruitment, (varies between 1 year old, e.g., North Sea cod and 3 years old, e.g., North East Arctic cod) and age\(_{max}\) defines the age of the oldest age class (varies between 6 classes, e.g., North Sea cod and 13 year classes, e.g., North East Arctic cod).

The number of individuals in each age class at year \(t\), \(N_{age,t}\), equals cohort abundance of the previous year multiplied by the survival rate (reciprocal of constant natural mortality rate, \(M\), and fishing mortality rate, \(F\)). All surviving mature individuals at the end of each year make the spawning stock biomass, SSB\(_t\), which annually produces recruitment, \(R_t\), through a stock-recruitment function (Equation 3), considering the respective recruitment year.

\[
SSB_t = \sum_{age=1}^{11} \mu_{age} * w_{age} * N_{age,t} \quad \text{Equation 2}
\]

with \(\mu_{age}\) and \(w_{age}\) being the age-specific (and dependent on the paper also time-dependent) probability of maturation and weight (in metric tons), respectively.

Data extraction, programming of the population model, statistical analysis and visualization was all performed in “R” (R Core Team 2017). To parameterize the model, time series on recruitment, SSB, abundance, fishing mortality, and life history traits for all 17 Atlantic cod stocks were extracted from publicly available assessment reports issued by the different fisheries institutions responsible (ICES [www.ices.dk], DFO [www.dfo-mpo.gc.ca], NAFO (Northwest Atlantic Fisheries Organization)
In the baseline stock-recruitment model, recruitment and SSB are linearly related (Ricker-type model; Ricker 1954):

\[ R_t = SSB_{t-1} \cdot e^{(a-b \cdot SSB_{t-1})} \]  

Equation 3

In the different articles, the population model was modified and the stock-recruitment model was extended by different components that could non-linearly affect recruitment production. The model was used for a single stock analysis (paper I), for contrasting two stocks (paper III) and comparing all 17 Atlantic cod stocks (paper II) by normalizing the data to reduce scale. In paper II the model was used to reflect on historic population dynamics, while in paper I+II the model was used for forward projections to future climate scenarios.

3.1.1 Stock-recruitment function with an Allee effect

If the Allee effect is not modeled mechanistically (e.g., De Roos & Persson 2002; Van Leeuwen et al. 2008), fish population models usually consider the Allee effect in a stock-recruitment model with at least one additional parameter in comparison to the classical Ricker and Beverton-Holt models (e.g., Chen et al. 2002; Gascoigne & Lipcius 2004; Cabral et al. 2013; Hilborn et al. 2014; Shertzer et al. 2014). Because of data limitation at low abundance (only 30.5% of the data considered in my research had recruitment information for stock sizes \( \leq 20\% \) of the maximum observed SSB), the fitting of an Allee effect stock-recruitment model to SSB and recruitment data did not yield high statistical significance for either of the stocks. In paper I, we therefore applied a meta-analysis of all Atlantic cod stocks following Keith and Hutchings (2012). We linearized the stock-recruitment relation by aggregating recruit-per-spawner ratios (a proxy for realized per capita growth rate) and SSB of all stocks. For the scenarios without an Allee effect, we simply fitted a Ricker stock-recruitment model (Ricker 1954) by applying linear regression to large SSB. For scenarios with an Allee effect, we applied a segmented regression to identify a breakpoint, the Allee effect threshold, below which the per capita growth rate decreased. The model was back-transformed and applied to the North Sea cod stock.

In paper II, we attempted a more mechanistic and stock-specific approach of modelling the Allee effect and considered, apart from spawner abundance, also changes in spawner weight and ocean warming as factors affecting recruitment production and leading to an
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Allee effect. For this calculation, spawner weight and spawner abundance were not considered as an aggregate (i.e., Equation 2+3), but as separate factors influencing recruitment. Recruitment production ($R_t$, Equation 1) was described by three separate sub-functions: The first one captured recruitment production as a sigmoidal function of spawner abundance that could show either a decline or constant recruitment production at low abundance depending on the stock-specific parametrization. Spawner abundance was considered by using the spawners’ average weight over the time-series (instead of time varying weight; for simplicity here called average weighing spawners). The second part of the recruitment function considered the divergence from average spawner weight as an additional factor influencing recruitment production. Weight changes were captured by the ratio between the average weighing spawners and spawners (SSB). A ratio of 1 indicated that weight of the average spawner and SSB was the same. An additional exponent indicated nonlinearity of the relation between spawner weight and reproductive output: If the exponent was $> 1$, increasing spawner weight led to an unproportionally strong increase in recruitment production (and vice versa, decreasing spawner weight lead to unproportionally strong decrease in recruitment, which could lead to or enhance an Allee effect) and if the exponent was $< 1$, recruitment production decreased unproportionally strong with increasing spawner weight. Thus, in contrast to many conventional stock-recruitment models (e.g., Ricker 1954; Quinn & Deriso 1999), SSB was not used as an aggregate, but heterogeneity in recruitment production among spawners of different weight was considered. Though these “maternal effects” have been included in models before (e.g., Marteinsdottir & Thorarinsson 1998; Brunel 2010; Shelton et al. 2015), this model allowed for stock-specific and nonlinear spawner weight and abundance effects on recruitment production.

The third and last component of the recruitment function in paper II was ocean temperature. The relation between SST and recruitment production was considered in a Lorentz function (also Cauchy distribution), which, dependent on the stock-specific parametrization, could show ambiguous temperature dependence. A negative SST dependence could support an Allee effect at low abundance.

Even though I refer to the Allee effect as a density-dependent phenomenon, it remains noted that I did not consider population or spawner density, but abundance to investigate the Allee effect. Some Allee effect mechanisms depend on population density rather than abundance (e.g., a lowered egg fertilization rate), but density data was not sufficient. Especially for fish stocks which are migratory and not confined to the borders of the
assessment area, the distinction between number and density is complex, depending largely on the spatial resolution (Stephens et al. 1999; Osorio-Olvera et al. 2019). Changes in aggregative behavior alter the population density and may indicate temporal changes in the strength of Allee effects (Neuenhoff et al. 2019). Thus, detection of Allee effects depends largely on the data, spatial and temporal resolution (e.g., Frank & Brickman 2000).

3.1.2 Stock-recruitment function with ocean warming

The temperature effect on Atlantic cod recruitment production is usually incorporated into the stock-recruitment function ($R$, Equation 3) as one additional, additive parameter without any further attention to the mechanism behind, and as a monotonic, density-independent, linear effect (e.g., Hilborn & Walters 1992; Clark et al. 2003; Planque et al. 2003) though recent studies do recognize time-variance (e.g., Olsen et al. 2011; Ottersen et al. 2013; Stige et al. 2013; Szuwalski et al. 2015). A density-independent, linear temperature effect has the advantage of an easier interpretation when studying multiple, interacting drivers of recruitment production, as in this PhD research. In paper I, the parameter describing SST dependence was extracted from the meta-study by Planque and Fredou (1999). In paper III, the recruitment model was fitted to time-series of recruitment, SSB and SST data. We assumed that environmental forcing on recruitment constitutes uncorrelated random white noise (Bjørnstad et al. 2004). For simulating ocean warming, ocean temperature was time-varying and a random draw from a normal distribution with mean equal to absolute SST (paper III) or the net increase in SST (paper I) and variance equal to observed SST variance.

Two different approaches were taken for modeling a nonlinear temperature dependence. In paper I+III, a nonlinear relation was fitted between log2 transformed recruitment anomalies and SST anomalies, following the approach by Planque and Fredou (1999). The function was individually chosen and stock-specifically fitted. In contrast, the Lorentz function in paper II was flexible enough to capture the diversity and ambiguous response of Atlantic cod recruitment to SST change. For some stocks, the Lorentz function found a temperature optimum within the observed range of data, which means that the direction of temperature dependence for these stocks changed over time after passing their temperature optimum. For stocks for which no temperature optimum was found, simulated SSB stayed on either side of the temperature curve (Figure 5).
Figure 5: Examples of the fitted Lorentz curve for the North Sea, Icelandic and Southern Grand Bank cod stocks. Temperature has a negative effect (left), ambient effect (center) or positive effect (right) on per capita growth rate within the observational range. Black dots show the data, white dots show the simulation. The star depicts the current position on the Lorentz curve.

3.1.3 Stock-recruitment function with ocean acidification

The effect of ocean acidification on Atlantic cod recruitment was experimentally quantified by Stiasny *et al.* (2016), who were the first to document acidification induced mortality estimates of Atlantic cod. Stiasny *et al.* (2016) kept eggs and larvae of Western Baltic cod and North East Arctic cod under control (~400–500 μatm) and high CO$_2$ levels (~1100 μatm, the global predicted end-century level of ocean acidification under the IPCC RCP 8.5 scenario; IPCC 2013) in two separate experiments until 25 and 22 days post-hatching respectively, and survival was monitored. The survival was absorbed into an additional, density-independent exponential term in Equation 3, describing the fraction of Atlantic cod in the early life history stages that survived the effect of acidification. Without ocean acidification, no recruitment died from ocean acidification, while under acidification survival of the North East Arctic cod reduced to 17 % and of the Western Baltic cod reduced to 4 % by year 2100. Mortality through ocean acidification was assumed to be density-independent as in (Stiasny *et al.* 2016; Voss *et al.* 2019; Hänsel *et al.* 2020), because of no evidence linking density-dependent mortality to changing CO$_2$ levels.

3.1.4 Model utility and limitations

In my PhD, I did not aim for perfection of a stock assessment or prediction model, but used the model as an explanatory tool, which has proven to be immensely useful for studying the drivers and mechanisms potentially leading to shifts and thus facilitates...
directing monitoring efforts (i.e., towards the change in variables or parameters, Figure 2), quantifying uncertainty (e.g., by accounting for the different ways the identified driver can affect the system) and identifying sources of uncertainty (e.g., knowledge or data gaps). This, in turn, supports the formulation of future research objectives.

The suddenness, complexity and scale-dependency of regime shifts and nonlinear dynamics make their investigation and calculation difficult. A regime shift (as depicted in Figure 2) may only be observed on a specific spatial and temporal scale and variable/parameter combination. Similar, relations between recruitment and environmental drivers may appear linear on a short time scale, but appear nonlinear when the time-series is extended. Application of “Early Warning Signals” to anticipate regime shifts (e.g., Scheffer et al. 2009; Dakos et al. 2012) requires that the decline in the resilience of a system can be inferred from changes in readily measurable statistics of the ecological time series. Thus, the quality of the data available is critical, which is in particular difficult in marine fish, because of spatial and temporal sampling limitations (Clements et al. 2015), short, noisy, temporally autocorrelated data (Litzow & Hunsicker 2016), age-size class diversity that dampens the effects of environmental stochasticity (“portfolio effect”; Schindler et al. 2010; Krkošek & Drake 2014) and difficulties in distinguishing variability due to a loss of resilience from variability due to other causes (Litzow et al. 2008).

With the proposed model, climate change impacts and in particular nonlinear response and regime shifts can be studied, though at the (intentional) cost of model complexity. It is thus important to note that the model delivers only one explanation for the observation, that uncertainty always remains and that the results of this research are based on certain model assumptions, some of which are elaborated here.

The model focuses on recruitment as a driver of population dynamics in general and environmentally induced recruitment changes in particular, though recruitment variability is likely a product of many more factors (see introduction and Hjort 1914; Hjort 1926; Houde 2016). Climate change impacts also other life stages, traits and the environment the population is interacting with, including fishing behavior (Watson et al. 2018). In particular relevant for this thesis is temperature-dependent body growth, as it can alter the age-size structure of a population (Daufresne et al. 2009; Neuheimer & Grønkjær 2012; Cheung et al. 2013; Tu et al. 2018), which in turn influences its recruitment production (Birkeland & Dayton 2005; Hixon et al. 2013), size-dependent trophic interactions (De Roos & Persson 2002; De Roos et al. 2003; Ling et al. 2009; Gårdmark et al. 2015;
Gårdmark & Huss 2020), vulnerability to size-dependent fishing, bet-hedging strategies (Hutchings & Myers 1993; Jørgensen et al. 2006; Lowerre-Barbieri et al. 2015) and thus resilience towards a changing environment (Hsieh et al. 2006; Rouyer et al. 2011). The model does not consider changes in life-history traits or body growth and the age-size structure remains relatively stable, which reduces possible “portfolio effects” (Schindler et al. 2010; Krkošek & Drake 2014). The impact of age-size changes on population resilience cannot be studied. In this model, if an increase in temperature enhances body growth, it could boost productivity, slow down stock degradation (paper I) and counteract some of the mortality losses found in paper III. Ultimately, the population’s net effect will then depend on the combination of local temperature and the individual body size, as the temperature-dependent body growth rate is expected to be inversely related to body weight (i.e., the larger individuals of North East Arctic cod may experience warmer waters, but slower body growth [Butzin & Pörtner 2016]). Life history traits for most Atlantic cod stocks are highly dynamic (e.g., appendix in paper II) and, in particular for population projections under future climate conditions, it would be important to consider the mechanisms that change body weight and life history traits (e.g., linking changes in spawner weight to body growth in paper II, considering temperature induced changes in age at size in paper I as in Neuheimer & Grønkjær 2012). Evolutionary adaptation of life-history traits could change the speed and magnitude of collapse and recovery dynamics (e.g., fisheries induced evolution could lead to a smaller equilibrium population size and slow down recovery or increase productivity and lower the risk of collapse [Heino et al. 2013; Dunlop et al. 2015; Nussle et al. 2016]). Apart from evolutionary changes, phenotypic plasticity in life history traits should be important when upscaling from individual fish to population level and predicting its resilience to climate change impacts (Crozier & Hutchings 2014; Gårdmark & Huss 2020; Little et al. 2020).

Fishing can also alter the size-structure of the population by targeting specific size classes (Marteinsdottir & Thorarinsson 1998; Murawski et al. 2001; Hutchings 2005; Brunel & Piet 2013). In this model, however, the selectivity of the fishery does not change over time and I thus implicitly assume that the fishery does not change its fishing strategies or technologies and that the availability of the fish to the fishery remains the same (no change in effort and catchability) in every scenario and under future conditions. Rebuilding an age-size truncated population is likely more complex than the results of this model imply, as feedback effects (e.g., trophic interactions (Walters & Kitchell 2001;
De Roos & Persson 2002; Van Leeuwen et al. 2008; Neuenhoff et al. 2018) may hinder population growth, and re-establishment of the size-structure would be required first. Because the model is not spatial, another important assumption is that within the (management) area of one stock, the (a-)biotic conditions are the same. Though the different cod stocks could be used to define the species’ climate envelope (e.g., Righton et al. 2010), the biological response to climate change is a product of exposure and sensitivity and thus the only aspects of weather and climate that affect individuals are those in its immediate vicinity (Helmuth et al. 2010). Extrapolating from average climate scenarios, which ignore local climate heterogeneity (AMAP 2018), the severity and duration of local weather events (Russell et al. 2009; Buckley & Huey 2016) can therefore lead to over- and underestimation of the population’s response to climate change in different areas. The thesis does consider an increase in fishing and temperature variance (paper I), but only as uncorrelated white noise (Bjørnstad et al. 2004), while the succession of several extreme events will likely strengthen the effect of variance on recruitment (Morales 1999; Heino et al. 2000; Schwager et al. 2006) and the risk of Allee effects, regime shifts and nonlinear behavior. Similarly, while the model does account for nonlinearity in the recruitment response to environmental change, the driver itself (i.e., warming, rise in CO2, increase in fishing pressure) is considered to change in the future only linearly, unidirectional (increase in warming, acidification, variation and fishing) and based on the mean prediction of global climate models (IPCC 2019). The relationship between temperature and pH level (paper III) is, however, not linear and, because other important factors, such as oxygen, are thermally limited, their combined effect is not additive (Pörtner & Farrell 2008). Further, the dynamic temperature sensitivity of Allee effects found in paper II cannot be considered when predicting a mean increase in temperature and ignoring occasional cooling events (such as the Allee effect in North East Arctic cod, which appeared during colder years, paper II).

The migratory behavior of fish also impacts climate exposure and response and can impacts population productivity by e.g., affecting reproductive energy (Färber et al. 2018), exposure to new prevailing ecosystem conditions and trophic interactions. Fish stocks that reach their environmental tolerance limit will be more adversely affected, which can strengthen the risk of regime shifts and collapse. Other spatial elements, such as drift of eggs and larvae from their advantageous habitat (e.g., due to wind and ocean currents, “aberrant drift”) and spatial constraints causing recruitment variability (e.g., member vagrancy; Sinclair & Iles 1989) or consideration of an optimal oceanographic
window; Cury & Roy 1989) could not be considered here. I interpreted data indicating little recruitment at low abundance as an Allee effect (paper I-II); little recruitment due to losses of pre-recruitment stages from physical processes were not considered here. While a spatial model might be realistic, the analysis of regime shifts and nonlinear behavior will become highly complex when adding another dimension. For example, Wang et al. (2014) find that adding a spatial dimension can lead to instability of the equilibrium points, driven by the joint effect of diffusion and the Allee effect. Regime shifts are often accompanied by an increase in spatial variance (Litzow et al. 2008), which are likely to interact with Allee effects at low abundance and further challenge their identification and research.

The data used in my research is not raw data, but was derived from stock-assessment models. They, too, are subject to model assumption, model uncertainty and stock expert bias (Schuch 2020), which translate to the model outputs and add uncertainty to this thesis’ results. An implicit assumption of the stock-assessment data is that it is representative for the entire actual habitat of the population (which may not be the case when e.g., the stock management area is not adjusted [Schuch et al. 2021]), that the stock is indeed one stock and not a stock complex composed of several sub-populations (e.g., Frank & Brickman 2000) and that the data reflects the actual abundance and density of the population without a change in the abundance-density relation. The abundance-density relation is critical for the study of recruitment production and Allee effects, as they depend on the abundance and encounter rate of spawners. For example, in the Ricker function (Equation 3), recruitment and SSB are linearly related, implying that every spawner contributes to recruitment production. However, not only can spawners deliberately skip spawning (Jørgensen et al. 2006; Skjæraasen et al. 2012), spawners can also be too far away to contribute to the reproductive process, which could compromise the use of abundance data when studying density-dependent phenomena.

Population dynamics of a stock complex would depend on the dynamics of the different sub-populations and their interaction (e.g., source-sink relations). Instead of biomass as a critical factor for collapse and recovery, it would be these linkages that are crucial (e.g., Frank & Brickman 2000; Dean et al. 2019). Though in some stocks their sub-structure has been acknowledged in the scientific assessment (e.g., North Sea cod [ICES 2020]), the assessment data is still aggregated on stock level. Similar to the consideration of the population as a single stock is the treatment of Atlantic cod as an isolated entity and ignoring any further species interaction. Atlantic cod is interconnected to its ecosystem
and its population behavior is a response to its interaction with the environment, other species and human intervention. For example, the temperature-dependent recruitment production considered here can be caused by direct temperature dependence of recruitment survival/production (Brander 2010; Drinkwater et al. 2010), or indirectly by the temperature-dependent occurrence of a *Calanus* species that early cod life stages prey on (Munk 1997; Beaugrand et al. 2003; Olsen et al. 2011). Similarly, the Allee effects found here, can be caused by direct density-dependence of recruitment production or they can be a result of species interactions. In the Gulf of St. Lawrence cod stock, for example, the Allee effect is likely caused by seals predating on the cod population (Neuenhoff et al. 2018) and in the Baltic cod stock by the reduced availability of right-sized sprat (Van Leeuwen et al. 2008). Thus, the model indirectly considers interactions with other species, though the implications differ in a multi-species perspective. If a species interaction is behind the (nonlinear) response to climate change, managing only Atlantic cod is likely not effective. Changes in the physical habitat and ecosystem in response to changes in cod abundance may not allow cod to re-populate its niche after depletion as easily as the results of this thesis suggest. Further, species-rich communities are thought to produce more temporally stable ecosystems, because of the complementary dynamics among species that perform similar ecosystem functions (“diversity–stability hypothesis” (Tilman 1996; Chapin Iii et al. 2000; Schindler et al. 2010). Similar to when considering age-size dynamics, considering more ecosystem information could lead to the result that no regime shift is found as a result of self-stabilizing effects of the ecosystem or because of more noise in the data and statistical signal blurring the analysis. While the first case may make the results of this thesis less severe, in the latter case, this could lead to an increased risk and impact as management cannot prepare for the possibility of regime shifts.

With these assumptions in mind, the results should be interpreted as equilibrium scenarios of an average, cod-typical stock projected to different climate scenarios. The model can be used to guide management, localize uncertainty and direct future research for more specific and local management based on population predictions. I therefore deliberately use “projections” instead of “predictions” to describe the results of this thesis and account for the assumptions they are based on (Caswell 2001; Massad et al. 2005). I believe that the model provides predictive capacity to fisheries management by guiding management efforts, localize uncertainty and direct future research for more specific and local management strategies. It thus contributes to a general understanding of the resource
dynamics and resource availability, which is important for achieving sustainability and blue growth.

3.2 A framework to analyze the precautionary approach

Paper IIII scrutinizes the precautionary approach in Canada’s fisheries management practices and compares the findings to practices in the EU in an analytical framework. For this, we looked mainly at grey literature and legal and policy documents (acts, regulations, decisions and agreements) to investigate compliance with key principles of the precautionary approach, which we identified as: 1) Definition of quantifiable criteria (reference points) for scientific assessment of the management objective (total allowable catch, TAC), 2) Evaluation of the attendant risks, and 3) Evaluation of what respective actions (harvest rules) will meet the objectives. Besides following scientific standards (objective, verifiable and replicable), this implies 4) a peer-review process to ensure that the best available evidence is used and 5) a transparent science advisory process. Building on findings by VanderZwaag et al. (2012), we further used a conceptual framework to distinguish science-based decisions from science-determined decisions in the setting of reference points, harvest control rules, and the TAC. Science-based decisions are the result of a consultation process regarding various stakeholders (VanderZwaag et al. 2012) and science is involved in the decision-making process, but its role is not always central, clearly defined and accountable. Often a public record of the policy decisions that clearly distinguishes science from non-science inputs is not available. That is, science cannot be identified as the starting point of the decision consultation (Figure 3). In contrast, science-determined decisions are those determined by scientists, using evidence analyzed by scientific models that are also applied elsewhere in the world (VanderZwaag et al. 2012). The science advice is transparent (accountable) and forms the basis for the decision consultation (horizontal process based on science advice; Figure 3).
4 RESULTS AND MANAGEMENT PERSPECTIVES FOR A SUSTAINABLE FISHERY

Fish stocks are exposed to a multitude of growing stressors, foremost related to fishing pressure and climate change, which impose challenges for sustainability and recovery. This thesis elaborates on factors and mechanisms that can change fish stock productivity in such a way that re-establishment of pre-collapse conditions (e.g., low fishing pressure) is either not sufficient (regime shift) or not possible (persistent climate change). I was in particular interested in factors that interact and jointly affect population dynamics. I observed that these factors vary within the same species, vary over time and vary in their form. I found, for example, additive interactions (e.g., ocean acidification adds additional mortality to negative temperature dependence in Western Baltic cod; paper III), antagonistic interactions (e.g., ocean warming compensates for acidification in North East Arctic cod; paper III) and synergistic interactions when a regime shift caused an impact much larger than the sum of the effects (e.g., an Allee effect; paper I+II). Several, for fisheries management relevant, conclusions emerge from this thesis: 1) recruitment dynamics are often transient and not linear (nonlinearity). 2) Allee effects and persistent climate change increase the risk of irreversible productivity changes (irreversibility). 3) Recruitment and population dynamics under climate change are difficult to predict (surprise).
4.1 Nonlinearity

In this thesis, nonlinear dynamics are caused by an Allee effect and by a nonlinear recruitment response to ocean warming. Although Allee effects are associated with an increased risk of population collapse (paper I+II and Courchamp et al. 1999; Chen et al. 2002; Dennis 2002; Gascoigne & Lipcius 2004) and delayed or absent recovery (Kuparinen et al. 2014a; Hutchings 2015; Kuparinen & Uusi-Heikkilä 2020), they are not considered in (Atlantic cod) fisheries management (only in the Gulf of Maine cod, Allee effects are considered as a source of uncertainty [Palmer 2014]). The Allee effect threshold is typically found much below limit biomass reference points. Hutchings (2014) estimated for 119 marine fish stocks on average an Allee effect reference point at 20% of the biomass level sustaining MSY, which resonates with our findings in paper I (Allee effect threshold at 23% of the biomass level sustaining MSY and 32% of the biomass limit reference point). Though the Allee effect threshold under current conditions is considerably lower than the management reference point, we find that ocean warming can shift the Allee effect threshold to higher biomass levels and reference points become un-precautionary if not adjusted. For the North Sea cod, we find that if ocean warming increases beyond +2 °C, current reference levels involve a high probability of collapse and low probability of recovery in presence of an Allee effect. Ocean warming strengthens the Allee effect in the North Sea cod and thus significantly increases the probability of collapse while reducing means and pace of fisheries management to avert the population’s collapse. Besides strengthening of the Allee effect in several other Atlantic cod stocks, we further find in paper II that the Allee effect can also be weakened and reversed if warming has a positive recruitment effect. This means that the Allee effect is not as static as generally assumed (e.g., Courchamp et al. 1999; Hutchings 2014 but very recently recognized in Berec 2019; Vet et al. 2020), but the form and the Allee (effect) threshold can change over time, making inclusion of Allee effects in fisheries reference levels difficult.

The interaction between warming and the Allee effect depends on the nature of the temperature dependence, i.e., its strength, direction and density-dependence. For several Atlantic cod stocks, we fitted a temperature-recruitment function showing an optimum of recruitment production (paper II). Stocks which benefitted from warming in the past but have now passed a temperature optimum are likely to show declines in recruitment production in the future. For example, extraordinary low SST supported recruitment production in the Kattegat cod in the past but future warming could negatively impact
recruitment production and “unmask” an inherent Allee effect (paper II). In other stocks, such as the Southern Gulf of St. Lawrence (paper II) and the North Sea cod (paper I+II), warming could further strengthen the Allee effect, thus squandering rebuilding efforts. Acknowledging the potential time-invariance and nonlinearity of recruitment response is important and brings to mind that the current observed recruitment relation is only a snapshot in time and of natural variability. In accordance with other studies (Myers 1998; Tamburello et al. 2019), I find that the temperature-recruitment relation weakens when updated with more data and that the sensitivity to temperature change varies over time, which supports consideration of nonlinear and time-variant environment-recruitment relations (Ottersen et al. 2013; Stige et al. 2013; Devine et al. 2014; Munch et al. 2018). The Ricker stock-recruitment function, as used here, has the major drawback of a linear approximation of the environmental effect. I find that in comparison to a linear relation, the impact of a nonlinear temperature function critically depends on the current stock’s position on the fitted curve. For North East Arctic cod, for example, we find an Allee effect during colder years, where the stock was exceptionally sensitive to cooling (paper II). We also find that future warming will increase the stock’s recruitment less than predicted from linear temperature models (Planque & Fredou 1999; Drinkwater 2005), because of a decrease in temperature sensitivity (paper II) and the stock’s approximation of an optimum (paper III appendix). Especially for stocks in close proximity of their temperature optimum, minute differences matter and can reverse the response to future environmental change (paper II). For these stocks, extrapolating from a linear stock-recruitment model and/or considering only unidirectional environmental effects would lead to wrong population predictions and management decisions with a high potential for negative ecological, social and economic consequences.

The thesis highlights the fact that the benefits of management interventions (e.g., reducing fishing pressure) are contingent upon the climate regime the system is experiencing in any given year. Thus, when environment–recruitment relationships underpin reference levels and fisheries decision-making in general, they should be re-evaluated on a regular basis as part of an adaptive management approach to ensure that they remain robust in the face of new data and continue to provide an accurate representation of recruitment production in light of a continuously changing climate. When nonlinearity is (suspected to be) present, using recent observations to predict the consequences of alternative management actions can improve management outcomes (e.g., Ianelli et al. 2012; Tamburello et al. 2019), as well as precautionary strategies that “buffer” reference levels.
to account for an Allee effect (e.g., Chen et al. 2002) and abundance fluctuations. The latter is particular important as fluctuations, e.g., related to interannual fishing variation or temperature change, increase the risk of passing climate and/or Allee effect thresholds, which could increase the probability of collapse (paper I and Scheffer et al. 2001). Extreme climate events could further exaggerate the risk.

4.2 Irreversibility

Productivity shifts caused by climate change or an Allee effect can be irreversible. The Allee effect per se does not lead to irreversible extinction. There is an important distinction between a weak and a strong Allee effect. Only the latter inflicts bistability by introducing an unstable equilibrium point below which realized per capita growth rate becomes negative and the population goes extinct (Figure 4 a and Berec et al. 2007; Courchamp et al. 2008). Extinction is a stable equilibrium, reinforced by a negative population growth rate. Once passing the Allee effect threshold (tipping point), attraction to the extinction equilibrium is stronger than attraction to the high biomass equilibrium and extinction becomes likely, especially if the underlying changes are not immediately halted (paper I and Beisner et al. 2003). Following this theoretical background, we find that in presence of a strong Allee effect, the North Sea cod cannot recover once collapsed, even if fishing is fully prohibited (paper I). Recovery would require negative fishing pressure, i.e., re-stocking (Figure 4 b), which is usually not possible for wild fish stocks.

We further find that prevention of population collapse critically depends on the climate regime and how fast fishing pressure is halted once the population drops below the Allee effect threshold and is “attracted” by the lower equilibrium. Due to the negative temperature-recruitment relation, ocean warming reduces the per capita growth rate and shifts the unstable equilibrium to higher biomasses (Allee effect type I variation in Walter et al. 2017, more empirical evidence in Berec 2019; Vet et al. 2020). Fishing pressure gradually reduces the interval between the stable (large population size) and unstable equilibrium, indicating a loss of resilience. As a result, additional stress from for instance climate change brings a higher risk to reduce the population to critical numbers and the population is more vulnerable to collapse (Stephens & Sutherland 1999). We find that a fishing moratorium is only sufficient for recovery when ocean warming remains within 2 °C and fishing is restricted within 10 years. If temperature rises beyond 2 °C, even immediate banning of fishing is not sufficient to guarantee recovery. If fishing is not fully
banned and a residual fishing pressure of e.g., \(0.1\, y^{-1}\) remains, recovery is only possible within 5 years, provided warming does not exceed 1 °C.

Though we focused only on the threshold for collapse, for rebuilding plans it would be helpful to identify the target biomass threshold level until which re-stocking would be necessary for the population to sustain itself. Such a level would be in proximity of the tipping point (Allee effect threshold), but would critically depend on the strength of the attraction basins (lower/higher equilibria) and the climate conditions and productivity regime influencing these (Wang et al. 2014; Cai et al. 2015). Fishing and climate change jointly reduce the resilience to the impact of an Allee effect and constitute together the boundaries for sustainability. Similar to Sguotti et al. (2019), we find that the system’s tipping points are an expression of both fishing pressure and ocean temperature, which can modulate each other.

We find that depletions aggravated by unfavorable climatic changes will be difficult to reverse. For several cod stocks, we find that Allee effect occurrence coincides with prolonged recovery (paper II), though we also find the magnitude of depletion to be an important determinant of recovery (paper II). These findings support the notion that a prolonged, degraded population state can become manifest, not only by an Allee effect, but because of an increased vulnerability to genetic, demographic and environmental stochasticity and a reduced capacity to tolerate and adapt to external stressors at low abundance (Hutchings & Myers 1993; Lande 1998; Marteinsdottir & Steinarsson 1998; Ottersen et al. 2006; Anderson et al. 2008; Hsieh et al. 2008; Shelton & Mangel 2011; Brown et al. 2012; Rouyer et al. 2012; Kuparinen et al. 2014a).

Another important determinant of recovery is the fishing history before depletion (Neubauer et al. 2013). Heavy fishing pressure and the alteration of density-dependent regulation at small population size can alter life-history traits and recovery behavior (Fudge & Rose 2008; Enberg et al. 2009; Neubauer et al. 2013; Eikeset et al. 2016; Nussle et al. 2016). In several cod stocks, prolonged low abundances coincides with a shift towards smaller, lighter spawners with lower productivity (paper II), which could have been caused by long-running and strong age- and size-selective fishing (Marteinsdottir & Thorarinsson 1998; Murawski et al. 2001; Hutchings 2005). Under a short-tailed age-size structure, the population can rely less on the increased quantity and quality of reproductive output by older, experienced and large fish (“BOFFFFs”; Marteinsdottir & Steinarsson 1998; Murawski et al. 2001; Birkeland & Dayton 2005; Hixon et al. 2013).

As the level of fishing mortality increases and the population size declines, the population
dynamics are increasingly dominated by recruitment dynamics and vulnerable to recruitment variability (Hsieh et al. 2006; Rouyer et al. 2011). This could also explain the strong impact of acidification found in the Western Baltic cod (paper III), which is strongly age and size truncated (Svedäng & Hornborg 2017). In this stock, smaller female spawners have been found to produce eggs with lower buoyancy, thus leading to a lowered reproductive success in the oxygen depleted waters of the Baltic Sea (Vallin & Nissling 2000; Hinrichsen et al. 2016). Thus, it is likely that the Western Baltic cod’s capacity to buffer increased recruitment mortality from CO₂ and to dampen environmental stochasticity had been eroded by its long-standing fishing history (Shelton & Mangel 2011; Rouyer et al. 2012).

The results show that fishing, climate change and the Allee effect can lower the population’s productivity, increase its vulnerability to other stressors and increase its risk to irreversible collapse, which emphasize the need for precautionary and fast management decisions. Even with precautionary reference levels, delays in acting on declines in population growth can significantly increase the risk of collapse. Especially nonlinear dynamics, such as posed by an Allee effect, require timely management response in order to prevent (prolonged) collapse (paper I and Brown et al. 2012; Neubauer et al. 2013). Delays in conservation measures caused by e.g., slow data collection and analysis, communication of science advice (paper IV), bureaucratic inertia and social resistance (Hutchings & Reynolds 2004; Agnew et al. 2009; Davies et al. 2009; Brown et al. 2012) or counterproductive governmental incentives (Sumaila et al. 2008; Sumaila et al. 2019) could be accounted for by more conservative reference points. Implementation of a full, prompt fishing moratorium is extremely difficult, and we show that even small residual fishing pressure e.g., through illegal fishing (Agnew et al. 2009) and bycatch (Davies et al. 2009) can increase collapse probability when in proximity to the tipping point (paper I). Similarly, re-opening the fishery to soon can impair recovery and nullify recovery efforts. The re-opening of the Northern Cod fishery in 2016, for example, took place despite biomass levels remaining below the limit reference point, and the biomass decreased by 30 % again in 2018 (DFO 2018b).

The permanent productivity changes discussed here signify that the baseline for assessment and management has changed, requiring management strategies that are adaptive to such a “shifting baseline” (Pinnegar & Engelhard 2008; Fluharty 2011; Klein & Thurstan 2016) in order to remain efficient. This could be operationalized by basing reference points on “prevailing environmental conditions” as attempted in the US
(www.fisheries.noaa.gov, a concrete example is Ianelli et al. 2012), and not on historic or long-term averages, as for many Atlantic cod stocks (ICES 2019b). Using such historic, long-term averages as a reference level may only work if the period of environmental forcing is short and without a clear long-time trend (Haltuch & Punt 2011). In order to account for a changing environment and productivity, recruitment dynamics should not be fixed (i.e., described by one specific stock–recruitment curve), but instead consider influences by the prevalent (environmental) conditions (e.g., the recruitment function of the North Sea cod was shaped first by food availability and then by sea temperature [Olsen et al. 2011]). If the carrying capacity shifts, this also challenges locating Allee effect thresholds and could imply that Allee effects occur at larger abundance than so far considered (paper II). To prevent stock collapse (paper I+III) and maintain realistic rebuilding targets (Britten et al. 2017), reference points should consider magnitude and pace of climate change, as well as the increased uncertainty under climate change.

4.3 Surprise
Regime shifts have strong, often unfavorable repercussions for the ecosystem and socio-economics and are likely to increase in frequency under climate change. Population dynamics under climate change and in particular, in presence of a regime shifts are difficult to predict and consider in fisheries management (King et al. 2015). One observation of this thesis is that there are always multiple drivers acting and often modulating each other. Several interactions have been found between the Allee effect, temperature and fishing (paper I+II) and temperature, acidification and fishing (paper III). These drivers, together with other factors, confine a “Safe Operating Space” (Scheffer et al. 2015; Carpenter et al. 2017), where the bounding level of each driver (“boundaries”) depends on another. We find that increasing climate pressure lowers the fishing pressure allowing for MSY (paper I+III). Conversely, drastically managing fishing, a stressor unrelated to climate change and which is easier to control, can enlarge the Safe Operating Space by compensating some climate change effects (Carpenter et al. 2017; Brander 2018a; Gaines et al. 2018; IPCC 2018) and mitigating climate change impacts (e.g., decreasing marginal effects, paper I). However, especially for North Sea cod and the Western Baltic cod, this thesis also shows that climate change and the Allee effect restrict possibilities for management adaptation and not all fish may be saved by limiting warming to the global target of 1.5 °C (paper I+III).
Besides mitigation strategies, fisheries management can also increase the population’s resilience (i.e., increasing steepness of the valley in Figure 2) by maintaining a balanced mix of age and size classes (Hsieh et al. 2006; Walsh et al. 2006; Anderson et al. 2008; Brunel & Piet 2013), sex ratio (Courchamp et al. 2008), sup-population structure (Frank & Brickman 2000; Sterner 2007; Kelly et al. 2009) and spatial resolution (i.e., locations of high spawner abundance [Hsieh et al. 2008; Ciannelli et al. 2013; Langangen et al. 2019]), which support the population’s productivity, counteract Allee effects and allow for bed hedging and buffer capacities. Thus, traditional practices of targeting spawner aggregations (potentially creating an “illusion of plenty”; de Mitcheson & Erisman 2012) and the largest individuals should be reconsidered. Instead, spatial management strategies should be emphasized (Fu & Fanning 2004; Svedäng et al. 2010), where the spatial structure of a population is monitored and catches are numerically and also geographically accounted for (Link et al. 2011). Local management strategies are important to consider the stock-specific response to climate change and reduce local stressors (e.g., fishing), and can still mitigate the impact of global stressors (e.g., ocean warming or acidification) (Russell et al. 2009).

Acknowledgement of the interconnectivity between drivers is further motivated by the ecosystem-approach, as species interact and their impacts propagate through the ecological network, which can lead to regime shifts (examples in introduction). Many fisheries management decisions do not include environmental drivers or indicators yet, but there are growing efforts towards multi-species and ecosystem-based management, especially for well-researched stocks such as from the Atlantic cod (Skern-Mauritzen et al. 2016). Though finding significant and/or stable recruitment-environment relations (Myers 1998; King et al. 2015; Szuwalski et al. 2015; Tamburello et al. 2019) and finding causal relations between simultaneously appearing factors is challenging, further work on establishing causal recruitment-environment relations and identifying mechanisms and drivers of Allee effects and regime shifts can aid in population prediction, directing monitoring efforts and managing key drivers.

Part of a holistic ecosystem approach is also the consideration of the human component as an integral element of fisheries. Though in this thesis fishing pressure is treated as an external driver of population dynamics, it is effectively a result of a socio-economic context in which the fishery operates with a policy and institutional framework in place. One example is the increase of catch quota in the Northern cod fishery despite its population being below the limit biomass reference level (DFO 2018b), which reflects
the strong industry interest in the stock and an unstructured, ambiguous decision-making of Canada’s fisheries management (paper IV). Another recent example are spatial restrictions in the North Sea, imposed by e.g., offshore wind farms, Natura 2000 protected areas and Brexit, which influence fishing grounds and thus change the fishing pressure stocks are exposed to. Further, in many places including the North Sea, Atlantic cod is fished in a mixed-species fishery, which can lead to conflicting management advice for the different species and the de facto fishing pressure relies on the tactical decisions of the fishery. The discard ratio of Atlantic cod in the North Sea is 20 % (ICES 2019b), and with the landing obligation, Atlantic cod becomes likely a choke species (Mortensen et al. 2018). Quota trading can still enhance cod fishing if no catch-quota balancing options are available (Oostdijk et al. 2020). The complexity of mixed fisheries can make management advise derived from a single species model, such as limited fishing activities or even a fishing moratorium on a single stock, ineffective and may jeopardize recovery of weak stocks. In the EU, the limitations of the traditional, single-species approach has been recognized and ICES advises an increasing number of stocks with a mixed fisheries approach by e.g. merging the various single-stock assessments and providing a range of catch scenarios (ICES 2014).

This thesis demonstrates that climate change brings uncertainties, which demands scientifically informed, proactive and precautionary management measures to protect the environment and manage risks. Synthesizing the findings from paper I-III in regard to the requirements of the role of science (paper IV) for successfully managing fish under uncertainty and climate change, several conclusions can be drawn. The thesis demonstrates that stock trajectories are governed by more factors than only fishing pressure (e.g., by the reduced age structure and resilience caused by strong historic fishing pressure in Western Baltic cod [paper II], climate effecting recruitment production [paper I-III], Allee effect dynamics hampering productivity [paper I+II]). Neglecting these factors can lead to management failure. For example, if an Allee effect suppresses recruitment production and therefore hampers stock rebuilding, implementing a fishing moratorium may not be effective or re-opening the fishery too early may lead to unforeseen population decrease. Thus, in the decision-making process and in particular in the ecosystem approach (Wilson 2009), science needs to be given authority to provide the best available information regarding the entire ecosystem, such as of potential Allee effects or environmental impacts. As science is a dynamic process and new scientific findings constantly advance the state of knowledge, scientific information, standards and
methods should be peer-reviewed regularly (PA key principle 4, paper IV). This becomes in particular much-needed in light of the fast pace of the changing environment and (nonlinear) population dynamics, where scientific information needs to be quickly updated, decision-making and implementation needs to be fast and adaptive (Fluharty 2011), irrespective of long-standing, rigid international practices such as the “relative stability” principle when allocating quota (Engler 2020; Schuch et al. 2021). Paper I+II for example, show how reference levels become ineffective when not accounting for productivity changes or letting industry set reference levels (paper IV). The change in the underlying biology can lead to misperception of the stock status, leading to risks greater than anticipated (e.g., collapse in Western Baltic cod [paper III] or North Sea cod [paper I]), but could also lead to increased precaution and a fishery that is underexploited (e.g., North East Arctic cod [paper III]), a safe but potentially costly scenario (Heino et al. 2013). Independent of the management target, scientifically determined, up-to-date reference levels (PA key principle 1, paper IV) are needed as objective, quantifiable criteria to assess stock status and progress and guide management. The (nearly) open-access and transboundary nature of many fisheries requires multi-lateral cooperation and transboundary governance (Sumaila & Pauly 2007; Stokke 2011; Palacios-Abrantes et al. 2020a; Østhagen 2020) based on internationally recognized scientific standards, in order to implement international policies (e.g., the Common Fisheries Policy in the EU) and reach global targets (e.g., the Aichi sustainability target; CPD 2011).

It is important that policy formulation is very clear in rendering science the according undivided responsibility (PA key principle 5, paper IV; e.g., no vague harvest control rule as of the southern Newfoundland cod stock [DFO 2016]) and giving science the platform to quickly inform management and intervene. This is further illustrated in paper I+II, where in presence of Allee effects and climate change, fishing pressure needs to be reduced quickly and strictly to avoid collapse. Because the magnitude of stock degradation is decisive for rebuilding (paper II and Neubauer et al. 2013; Hutchings 2015), fishing restrictions need to be immediately in place once a stock is falling below sustainable levels. When in defiance of a scientifically advised moratoria, fishing continues (e.g., because the management decision deviates from the advice or as a result of non-compliance), rebuilding efforts are hampered and the population may irreversibly collapse (paper I). Conservation efforts can be slowed down by governmental stimuli, such as fisheries subsidies (Sumaila et al. 2008; Sumaila et al. 2019), if they are not in line with the population state. Further, if it is not possible to disentangle such economic
incentives from the scientific advice and identify who holds the respective accountability for the ecological state, the credibility of the scientific advice may be weakened. Management failure can lead to mistrust in management and the science, which can motivate non-compliance with regulations and further hamper management success. To promote trust in management decisions and management efficiency, the decision-making process should be clearly structured and transparent, ensuring scientific integrity and a well-defined role of science that is publicly distinguishable from decision-makers (PA key principle 5, paper IV). Further, science assessment needs to inform not only on immediate and future yields but also on the uncertainty and risks involved when e.g., diverging from the science advice (PA key principle 2, paper IV). Such a scientific risk evaluation becomes in particular emergent as this thesis shows how uncertainty is an integral part of climate change management. For example, fishing North Sea cod at the currently advised fishing pressure may be sustainable now, but can lead to a 50 % probability of collapse, when the ocean warms and in presence of an Allee effect (paper I). Providing a scientific evaluation of different catch options (PA key principle 3, paper IV and ICES 2014) or a risk analysis that explores potential (nonlinear) relationships worthwhile further study and the extent to which management strategies are likely to be robust to these could account for the high uncertainty involved when managing fish under climate change (Chen et al. 2002; Punt et al. 2013). While the acceptable level of risk depends on the management objective, it is the responsibility of science to inform about the uncertainty and attendant risks (PA key principle 2, paper IV).

4.4 Future research

Though some future research suggestions have been mentioned in the previous chapter, I here outline the largest research gaps for informing fisheries management under climate change. While the effects of temperature change on Atlantic cod distribution, growth and recruitment have been studied extensively (e.g., Ottersen et al. 1994; Brander 1995; Planque & Fredou 1999; Drinkwater 2005; Stige et al. 2006), ocean acidification studies are limited by the lack of empirical studies, in particular regarding acidification effects on different life cycle components. Such information would be important to build a population model that considers environmental impacts on all life history traits and the entire life cycle (not only recruitment as in this thesis), which is necessary to make more realistic future predictions. While paper I+III address some stock-specific response to climate change, more stock-specific experiments would be desirable in order to relate...
climate change impacts to life-history and thus other species, maybe even outside the marine realm (Pinsky et al. 2019).

Some of my research’s results advocate for more spatial management strategies (e.g., a fishing moratorium relevant for a mixed fishery could be more efficient by closing fishing areas instead of restricting fishing), which could be concretized with a spatial model. Such a model requires spatially resolved data; stock-assessment would not be sufficient, but probably “raw” sample data should be used, which would first need to be standardized and rarely contain recruitment estimates, let alone information on pre-recruitment stages.

Further, to study local climate change impact, more local abiotic data for the physical environment is needed, including depth-specific data, as fish also move downwards in response to changing environmental conditions (Freitas et al. 2015; Ingvaldsen et al. 2017). Stock-specific experiments on the impact of exposure duration to elevated temperature and CO$_2$ levels are needed, which could link sensitivity to local climate variability and elaborate on stock-specific and multi-driver (i.e., temperature and CO$_2$) optima and threshold levels. This could provide information on range shifts as fish species close to their environmental limits of their distribution would be the first to shift range (Brunel & Boucher 2006; Campana et al. 2020), but could be restricted by other environmental factors (e.g., warmer temperatures may promote poleward migration, but ocean acidification, changing ocean currents, nutrient inflow or the photoperiod may constrain migration [Kaartvedt & Titelman 2018; Steiner et al. 2019; Sandø et al. 2020]).

More multi-driver consideration could aid predicting populations under multi-emission (different, combined temperature and CO$_2$) scenarios and identifying and managing environmental sustainability boundaries (“Safe Operating Space”; Carpenter et al. 2017; Brander 2018a; Gaines et al. 2018; IPCC 2018).

For an ecosystem-management approach and multi-species management advice, which concerns many Atlantic cod stocks, consideration of the interactions with the environment and other species is important (Pikitch et al. 2004). The observed response to climate change often is not, as simplified here, a direct response, but rather an indirect response to changes in prey or predators. Climate change propagates through the food web and trophic interactions and can modify and mediate the impact of stressors and of the management strategies (Kadin et al. 2019). This requires identification of the ecological interaction and quantification of the climate change effect on the interacting species and the interaction itself (e.g., change of density-dependence with warming [Olsen et al. 2011]), which remains challenging. Environmental variability interacting with complex
Trophic interactions can blur signals in time series data (Schindler et al. 2010; Oken & Essington 2015) and further challenges the study of regime shifts and nonlinear effects in an ecosystem context. How to study these complex dynamics on a broad, multidimensional scale (e.g., Rocha et al. 2018) is a question for future research.

The thesis shows that predicting population dynamics under climate change involves a lot of uncertainty and thus translating uncertainty into risk management becomes an increasingly important part of fisheries management. The task of scientific models is therefore to consider this uncertainty and communicate the impact effectively. In place of deterministic, parametric population models (as used in this thesis), a probabilistic, Bayesian modeling approach could improve incorporating uncertainty of different sources. This is in particular useful in a state-space modeling framework, as the random variability of both the dynamics of the population (e.g., age-dependent species interaction [Patin et al. 2016]) and of the data (e.g., regarding natural [Cadigan & Marshall 2016] or fishing mortality [Aeberhard et al. 2018]). Because nonlinear dynamics and non-normal errors (uncertainty) can be considered (Carlin et al. 1992; Millar & Meyer 2000; Rivot et al. 2004) as well as noisy data (Rivot et al. 2004; Dennis et al. 2006), this approach is in particular useful for studying regime shifts and nonlinear dynamics and increase the information available for fisheries management and better quantify the uncertainty of parameters of interest for management. A different approach to considering uncertainty in models are “ensemble models”, which combine different models and provide a unified set of predictions for the same quantity of interest (e.g., climate forecast from coupled climate models [IPCC 2019] or some covid-19 forecasts in the U.S. based on different models [https://viz.covid19forecasthub.org/]). This approach uses a broader knowledge base and the sensitivity to individual model assumptions (or threshold definitions such as “When is a population considered collapsed?” paper I+II), model bias and uncertainty is reduced, which can substantially improve estimates of population status and trend (Brodziak & Piner 2010; Anderson et al. 2017), also when data is limited (Rosenberg et al. 2018). Model ensembles expand the range of hypotheses that can be explored (Dietterich 2000; Brodziak & Piner 2010; Rossi et al. 2019) and allow to assess the overall uncertainty and risk effectively (Jardim et al. 2021), which can improve future scientific advice and fisheries management under climate change.

Based on the results of this thesis and independent of the model complexity, I suggest that future research (models) considers 1) multiple drivers and multi-emission scenarios, 2) both magnitude and pace of climate change, 3) variance and extreme events as part of
climate change and 4) propagating climate induced uncertainty in order to inform decision-making under climate change.
5 CONCLUSION

There is increasing human stress imposed on the oceans with the North Atlantic Ocean and the Arctic as focal areas of blue growth, and increasing pressure from fishing and climate change, jeopardizing the future of one of its most prominent species, Atlantic cod. This thesis tackled the question “What drives the collapse and what drives the recovery of Atlantic cod?” by analyzing how different stressors can interactively affect its recruitment dynamics. This PhD thesis showed how managing fishing can mitigate some climate change effects and can strengthen climate change resilience. Fisheries management interventions are, however, contingent upon the climate regime and the different Atlantic cod stocks differ strongly in their climate change response. Several stocks display nonlinear recruitment dynamics, posed for example by an Allee effect, which challenge fisheries management by increasing the risk of population collapse, recovery failure and the level of uncertainty.

Climate change and the current covid-19 pandemic illustrate that the importance of nonlinearity and potential tipping points in order to prevent unintended runaway processes, is not restricted to natural resource management. Low predictability, high uncertainty and future risk emphasize the need to apply precautionary management strategies with science playing a central role. For managing Atlantic cod under climate change, this implies scientifically informed, stock-specific, adaptive, precautionary ecosystem-based management strategies that consider multiple interacting drivers, the magnitude, pace and variance of climate change and high uncertainty.
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Implications of Allee effects for fisheries management in a changing climate: evidence from Atlantic cod

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Highlights

- Ocean warming increases Allee effect strength in North Sea cod and increases the risk of population collapse and recovery failure.
- Ocean warming restricts means and pace for preventing and reverting collapse.
- If sea surface temperature rises beyond 2°C, even immediate banning of fishing is not sufficient to guarantee recovery of North Sea cod.
- Once the population collapses, rebuilding measures will be squandered and collapse will very likely be irreversible.
- Variance in fishing increases the probability of collapse, especially in presence of an Allee effect.
Implications of Allee effects for fisheries management in a changing climate: evidence from Atlantic cod

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Abstract. There are concerns that increasing anthropogenic stressors can cause catastrophic transitions in ecosystems. Such shifts have large social, economic, and ecological consequences and therefore have important management implications. A potential mechanism behind these regime shifts is the Allee effect, which describes the decline in realized per capita growth rate at small population density. With an age-structured population model for Atlantic cod, Gadus morhua, we illustrate how interactions between human-induced stressors, such as fishing and climate change, can worsen the impact of an Allee effect on populations by promoting hysteresis. Therefore, the risk of population collapse and recovery failure is exacerbated and the success of preventing and reverting collapse depends on the climate regime. We find that, in presence of the Allee effect, a fishing moratorium is only sufficient for recovery when sea surface temperature rise remains within 2°C and fishing is restricted within 10 yrs. If sea surface temperature rises beyond 2°C, even immediate banning of fishing is not sufficient to guarantee recovery. If fishing is not fully banned and a residual fishing pressure remains, the probability of recovery is further decreased, also in the absence of an Allee effect. The results underscore the decisive role of Allee effects for the management of depleted populations in an increasingly human-dominated world. Once the population collapses and its growth rate is suppressed, rebuilding measures will be squandered and collapse will very likely be irreversible. We therefore emphasize the need for proactive management involving precautionary, adaptive measures and reference points. Our studies show that climate change has the potential to strengthen Allee effects, which could increasingly challenge fisheries management.

Key words: Allee effect; Atlantic cod; climate; collapse; fisheries management; hysteresis; marginal effect; proactive management; recovery; regime shift; resilience; tipping points.

INTRODUCTION

Ecological regime shifts describe the abrupt and persistent change of the community structure that involves multiple variables and key species (Scheffer et al. 2001, Scheffer and Carpenter 2003, Conversi et al. 2015). A potential population ecological mechanism that can lead to a regime shift is the Allee effect (Jiang and Shi 2010, Dai et al. 2012, Dakos et al. 2012). A demographic Allee effect emerges if the realized per capita population growth rate ($r_{\text{realized}}$, a metric of average individual fitness accounting for density dependence) reduces with declines in population abundance (Courchamp et al. 1999, Hutchings 2015). If the Allee effect is strong, there is a critical threshold in population density or size (the Allee threshold), below which $r_{\text{realized}}$ drops below zero. In deterministic settings, this causes bistability and the population will go extinct below the Allee threshold (Berec et al. 2007, Courchamp et al. 2008).

In depleted fish populations, the Allee effect, also called depensation in fisheries ecology, has long been suggested as an explanation for the observed lack of recovery despite substantial fishing reductions (Hutchings 2001, 2015). An iconic example is the collapse of Atlantic cod, Gadus morhua, off the coast of Canada in 1992. Biomass levels declined by 99.9% (Hutchings and Reynolds 2004) and have not recovered since, despite a commercial fishing moratorium.

Even though marine fishes are one of the most data rich taxonomic groups, approaches to study Allee effects have been limited by a paucity of data at low abundance levels and the difficulty of performing appropriate experimental studies. As a result, there remains a great deal of uncertainty surrounding the prevalence of Allee effects in marine fishes (Myers et al. 1995, Liermann and Hilborn 1997, Gregory et al. 2010). Yet, Allee effects have been suggested for various marine fish such as Atlantic herring, Clupea harengus (Saha et al. 2013, 2015).
Peralá and Kuparinen 2017), shallow-water cape hake, Merluccius capensis (Vergnon et al. 2008), and Pacific salmon, Oncorhynchus spp. (Liermann and Hilborn 2001, Chen et al. 2002), with empirical evidence arguably strongest for Atlantic cod (Rowe et al. 2004, Keith and Hutchings 2012a,b).

Suggested mechanisms for an Allee effect in marine fish are related to difficulties in finding mates (Rowe et al. 2004), reduced antipredator vigilance due to a smaller school size (Clark 1974, Saether et al. 1996), lowered egg fertilization rate, and decreased genetic variation among offspring (Rowe and Hutchings 2003, Courchamp et al. 2008). Possible Allee effect mechanisms in Atlantic cod include increased predation on adult fish (Swain and Chouinard 2008, Kuparinen and Hutchings 2014, Swain and Benoit 2015) and altered food webs (Walters and Kitchell 2001, Frank et al. 2011).

The recent IPCC report highlights the increased risk to fisheries as global warming reaches beyond 1.5°C (IPCC 2018). Climate change has been implicated in large-scale marine regime shifts (Hare and Mantua 2000, Parsons and Lear 2001, Benson and Trites 2002, Beaugrand 2004, Lees et al. 2006, Beaugrand et al. 2008, Möllmann and Diekmann 2012, Conversi et al. 2015, Rocha et al. 2015) and these shifts are likely to increase in frequency. In Atlantic cod, climate change is found to have a negative effect on recruitment for stocks located at the southern end of the species range (Drinkwater 2005, Stige et al. 2006). In the North Atlantic Ocean, both increasing seasonal temperature variability and higher average temperatures are expected (Taboada and Anadon 2012, IPCC 2013, Pörtner et al. 2014).

While both climate change and the Allee effect have been at the origin of regime shifts, it is unclear how the combination of climate change and the Allee effect impacts populations. Environmental variability can decrease population resilience to fishing and increase uncertainty of recovery, especially if recruitment is compromised by an Allee effect (Dennis 2002). Considering a density-independent effect of temperature on recruitment, increasing temperatures may reduce per capita growth rate and shift the Allee threshold to higher biomasses (see also Allee effect variability types I in Walter et al. [2017]). As a result, the depressed per capita growth rate could have unforeseen consequences for fishing activities.

Successful fishery management strategies must account for the potential interaction between climate and an Allee effect. Less favorable climate reduces the maximum fishing pressure the population can withstand and the population collapses at unanticipated high biomass levels, which requires more conservative reference points (Fig. 1a). The Allee effect imposes a concrete time frame where fishing restrictions are sufficient to prevent collapse, and this time frame narrows with increasing temperature. Further, to recover the population it is not sufficient to reduce the fishing pressure to pre-collapse levels or even zero. Instead, negative fishing pressure, i.e. re-stocking may be necessary (Fig. 1b), which is usually not possible for wild stocks. This is, because of the bistability that arises with the presence of an Allee threshold, which introduces an unstable equilibrium point, because below it $r_{realized}$ becomes negative and the population goes extinct. Extinction is a stable equilibrium, which is reinforced by a negative population growth rate. A shift to the lower equilibrium can occur as a result of a shock event and/or slow changes in the underlying variables and internal feedbacks that define the ecological system (Beisner et al. 2003). Once passing the tipping point, attraction to the extinction equilibrium is stronger than attraction to the high biomass equilibrium and extinction becomes very likely if the underlying changes are not immediately halted.

In case of the Allee effect, fishing pressure gradually reduces the interval between the two equilibrium population sizes, with the result that additional pressure from climate change will be more likely to reduce the population to critical numbers and the population will be more vulnerable to extinction (Stephens and Sutherland 1999). Fishing and climate change are human-induced stressors, which jointly reduce the resilience of the population to the impact of an Allee effect, but only fishing pressure can be controlled by managers. Therefore, once the tipping point is passed, a fast fisheries management response is necessary.

The return path between the two stable equilibrium states can be different from the outgoing path, a phenomenon called hysteresis (Beisner et al. 2003). Because once collapsed, there are no or very few individuals left to produce recruitment, even successful attempts to restore the “original” environmental variables may not result in the recovery of the population (Fig. 1b). Increasing temperature shifts the hysteresis region to appear at even lower fishing values.

Incorporating these factors into a precautionary approach to fisheries management remains challenging (Selkoe et al. 2015). Using North Sea cod as a case study, we illustrate how the interaction between fisheries management strategies (fishing pressure, variability in fishing pressure and delayed management action), directed environmental change (increasing temperature and temperature variability), and an Allee effect can impact the population dynamics and recovery of this population. In light of these results, we identify appropriate strategies that incorporate a precautionary approach to fisheries management. While Allee effects in marine systems may have been uncommon in the past, climate change has the potential to strengthen Allee effects, which could increasingly challenge fisheries management.

**MATERIAL AND METHODS**

We developed an age-structured model linked with a stock-recruitment function accounting for (1) absence
and presence of an Allee effect and (2) effects of increasing sea surface temperature, SST. We used Atlantic cod as a case study, as it is a species of high economic and cultural value and for which there is evidence of an Allee effect (Keith and Hutchings 2012b, Cabral et al. 2013). We chose to focus on North Sea cod, where recruitment productivity is found to be negatively affected by increasing temperature (Planque and Fredou 1999, OBrien et al. 2000, Clark et al. 2003, Portner et al. 2008). A 1°C increase of SST is predicted to reduce recruitment production by 50% (Planque and Fredou 1999, Drinkwater 2005). The North Sea cod was MSC certified in 2017, but the most recent assessment found its fishing activity to be unsustainable and biomass levels dropped again below the limit reference point (ICES 2019).

Modeling the Allee effect

We applied the meta-analysis by Keith and Hutchings (2012b) to Atlantic cod stocks only, to parameterize a recruitment function with an Allee effect and one without an Allee effect. Of the 19 Atlantic cod stocks represented in the Ransom A. Meyers (RAM) legacy database (Ricard et al. 2012; available online) www.ramlegacy.org, we extracted recruit-per-spawner ratios as a proxy for $r_{\text{realized}}$ and fitted a segmented regression to the standardized recruit-per-spawner ratios and spawning stock biomass, SSB (see Appendix S1 for detailed description). The segmented package in R (Muggeo 2008), was used to estimate a breakpoint at 13.47% maximum SSB (SSBMAX) with a standard error of 1.7 (Appendix S1: Table S4). The Davies test (Davies 2002) tests for a non-zero difference in the slope parameters of the segmented relationship and was highly significant ($p < 0.01$). We used the breakpoint as the Allee effect threshold, SSBAT. SSBAT is the biomass threshold below which $r_{\text{realized}}$ starts to decrease. It translates to 34,045.02 metric tons for North Sea cod. For a sensitivity analysis of the breakpoint estimates to the number of stocks considered and the uncertainty level of the individual estimates, see Appendix S1: Tables S4–S6.

For SSB above the Allee effect threshold, we used the same function as for the scenario without an Allee effect. For this, we fitted a Ricker stock-recruitment model (Ricker 1954) by applying linear regression to the standardized recruit-per-spawner ratios of SSB above 40% SSBMAX (Appendix S1: equation S2). For the Allee effect scenario, we extended the stock-recruitment function by an additional parameter, $c$ (Eq. 1), to model the
observed decline in recruit-per-spawner ratios below the Allee effect threshold (Fig. 2). Even though \( r_{\text{realized}} \) drops well below 1 (0.4) at positive SSB after back-transformation, the modeled Allee effect is considered a strong Allee effect, because of the exponential shape of the stock-recruitment function at low SSB. See Appendix S1, for details on fitting the stock-recruitment functions and an analysis of how our results depend on the values of parameter \( c \).

Temperature dependency

We assumed a linear relationship between recruitment and temperature following, e.g., Hilborn and Walters (1992), Clark et al. (2003), Planque et al. (2003), and Ottersen et al. (2013) and because of its easier interpretation when the Allee effect itself is already a nonlinear function. In Appendix S2, we also consider a nonlinear temperature function. We extended the stock-recruitment function by an additional parameter \( d \) to account for the linear dependence on sea surface temperature documented by Planque and Mirodatos (1999) (Eq. 1). Note that \( d \) reflects the change in recruitment with a 1°C change in the average ambient spawning SST (e.g., 7.95°C for the North Sea). We assumed that environmental forcing on recruitment constitutes uncorrelated random white noise (Bjørnstad et al. 2004). Therefore, in our model, SST, is time varying and a random draw from a normal distribution with mean \( \text{SST} \) and variance \( \sigma_{\text{SST}}^2 \). To reflect current climate conditions, \( \text{SST} \) is zero and \( \sigma_{\text{SST}}^2 \) is equal to the observed variance in North Sea SST, 0.426°C (\( \text{SST} \) was extracted for the years of SSB and was provided by NOAA/OAR/ESRL Physical Sciences Division; available online).4

Population dynamics

Recruitment, \( R_t \), is dependent on whether SSB is below or above the Allee effect threshold and given by

\[
R_t = \begin{cases} 
\text{SSB}_{\text{MAX}} - \frac{1}{e^{a}} \frac{e^{b}}{e^{c}} \text{SSB}_{\text{MAX}} & \text{if } \text{SSB}_{\text{MAX}} \geq \text{SSB}_{\text{MAX}} \\
\left( \frac{\text{SSB}_{\text{MAX}}}{\text{SSB}_{\text{MAX}}} \right) e^{c} \text{SSB}_{\text{MAX}} & \text{if } \text{SSB}_{\text{MAX}} < \text{SSB}_{\text{MAX}}.
\end{cases}
\]

The parameter \( e \) captures the interannual recruitment variation and is parameterized using the residuals from the fitted linear regression model (Appendix S1: Eq. S2). The parameter \( e \) is a random draw from a normal distribution with mean equal to the residual average of North Sea cod, \( \bar{e} = 1.7 \), and standard deviation equal to the standard deviation of the residuals of North Sea cod, \( \sigma_e = 0.63 \), which is close to the value documented for marine fish (Beddington and Cooke 1983, Smith and Punt 1998). The exponent \( e^c \) is lognormally distributed so that annual recruitment production, \( R_t \), also follows a lognormal distribution (Maunder and Deriso 2003, Metz and Taylor 2011, Devine et al. 2014).

We combined the back-transformed Atlantic cod stock-recruitment functions with a time-discrete cohort model with reproduction and harvesting happening annually at the beginning and end of the year, respectively. The number of individuals in each age class at year \( t \), \( N_{\text{age},t} \), equals cohort abundance of the previous year multiplied by the survival rate (reciprocal of constant natural mortality rate, \( M_{\text{age}} \) and time varying fishing mortality, \( F_t \)). \( F_t \) is a random draw from a log-normal distribution with mean equal to the imposed logarithmic fishing pressure, \( \bar{F} \), and variance \( \sigma_F^2 \) equal to logarithmic variance. The log-normal distribution prevents negative values for \( F_t \). In our baseline simulations, we vary \( \bar{F} \) and assume variance equal to the observed log variance level in fishing age classes 2-4 (0.210 yr\(^{-1}\); ICES 2016). The realized fishing mortality in the North Sea fluctuates from year to year on average by 6%, but interannual changes up to 27% have been observed (ICES 2016). All age classes were exposed to the same fishing mortality, except 1-yr-olds, which were considered too small to be caught (ICES 2016). The last age class was treated as a plus group, combining all individuals beyond the age of 11. The number of individuals in each age class is given by

\[ R_t = \begin{cases} \text{SSB}_{\text{MAX}} - \frac{1}{e^a} \frac{e^b}{e^c} \text{SSB}_{\text{MAX}} & \text{if } \text{SSB}_{\text{MAX}} \geq \text{SSB}_{\text{MAX}} \\
\left( \frac{\text{SSB}_{\text{MAX}}}{\text{SSB}_{\text{MAX}}} \right) e^c \text{SSB}_{\text{MAX}} & \text{if } \text{SSB}_{\text{MAX}} < \text{SSB}_{\text{MAX}}.
\end{cases} \]

4https://www.esrl.noaa.gov/psd/
The threshold of 5% $SSB_{MAX}$ was chosen for the reason that $SSB$ had at any point of time declined and remained below the Allee effect threshold in every scenario. Each scenario was repeated 100 times and simulated with and without an Allee effect. For each scenario, the probability of collapse and population recovery by repeatedly calculating different scenarios to illustrate see Appendix S3: Fig. S1). Thus, cases that declined again after recovery were still considered recovered. However, because $F$ was substantially reduced in these cases, there were only very few cases that had declined again after recovery.

Simulated and predicted probability of collapse and recovery

We first looked at the simulated probability of collapse and recovery by repeatedly calculating different scenarios and counting the times of collapse and population recovery after depletion, respectively. In a second analysis, we fitted a logistic regression model to the outcome of different simulated scenarios to predict the probability of collapse and recovery. Collapse and recovery scenarios are simulated separately, because they differ in the parameters considered. Each scenario was initialized by simulating population dynamics for 500 yrs without fishing pressure, no temperature increase and without an Allee effect, to find the equilibrium population size. We then simulated different scenarios by exposing the population for 500 yrs to different variables.

For the simulated probability of collapse (Fig. 3a, b), mean SST, $SST$, was, in each scenario, increased up to $4.5^\circ C$ according to the predictions for year 2100 under the RCP8.5 scenario (IPCC 2014) and predictions from the Hadley Centre for Climate Prediction and Research for year 2099 in the North Sea (Sheppard 2004). Mean fishing pressure, $F$, was increased up to $1$ yr$^{-1}$, which is well above the level consistent with achieving maximum sustainable yield ($F_{MSY} = 0.31$ yr$^{-1}$; ICES 2018a). Variance in $SSST$ and $F$ remained at observed levels and initial $F$ was set to $0.8$ yr$^{-1}$ to ensure that biomass would drop below the Allee effect threshold in every scenario. Each scenario was repeated 100 times and with and without an Allee effect. For each scenario, the probability of recovery was estimated as the proportion of recovered population states. The population was classified as recovered if $SSB$ had fallen below the Allee effect threshold at any point of time and subsequently recovered and remained at least for one generation at levels above the Allee effect threshold (for an illustration see Appendix S3: Fig. S1). Thus, cases that declined again after recovery were still considered recovered. However, because $F$ was substantially reduced in these cases, there were only very few cases that had declined again after recovery.

For the predicted probability of collapse the presence of an Allee effect (AE; binary) was sampled and the parameters $SSST$, $F$, $\sigma_{SSST}^2$, $\sigma_F^2$ were drawn from uniform distributions in a Monte Carlo Analysis. $SSST$ varied between $-0^\circ C$ and $+4.5^\circ C$, $F$ varied between $0$ and $1.5$ yr$^{-1}$. Variance levels were altered with maximum levels according to a doubling of observational values. Fishing variance varied between $0$ and $0.297$ yr$^{-1}$ and, SST variance varied between $0^\circ C$ and $0.853^\circ C$. 1500 scenarios were drawn and a logistic linear regression was fitted with the response variable, $Y$, equal to the population status (collapsed, not collapsed):

$$Y_i = \beta_0 + \beta_1 \times AE + \beta_2 + SST + \beta_3 \times F + \beta_4 \times \sigma_{SSST}^2 + \beta_5 \times \sigma_F^2 + \epsilon_i$$

(4)

For the predicted probability of recovery the presence of an Allee effect was sampled and the parameters $SSST$, $\sigma_{SSST}^2$, $\sigma_F^2$, mgmt. delay, and fishing during moratorium
were drawn from uniform distributions. For SST, $F$, $\sigma_{SST}^2$, and $\sigma_F^2$ distributions were the same as for the predicted probability of collapse. In addition, the management delay was drawn and varied between 0 and 30 yrs and the residual fishing pressure was sampled and varied between 0 and 0.2 yr$^{-1}$. Initially 3,000 scenarios were drawn, of which 1,500 cases where biomass had dropped below the Allee effect threshold were randomly chosen. Based on these 1,500 cases, a logistic linear regression was fitted with the response variable, $Y_i$, equal to the population status (depleted, depleted and recovered):

$$Y_i = b_0 + b_1 \cdot AE + b_2 \cdot SST + b_3 \cdot F + b_4 \cdot \sigma_{SST}^2 + b_5 \cdot \sigma_F^2 + b_6 \cdot \text{mgmt.delay} + b_7 \cdot \text{fishing during moratorium} + \varepsilon_i.$$  

For details on model choice, regression analysis, and values of coefficients ($b_0$–$b_7$) see Appendix S3.

**RESULTS**

**Allee effect decreases resilience to fishing pressure and increasing SST**

First, we analyzed how the Allee effect affects the probability of collapse at increasing levels of SST and fishing pressure, $F$. In presence of an Allee effect, more population trajectories collapse and the tolerated level of cumulative stress from both fishing pressure and increasing temperature is lower (Fig. 3a, b). Without an increase in temperature and without an Allee effect, a fishing pressure of 0.8 yr$^{-1}$ still keeps the probability of collapse below 50%, whereas in the presence of an Allee effect, 0.8 yr$^{-1}$ would increase the probability of collapse to 90%. Using the $F_{\text{MSY}}$ of 0.31 yr$^{-1}$ naively, in spite of rising temperature levels, will result in a 50% probability of collapse at +2.5°C in the absence of an Allee effect and at +2.1°C in the presence of an Allee effect. At high levels of both $F$ and SST, the population collapses irrespective of whether an Allee effect is present. For
example, when the ambient SST rises to the globally predicted maximum for the North Sea region (Sheppard 2004, IPCC 2014), fishing beyond \( F_{\text{MSY}} \) would result in population collapse even in absence of an Allee effect, making the additional, i.e., marginal, impact of an Allee effect disappear.

Analyzing the marginal effects shows when Allee effects matter and are useful to locate tipping points. The increase in SST interacts with the Allee effect by further lowering the already suppressed recruitment production. As a result, the tipping point is moved to lower biomasses, which in turn allows for lower fishing pressure (Fig. 1b). In the region of the tipping point, the impact of the Allee effect on the probability of collapse is highest. Fig. 4 shows the marginal effects of the Allee effect on the probability of collapse. While the probability of collapse increases with increasing level of pressure (increasing number of red cells; Fig. 4), the marginal effects of the Allee effect are highest only at intermediate (increasing number of red cells; Fig. 4), the marginal effects of the Allee effect are highest only at intermediate levels of \( T \) and SST. We find that the Allee effect can increase the probability of collapse up to 88 percentage points and, depending on the cumulative level of stress the Allee effect can be decisive over whether the population collapses or not (encircled cells; tipping points). For example, at \( +3^\circ \text{C} \), passing a fishing pressure just above 0.1 yr\(^{-1} \) could lead to population collapse in presence of an Allee effect. Therefore, at \( +3^\circ \text{C} \), the tipping point is between \( > 0.1 \) yr\(^{-1} \) and \( < 0.2 \) yr\(^{-1} \). At \( +2^\circ \text{C} \), the tipping point is between \( > F_{\text{MSY}} \) and \( < 0.45 \) yr\(^{-1} \) (probably closer to \( F_{\text{MSY}} \) because of the already elevated marginal effect of 22.6 percentage points). From Fig. 1 we know that in a fully deterministic model the tipping point would be at 0.3 yr\(^{-1} \).

In line with Fig. 3, the marginal effects of the Allee effect are minimal at very low stress levels (the population never falls below the Allee effect threshold) and very high cumulative stress levels (the population always collapses anyway). On average, the Allee effect increases the probability of collapse by 5.66 percentage points (Appendix S3: Table S4).

The predicted probability of collapse according to the best fit logistic model is shown in Fig. 6a, b. The fitted model slightly underestimates the probability of collapse in comparison to the simulated probability of collapse in Fig. 3a, b. The fitted model confirms the overall increase of population collapse by the Allee effect (log odds increase by 5.6, Appendix S3: Table S3). The regression model shows that temperature, fishing pressure and fishing variance (Appendix S3: Table S3) increase the predicted probability of collapse, and even stronger so in the presence of an Allee effect (marginal effects with Allee effect; Appendix S3: Table S4). We found mean temperature to positively interact with mean fishing pressure. The log odds of fishing increase with increasing mean temperature. Variance of temperature was found to be nonsignificant, while the variance of fishing mortality is highly significant and interacts negatively with mean temperature. Thus, the effect of variance in fishing on the probability of collapse decreases with increasing mean temperature. For example, at \( +0^\circ \text{C} \), the log odds of variance in fishing on the probability of collapse are 2.56, but at \( +2^\circ \text{C} \), they are only 0.98.

**Allee effect decreases opportunities to prevent and revert population collapse**

As a result of the hysteresis, the trajectory of recovery differs from the collapse trajectory and restoration of pre-collapse conditions (e.g., reducing fishing pressure) may not be sufficient to recover the population. Without an Allee effect, a management delay of implementing a moratorium has no effect on recovery and restricting fishing pressure to \( \leq 0.1 \) yr\(^{-1} \) is sufficient to recover the population independent of when fishing is restricted (Fig. 3a, Fig. 6a). Only when SST passes \( +3.5^\circ \text{C} \), the probability of recovery decreases heavily.

In contrast, the probability of recovery in presence of an Allee effect is heavily dependent on the combination of the management delay and temperature. Generally, higher SST decreases the probability of recovery and the allowable delay in management actions. In the presence of the Allee effect, restricting fishing pressure to 0.1 yr\(^{-1} \) is only sufficient for recovery when SST rise remains below \( +2^\circ \text{C} \) and fishing is restricted within 5 yrs (Fig. 3d). At SST around the globally predicted maximum for the North Sea region (Sheppard 2004, IPCC 2014), even immediate restrictions (no management delay) of fishing are not sufficient to guarantee recovery in the presence of an Allee effect. This is reflected in the interaction term of the best fit logistic regression model for the predicted probability of recovery (Appendix S3: Table S3). Without an Allee effect, the management delay decreases the log odds of the probability of recovery by \(-0.04 \), while the presence of an Allee effect increases the log odds of the management delay to \(-0.45 \), which restricts recovery significantly (Fig. 3d, Fig. 6d). The fitted model confirms the overall decrease of population recovery by the Allee effect (log odds of probability of recovery decrease by 6.3; Appendix S3: Table S3). The regression model shows that temperature, fishing pressure, the management delay, and residual fishing pressure decrease the predicted probability of recovery (Appendix S3: Table S3). In the absence of an Allee effect, recovery is mainly governed by the combination of SST and the residual fishing mortality (Appendix S3: Table S4).

The Allee effect has a very high impact on the probability of recovery. On average, the Allee effect decreases the probability of recovery by 76.58 percentage points (Appendix S3: Table S4). The marginal effects increase with increasing temperature and management delay (increasing number of red cells; Fig. 5) and are highest at the highest cumulative stress levels. This is, because without the Allee effect, even at the highest pressure levels, the population still recovers (encircled cells, Fig. 5), while the hysteresis of the Allee effect hampers
recovery and increasingly so at high SST. Only at temperatures > +4.5 °C would the marginal effect decline, because then recovery is also hampered without an Allee effect (Fig. 3c).

Fig. 6c, d shows the predicted probability of recovery according to the regression model. It overestimates the probability of recovery. For example, at +1 °C the predicted probability of recovery is still 50% at a management delay of 8 yrs if fishing is restricted to 0.1 yr⁻¹, while Fig. 3c suggests at these pressure levels a 0% probability of recovery. If fishing is fully banned, management has more time to intervene and recovery at +1 °C is still likely at a delay of 15 yrs (Fig. 6c). At +2 °C however, even a full fishing ban cannot guarantee recovery.

**DISCUSSION**

**Interaction between climate, fishing, and the Allee effect**

Theory suggests that an Allee effect can cause irreversible regime shifts (Courchamp et al. 2008). We investigated how the presence of an Allee effect, directed SST change and fishery management can interact and synergistically affect the probability of collapse and recovery. Their interaction strongly influences the population responses; for example, if the temperature increase remains < 1 °C, the population can withstand moderate increases in fishing pressure. The Allee effect influences population dynamics primarily when the cumulative effects of SST and fishing pressure are at intermediate levels of SST and fishing pressure. Depending on the level of cumulative stress, the Allee effect can be decisive over whether the population collapses or not (encircled cells). At these combinations of SST and fishing pressure, a tipping point is likely to be crossed. Estimated standard errors are shown in brackets.

![Marginal effect of Allee effect on probability of collapse](image_url)

**Fig. 4.** Marginal increase of the probability of collapse associated with the Allee effect at increasing temperature and fishing level. The marginal effects are calculated with the fitted logistic regression model for the probability of collapse. While the probability of collapse increases with increasing cumulative stress level (colored cells), the marginal effect of the Allee effect is highest at intermediate levels of SST and fishing pressure. Depending on the level of cumulative stress, the Allee effect can be decisive over whether the population collapses or not (encircled cells). At these combinations of SST and fishing pressure, a tipping point is likely to be crossed. Estimated standard errors are shown in brackets.
changes in recruitment production, survival, food, and predator abundance can alter the temperature and the stock-recruitment relationship (Ottersen et al. 2013, Stige et al. 2013). The sensitivity to temperature increase and the probability of collapse and recovery depends on the Allee effect strength and “Allee slope” (Appendix S1: Table S7, Fig. S4). While the response of Atlantic cod to future warming has been intensively studied, little is known about the mechanisms leading to Allee effects in marine fish (Myers et al. 1995, Liermann and Hilborn 1997, Gregory et al. 2010). Thus, synergistic effects remain unknown and additional experimental research is needed. Nevertheless, unraveling mechanisms at low population abundance and detecting tipping points is often only possible when tipping points have passed and recovery is difficult if not impossible. The collapse of Northern cod is a particularly painful reminder in this regard.

The influence of variability

As a tipping point is approached, exogenous drivers and natural variation can induce a catastrophic shift to the alternative stable state (Scheffer et al. 2001). In our model, variation in recruitment production, fishing pressure and SST were stochastic elements. Variance in fishing increased the probability of collapse and even stronger in the presence of an Allee effect (Appendix S3: Table S4).

In heavily exploited fish stocks, demographic instability may be elevated through unbalanced targeting of specific age cohorts (Gilpin and Soulé 1986, Lande 1998, Dennis 2002, Hsieh et al. 2006, Anderson et al. 2008, Rouyer et al. 2012). In our simulations, fishing mortality was applied as a non-selective strategy and therefore did not lead to demographic variability. Selective fishing (removing the largest individuals) would elevate population variability and have a detrimental impact on the population.

Variance in temperature was not found to be significant for the predicted probability of collapse or recovery (Appendix S3: Table S3). In our simulations, we assumed temperature to follow a white noise process, causing unusually weak or strong year classes, but rarely leading to a succession of weak or strong year classes, as in the case of autocorrelated noise. If ocean SST is autocorrelated (Vasseur and Yodzis 2004, Rouyer et al. 2010), the succession of weak or strong recruitment years is likely to strengthen the effect of SST variance on recruitment (Morales 1999, Heino et al. 2000, Schwager et al. 2006), which would increase or decrease the risk and consequences of Allee effects.

Incorporating Allee effects in fisheries management

The interaction between climate and the Allee effect has repercussions for fisheries management. Restoration of the pre-collapse conditions may not lead to recovery due to hysteresis (Fig. 1b). Additionally, climate change is beyond the control of fisheries managers. Our results highlight the need to reduce the stressors unrelated to
climate change, which can be controlled, e.g., fishing mortality (Carpenter et al. 2017, Brander 2018, IPCC 2018). While reductions in fishing mortality are one of the most important factors for recovery (Wakeford et al. 2009), we find that fishing restrictions only lead to recovery when fishery management action is not unduly delayed (i.e. ≤ 10 yrs), incidental mortality during the moratorium remains as low as possible, and climate change impacts are moderate (i.e. ≤ +2°C; Fig. 6d).

The implementation of a full fishing moratorium is extremely difficult, especially if the population has a longstanding commercial fishery. Delays in data collection and analysis, communication of science advice, bureaucratic inertia, and social resistance may slow the implementation of the necessary management actions (Hutchings and Reynolds 2004, Brown et al. 2012). Continuation of fishing pressure after a moratorium e.g., through illegal fishing (Agnew et al. 2009) and bycatch (Davies et al. 2009), which is especially a challenge for mixed fisheries such as the North Sea cod fishery, increases the likelihood of reaching a tipping point (Fig. 3d, Fig. 6d). Even in absence of an Allee effect, the combination of high levels of SST and the continuation of high fishing pressure during recovery can be harmful (Appendix S3: Table S4). Similarly, reopening the fishery too soon can impair recovery and nullify recovery efforts. For example, the Northern Cod fishery latest reopening in 2016 took place despite biomass levels remaining below the limit reference point, and the biomass decreased by 30% again in 2018 (DFO 2018).

Our findings support the notion that a degraded population state is to be avoided because of its increased risk of irreversible collapse (Lande 1998, Kuparinen et al. 2014), especially considering the limited ability of degraded populations to adapt evolutionarily to changed conditions (Kuparinen et al. 2014). Heavy fishing pressure and the alteration of density-dependent regulation at small population size could alter life history traits and recovery behavior after collapse (Fudge and Rose 2009).
In fisheries, precautionary measures are usually implemented with limit biomass reference points (ICES 2018a, b), but constant limit reference points may not be precautionary under directed environmental change, for highly variable populations, or when there are delays in management action to reduce fishing pressure (Brown et al. 2012, Dickey-Collas 2016, ICES 2018b). While $F_{MSY}$ may be optimal under current climatic conditions, this level of fishing has a 50% probability of collapse when SST increases by 2.5°C, and leads to certain collapse if SST increases by 3°C (Fig. 3a). In the presence of an Allee effect current $F_{MSY}$ would already lead to certain collapse at an increase in SST of 2.5°C (Fig. 3b). Management measures that do not account for time varying productivity are inherently non-precautionary. The current limit reference point for North Sea cod is estimated to yield above-average recruitment based on historic values (ICES 2018a). This is comparable to the Allee effect threshold, which indicates highest per capita production. However, the findings indicate that the validity of these reference points depends heavily on when and how much fishing pressure is reduced and on the productivity baseline. We defined populations as recovered once biomass reached the limit reference point (Allee effect threshold), but this is only the point when recruitment production is not impaired anymore and could support stock rebuilding. Other modelling results indicate that full rebuilding to the original state in terms of genetic and phenotypic stock structure could be much slower than only biomass recovery alone would suggest (Dunlop et al. 2009, Enberg et al. 2009).

Fisheries management is challenged by the increasing effort towards recovery and rebuilding programs and the need to define appropriate target reference points while productivity baselines are shifting. Adaptive management strategies and regular re-assessments of management reference levels are important, especially when recruitment dynamics and their response to climate change are not well known or difficult to predict (Ottersen et al. 2013, Stige et al. 2013, Munch et al. 2018).

Acknowledgments

A. M. Winter, A. Richter, and A. M. Eikeset conceived jointly the study idea. A. M. Winter programmed the model, carried out the simulations, visualized the results, and drafted the manuscript. All authors contributed to the analysis, final writing and revisions of the manuscript. The authors wish to thank Jeffrey A. Hutchings for helpful discussions and the reviewers for valuable suggestions that helped improving the manuscript substantially. The authors acknowledge funding by NordForsk through the projects GreenMAR and TerMARisk (Project Number 51513) and from the Norwegian Research Council under the MARIN–FORSK program through the project Fishtech (Project Number: 280541) (A. Richter) and through the POLARPROG project STOCKSHIFT (Project Number: 257614).


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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1994/full

Data Availability

All data used in this study were extracted from publicly accessible data bases. No new data were used. Data for North Sea cod was extracted from the publicly available data base provided by ICES (www.ices.dk), sea surface temperature data were provided by the Earth System Research Laboratory, Physical Sciences Division, NOAA (www.esrl.noaa.gov/psd). Spawning stock biomass and recruitment data of other Atlantic cod stocks were taken from the Ransom A. Meyers (RAM) legacy database (www.ramlegacy.org). A summary of the exact parameter values used in the population model is found in the Supporting Information. The R code used in the current study's analyses is available in the Supporting Information (Metadata S1, Data S1) and is directly executable with the attached data file.
Appendix S1: Obtaining the (Ricker) stock-recruitment function from standardized recruit-per-spawner ratios

Implications of Allee effects for fisheries management in a changing climate: evidence from Atlantic cod

Ecological Applications

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²Environmental Economics and Natural Resources Group, Sub-Department of Economics, Wageningen University, 6700 EW Wageningen, The Netherlands
Appendix S1: Obtaining the (Ricker) stock-recruitment function from standardized recruit-per-spawner ratios

We used a Ricker stock-recruitment model (Ricker 1954) for the simulation scenarios without an Allee effect in accordance with (Keith & Hutchings 2012a, b). Because the Ricker model can be linearized by log transformation of the estimates, we could fit the Ricker model by linear regression. For this we first extracted recruit-per-spawner ratios, used as a proxy for $r_{realized}$, and spawning stock biomass, SSB, of the 19 Atlantic cod ($Gadus morhua$) stocks represented in the RAM legacy database (Ricard et al. 2012). We log-transformed the ratios for normalization, following the approach by Keith and Hutchings (2012b). To reduce scale variance between stocks, recruit-per-spawner ratios were standardized by the species’ mean (bar) and standard deviation (SD). The log-transformed and standardized recruit per spawner ratios are given by:

$$Z_i = \frac{\log \left( \frac{R}{SSB} \right)_i - \log \frac{R}{SSB}}{\text{SD} \left( \log \frac{R}{SSB} \right)_{\text{bar}}},$$

(eq. S1)

where $i$ stands for each individual data point.

SSB was then normalized to the stock’s maximum observed spawning stock biomass, $SSB_{MAX,j}$ as a proxy for stock $j$ specific carrying capacity. In R (R Core Team 2017) we then estimated the linear model to $Z_i$ and normalized SSB (eq. S2). We only included data points where SSB was larger than 40 % of $SSB_{MAX,j}$, because these biomasses typically show compensatory dynamics (Keith & Hutchings 2012b). Table S1 shows the regression fit.

$$Z_i = a_z + b_z \times \frac{SSB_j}{SSB_{MAX,j}} + \varepsilon_i \quad \text{with} \quad \frac{SSB_j}{SSB_{MAX,j}} > 0.4$$

(eq. S2)
\( \varepsilon_i \) are the residuals of the fitted model, which are normal distributed around a residual average of 0 with a standard deviation of 0.98.

Table S1: Regression coefficients of the linear regression of standardized recruit-per-spawner estimates.

<table>
<thead>
<tr>
<th>parameter</th>
<th>estimate</th>
<th>standard error</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>( a_z )</td>
<td>0.353</td>
<td>0.213</td>
<td>1.659</td>
<td>&lt; 0.10</td>
</tr>
<tr>
<td>( b_Z )</td>
<td>-0.718</td>
<td>0.308</td>
<td>-2.332</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>adjusted ( R^2 )</td>
<td></td>
<td></td>
<td></td>
<td>0.016</td>
</tr>
</tbody>
</table>

To use the Ricker stock-recruitment function in our population model, we solved equation S2 for recruitment, \( R \). In particular, parameter \( a_z \) was multiplied with \( \text{SD} \left( \log \frac{R}{SSB} \right) + \log \left( \frac{R}{SSB} \right) \) and \( b_Z \) was multiplied by \(-1 \left( \text{SD} \left( \log \frac{R}{SSB} \right) * \frac{1}{SSB_{\text{MAX},j}} \right) \). Because \( SS_{\text{MAX}} \) is stock specific, we considered here \( SS_{\text{MAX}} \) of the North Sea cod stock (\( SS_{\text{MAX}} = 252747 \) tonnes). North Sea cod is located at the southernmost species distribution range where recruitment productivity is found to be negatively affected by temperature rise (Planque & Fredou 1999; O’Brien et al. 2000; Clark et al. 2003; Pörtner et al. 2008).

For variation on recruitment, we selected only the North Sea cod specific residuals from \( \varepsilon_i \) in eq. S2. The North Sea cod stock is in the upper species’ range, so its stock-specific residual average is positive (\( \bar{\varepsilon} = 1.7 \), Fig. S1). In the final stock-recruitment model (eq. S3), interannual recruitment variation \( \varepsilon_t \) is a random draw from a normal distribution with mean equal to the residual average of North Sea cod, \( \bar{\varepsilon} = 1.7 \), and standard deviation equal to the standard deviation of the residuals of North Sea cod, \( \sigma_{\varepsilon} = 0.63 \). This follows the common assumption that recruitment variation follows a normal distribution constrained by the standard deviation of the logarithm of the annual recruitment residuals, which is usually around 0.6. (Beddington...
& Cooke 1983; Smith & Punt 1998). The exponent $e^{\varepsilon t}$ is lognormal distributed so that annual recruitment production, $R_t$, follows a lognormal distribution (Maunder & Deriso 2003; Methot & Taylor 2011; Devine et al. 2014).

![Figure S1: Total residuals of the fitted regression model and North Sea cod specific residuals (red dots). The average of the North Sea cod specific residuals is 1.7, the standard deviation is 0.63.](image)

The final Ricker stock-recruitment function producing yearly recruitment, $R_t$, in numbers is:

$$R_t = SSB_{t-1} \cdot e^{(a-b \cdot \text{SSB}_{t-1})} \cdot e^{\varepsilon_t}$$

(eq. S3)

with $a = a_z \cdot \text{SD} \left( \log \frac{R}{\text{SSB}} \right) + \log \frac{R}{\text{SSB}}$ and $b = -b_z \cdot \text{SD} \left( \log \frac{R}{\text{SSB}} \right) \times \frac{1}{\text{SSB}_{\text{MAX},t}}$ and SSB in kilotonnes. Table S2 shows all the values used in the final stock-recruitment function. The stock-recruitment function simulates recruitment comparable to the recruitment data (Fig. S2).
Figure S2: Comparison of the recruitment data and the recruitment production according to the stock-recruitment function.

Table S2: Parameters of the Ricker based stock-recruitment function (equation 1 in main text) using the North Sea cod stock (SSB\textsuperscript{MAX}) as a case study.

<table>
<thead>
<tr>
<th>parameter</th>
<th>value</th>
<th>description</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>0.04</td>
<td>back-transforming regression of standardized recruit-per-spawner ratio: $a = a_1 \cdot 5D (\log \text{SSB}) + \log \text{SSB}$</td>
</tr>
<tr>
<td>b</td>
<td>3.143e-0.6</td>
<td>back-transforming regression of standardized recruit-per-spawner ratio: $b = -b_1 \cdot 5D (\log \text{SSB}) \cdot \frac{1}{\text{SSB}^{MAX}}$</td>
</tr>
<tr>
<td>c</td>
<td>0.6991</td>
<td>no Allee effect, Allee effect</td>
</tr>
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<td>d</td>
<td>log 2^{-0.98}</td>
<td>Planque &amp; Fredou 1999</td>
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<td>extracted from total residuals of fitted model; North Sea cod specific</td>
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<td>$\sigma$</td>
<td>0.63</td>
<td>extracted from total residuals of fitted model; North Sea cod specific</td>
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For simulating the population model, ICES life history traits of the North Sea cod stock were used (Table S3).

Table S3: Life history parameters of North Sea cod. Probability of maturation, catch weight at age and natural mortality from ICES (ICES 2016). Values were averaged over the time period of SSB and recruitment data available (1964-2007). Parameters are used in equation 2 and 3 in the main text.
For the Allee effect scenario, recruitment production followed the Ricker function only at biomasses above the Allee effect threshold. Below the threshold, per capita growth rate decreased. The Allee effect threshold at 0.1347 (13.47 % SSB\textsubscript{MAX}) was found by segmented regression analysis with equation S2 in R (Muggeo 2008). The Davies test (Davies 2002) was used to test for a non-zero difference in the slope parameters of the segmented relationship and was highly significant (p < 0.01).

Sensitivity of the estimated breakpoint to the number of stocks considered was analysed by stepwise removing the number of stocks used in the analysis (Table S4).

<table>
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<tr>
<th>age class</th>
<th>probability of maturation, μ</th>
<th>weight [kg], w · 1000</th>
<th>natural mortality, M [y⁻¹]</th>
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</table>
Table S4: Break point and standard error and number of stocks at low abundance of the segmented regression analysis after removing each of the Atlantic cod stocks. Abbreviations of the cod stock names: COASTNOR = Norwegian Coastal cod, CODNEAR = North East Arctic cod, COD5Zjm = cod in a DFO area 5Zjm, COD2J3KLIS = cod in a DFO area 2J3KL, inshore, COD3PS = cod in a DFO area 3PS, COD3Pn4RS = cod in DFO area 3Pn4RS, COD4TVn = cod in DFO area 4TVn, COD3M = cod in NAFO area 3M, COD3NO = cod in NAFO area 3NO, CODGB = cod at Georges Bank, CODGOM = cod at Gulf of Maine, CODFAPL = cod at Faroe Islands, CODICE = Icelandic cod, CODBA2224 = Baltic cod in ICES area 2224, CODBA2532 = Baltic cod in ICES are 2532, CODKAT = cod in Kattegat, CODIS = Irish Sea cod, CODVla = COD in ICES are V1a, CODNS = North Sea cod.

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<th>break point</th>
<th>standard error</th>
<th>number of stocks &lt; 10%</th>
<th>number of stocks &lt; 20%</th>
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<td>0.017</td>
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To test the sensitivity of the breakpoint estimate to the uncertainty level in the individual estimates of SSB and $R$, we replaced the $R$ and SSB data from the data base with simulated data.
and re-ran the breakpoint analysis and Davies test (Table S5, S6). To simulate the data, we used ICES stock assessment reports to find estimates of data uncertainty, which are not provided by the RAM data base. Of those 5 stocks that showed patterns of an Allee effect, only for 2 stocks the 95 % confidence intervals for SSB and $R$ were reported. We estimated the standard deviation by dividing the length of the confidence interval by the number of standard errors. In a large sample size, a 95 % confidence interval is assumed to be 3.92 standard errors wide, thus $SD = (\text{upper limit}-\text{lower limit})/3.92$. The largest average standard deviation found for recruitment estimates was 125884 and for the SSB 46649 (from the North East Arctic stock). For each recruitment and SSB data point in the RAM data base, we simulated new recruitment and SSB data from a normal distribution with a standard deviation equal to the higher average estimate found ($SD = 125884$ for recruitment and $SD = 46649$ for SSB) and mean equal to the original estimate. We did this 100 times and repeated the breakpoint analysis and the Davies test for each run.

We found in 21 cases, no breakpoint at $\geq 10 \% \text{SSB}_{\text{max}}$. Thus, if individual estimates are given with 95 % certainty and considering the largest average $SD$ documented for Atlantic cod, there is a 21 % chance that no Allee effect is found. We also tested the times an Allee effect is found when assuming individual estimates are given only with a 90 % certainty ($SD = (\text{upper limit}-\text{lower limit})/3.29$). In 38 cases no breakpoint was found at $\geq 10 \% \text{SSB}_{\text{MAX}}$. Thus, when individual estimates are given with 90 % certainty and considering the largest average standard deviation, there is a 38 % chance that no Allee effect is found.
Table S5: Breakpoint values and their significance for simulated recruitment and SSB data assuming a 95% certainty level of the individual estimates. The values are shown for each of the 100 runs. Cases where a breakpoint was found below 10% $\text{SSB}_{\text{MAX}}$ are not considered Allee effect thresholds (in bold).

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Table S6: Breakpoint values and their significance for simulated recruitment and SSB data assuming a 90% certainty level of the individual estimates. The values are shown for each of the 100 runs. Cases where a breakpoint was found below 10% SSB\textsubscript{MAX} are not considered Allee effect thresholds (in bold).

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The decrease of the per capita growth rate below the estimated Allee effect threshold was found in accordance with the median recruit-per-spawner ratios at SSB below 10 % SSBB_{\text{MAX},j} (Fig. 2, equation 1 in main text). The steepness of the decrease is reflected by parameter $c$ in the stock-recruitment function (Table S2, equation 1). We also tested the influence of different values of $c$ (Table S7, Fig. S3) on our results. We fitted for each Allee effect scenario the same logistic regression models for the probability of collapse and recovery as in Appendix S3. We then estimated the marginal effect (M.E.) of the Allee effect and the predicted probability of collapse and recovery in presence of an Allee effect and without an Allee effect, at different values of $c$. 

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Figure S3: Different Allee effect scenarios based on the steepness of decline in recruitment per spawner ratio. Scenario a) is a strong Allee effect according to the Atlantic cod data, while b) – e) are hypothetical and weaker Allee effect scenarios.

Table S7: Different Allee effect scenarios defined by the steepness of decline in recruitment per spawner ratio (parameter $c$), resulting in different minimum recruitment per spawner ratios at lowest SSB. The marginal effect (M.E.) on the probability of collapse and recovery is shown.

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<th>M.E. recovery</th>
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<td>b)</td>
<td>92.92</td>
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<td>0.43</td>
<td>69.91</td>
<td>5.66 (0.54)</td>
<td>-76.58 (0.90)</td>
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The marginal effect of the Allee effect decreases with decreasing Allee effect strength, as well as the predicted probability of collapse (Table S8). At +2 °C and $F_{MSY}$, the predicted probability of collapse in presence of the Allee effect varies between 85 % and 100 % for scenario a) – d)
and is around 47% with a very weak Allee effect (e)) (Table S8, Fig. S4). The marginal effect on the probability of collapse does not vary much (1 - 6 percentage points). The difference between Allee effect scenarios is mainly noticeable for recovery. At +3 °C and a time lag of 20 years, recovery is nearly 0% in scenario a) and b), but still between 96% and 100% for all other scenarios. The strongest Allee effect decreases the probability of recovery on average by 77 percentage points, the weakest Allee effect decreases the probability of recovery on average by 4 percentage points. Of course, the Allee effect strength does not influence the cases when no Allee effect is present.

Figure S4: Predicted probability of collapse and recovery at different Allee effect strength. The broken lines show the predicted probability when no Allee effect is present. Light grey broken lines show the values at which the predicted probability of collapse (+2.3 °C) and recovery (20 years) was calculated (Table S8).

As expected, the results, in particular the probability of recovery, are highly sensitive to the Allee effect strength. However, it is not the exponential form of the Allee effect in scenario a) (Fig. S3), but rather the minimum recruitment per spawner ratios below the Allee effect threshold, which determines the impact of the Allee effect. For example, at $c = 20$ where the
exponential form is less pronounced and the minimum recruitment per spawner ratio is 93, the predicted probability of recovery is still close to scenario a).

Table S8: Predicted probability of collapse and recovery in presence of an Allee effect (A.E) and without an Allee effect (noA.E.) The predicted probability of collapse was estimated at + 2.3 °C and $F_{MSY}$ and the predicted probability of recovery was estimated at + 3 °C and a management delay of 20 years.

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<td>$P(\text{noA.E.})$</td>
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<tr>
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<td>18.77 (8.77)</td>
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<td>d)</td>
<td>85.17 (8.90)</td>
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References


Appendix S2: Fitting a nonlinear function for the relation between recruitment and temperature

Implications of Allee effects for fisheries management in a changing climate: evidence from Atlantic cod

*Ecological Applications*

Anna-Marie Winter¹, Andries Richter¹,², Anne Maria Eikeset¹

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²Environmental Economics and Natural Resources Group, Sub-Department of Economics, Wageningen University, 6700 EW Wageningen, The Netherlands
Appendix S2: Fitting a nonlinear function for the relation between recruitment and temperature

We assumed a linear and constant temperature dependence of the recruitment production following Planque and Fredou (1999). We used their linear relationship, because it is the simplest form and the interaction with an Allee effect, which itself is already a nonlinear function, is easier to interpret. However, we also tested the impact of a non-linear temperature function. For comparison to the linear scenario, we again kept the Ricker stock-recruitment function and fitted the non-linear term to recruitment anomalies (recruitment change with temperature). To remain consistent with Planque and Fredou (1999), we log2 transformed recruitment and SST anomalies. The log2 transformation stabilizes variance and gives an easy interpretation: a change of 1 indicates that an increase of 1°C is associated with a twofold increase in recruitment.

The function between the log2 transformed recruitment anomalies and SST anomalies was fitted with the Nonlinear Least Squares function in R:

\[ d = \log_2(R_{\text{anom},i}) = -\text{SST}_{\text{anom},i}^2 - a_T \times \text{SST}_{\text{anom},i} + b_T \]  
(eq. S1)

The fitted parameters \(a_T\) and \(b_T\) are shown in Table S1.

Table S1: Fitting parameters for the non-linear function between recruitment and SST anomalies.

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<td>(a_T)</td>
<td>1.085</td>
<td>0.258</td>
<td>4.212</td>
<td>0</td>
</tr>
<tr>
<td>(b_T)</td>
<td>0.342</td>
<td>0.151</td>
<td>2.271</td>
<td>&lt; 0.05</td>
</tr>
</tbody>
</table>

residual standard error: 1.096 on 51 degrees of freedom
The non-linear temperature dependence was incorporated into the stock-recruitment function as:

\[ R = SSB_{t-1} \cdot e^{(a-b \cdot SSB_{t-1})} \cdot e^c \cdot e^{\log(d)} \]  

(eq. S2)

where parameter \( d \) is estimated from equation S1 and back transformed. The yearly anomaly of SST, \( \text{SST}_{\text{anom},i} \) (eq. S1), is in the simulations a random draw from a normal distribution with mean \( \text{SST} \) equal to the mean increase and variance equal to observed variance in SST.

Figure S1: Simulated probability of collapse and recovery when the relation between temperature and recruitment is nonlinear. \( a \) and \( b \) show the probability of collapse at increasing temperature and fishing level. \( c \) and \( d \) show the probability of recovery at increasing temperature level and management delay in imposing a fishing moratorium. A residual fishing pressure of 0.1 \( y^{-1} \) remains despite the moratorium.
In comparison to the linear relation, the non-linear dependence causes recruitment production to decline more rapidly with increasing temperature (Fig. S1). This causes an increased probability of collapse. For example, at $F_{MSY}$ the 50% probability of collapse is around +1.2 °C with the non-linear function, while with a linear function it is at around +2.5 °C (+2.1 °C with an Allee effect). At +3 °C the probability of collapse is 100% with the non-linear function, independent of the fishing pressure and whether there is an Allee effect. With the linear function, the probability of collapse is only 100% above a fishing pressure of 0.3 y$^{-1}$. Without an Allee effect, the probability of recovery is with the linear temperature function still 100% at +3.5 °C, while recovery with the non-linear function is only possible < +2 °C. With an Allee effect, recovery is possible if fishing is restricted within 5 years and SST remains < +3 °C in the linear temperature scenario. In the non-linear scenario, recovery is only possible at ≤ +1 °C.

The fitted non-linear function suggests highest recruitment production between -0.5 and zero temperature anomaly and only then, recruitment production is higher than in the linear case (Fig. S2). At stronger negative and positive anomalies, recruitment production is lower with the non-linear temperature dependence.
Figure S2: Comparison of the linear temperature function (black lines) and the non-linear temperature model (blue lines). The left panel shows the relation between anomalies of North Sea cod recruitment and SST in the North Sea. The right panel shows the stock-recruitment model plotted at different temperature scenarios.
Appendix S3: Fitting a generalized linear model for the predicted probability of collapse and recovery

Implications of Allee effects for fisheries management in a changing climate: evidence from Atlantic cod

Ecological Applications

Anna-Marie Winter¹, Andries Richter¹,², Anne Maria Eikeset¹

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²Environmental Economics and Natural Resources Group, Sub-Department of Economics, Wageningen University, 6700 EW Wageningen, The Netherland
Appendix S3: Fitting a generalized linear model for the predicted probability of collapse and recovery

We fitted two separate generalized linear regression models to the outcome of different simulated scenarios to predict the probability of collapse and recovery. Collapse and recovery scenarios were simulated separately, because they differ in the parameters considered. Each scenario was initialized by simulating population dynamics for 500 years without fishing pressure, no temperature increase and without an Allee effect, to find the equilibrium population size. We then simulated different scenarios by exposing the population for 500 years to different variables. For each simulation, parameters were drawn from uniform distributions in a Monte-Carlo analysis (see main text for information on the minimum and maximum values of the different parameters). The regression models show the relative contribution of the different variables for the probability (log odds) of collapse and recovery. The best fit logistical regression models (Table S3) were chosen based on the Akaike Information Criterion (AIC) and likelihood ratio test (ANOVA).

For predicted probability of collapse, we ran in total 1500 independent simulations scenarios where we varied i) presence and absence of Allee effect, ii) mean temperature increase, iii) mean fishing pressure iv) variance in temperature and v) variance in fishing. The logistic model was fit to the population status collapsed/not collapsed. The population was defined as collapsed when it degraded to or below 5% of the maximum observed spawning stock biomass, SSB_{MAX}, and remained degraded for at least one generation (8 years) in accordance with Yletyinen et al. (2018).

For the predicted probability of recovery, we were only interested in cases that had dropped below the Allee effect threshold in order to analyse the probability of recovery. We therefore ran 3000 simulations, of which 1500 cases where biomass dropped below the Allee effect
threshold were randomly chosen. In addition to \( i)-v \), \( vi \) the management delay (“mgmt. delay”) until a fishing moratorium was implemented and \( vii \) the residual fishing pressure during the moratorium (“fishing during moratorium”) was varied between scenarios. The residual fishing pressure was considered to reflect bycatch or illegal fishing (Agnew et al. 2009; Davies et al. 2009). The logistic model was fitted to the population status depleted and recovered/not recovered. The population was declared recovered when it remained above the Allee effect threshold for at least one generation (8 years). Figure S1 illustrates the different definitions for population status used.

Figure S1: Illustration of the different definitions for collapsed and recovered. The population is declared collapsed once biomass fell below 5 % \( SSB_{\text{MAX}} \) and remained there for at least one generation. The population was recovered, once biomass increased above the Allee effect threshold again and remained there for at least one generation. If biomass was above the collapse threshold, but below the Allee effect threshold (or above the Allee effect threshold, but for less than one generation), the population was considered as rebuilding. The population could degrade again, after it had recovered. However, because fishing was then still restricted, this
could only happen due to very high temperature pressure (which happened in only 0.8 \% of the cases).

**Probability of collapse**

Out of the total number of 1500 independent simulations scenarios, 987 population trajectories degraded below the 5 \% of SSB_{MAX} threshold and were therefore declared as collapsed. The best model fit for the probability of collapse includes two interaction terms between fishing variance and fishing and temperature (model (3), Table S1). See the results section in the main text for interpretation of the coefficients and interaction terms of all fitted models.
Table S1: Generalized linear regression models for probability of collapse (log odds). The three nested and best fit models with increasing number of interactions are shown. $\beta$s from equation 4 in main text are the coefficients for Allee effect ($\beta_1$), temperature ($\beta_2$), fishing ($\beta_3$), fishing variance ($\beta_5$) and the constant ($\beta_0$). Temperature variance was found to be not significant ($\beta_4 = 0$).

<table>
<thead>
<tr>
<th></th>
<th>Collapse</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(1)</td>
<td>(2)</td>
<td>(3)</td>
</tr>
<tr>
<td>Allee effect</td>
<td>2.272***</td>
<td>5.177***</td>
<td>5.609***</td>
</tr>
<tr>
<td></td>
<td>(0.391)</td>
<td>(0.876)</td>
<td>(0.963)</td>
</tr>
<tr>
<td>Temperature</td>
<td>7.236***</td>
<td>10.856***</td>
<td>13.309***</td>
</tr>
<tr>
<td></td>
<td>(0.675)</td>
<td>(1.500)</td>
<td>(1.967)</td>
</tr>
<tr>
<td>Fishing</td>
<td>4.550***</td>
<td>6.889***</td>
<td>7.701***</td>
</tr>
<tr>
<td></td>
<td>(0.421)</td>
<td>(0.939)</td>
<td>(1.100)</td>
</tr>
<tr>
<td>Fishing variance</td>
<td>0.544***</td>
<td>0.804***</td>
<td>2.568***</td>
</tr>
<tr>
<td></td>
<td>(0.200)</td>
<td>(0.308)</td>
<td>(0.704)</td>
</tr>
<tr>
<td>Fishing : Temperature</td>
<td>1.409***</td>
<td>1.549***</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.212)</td>
<td>(0.240)</td>
<td></td>
</tr>
<tr>
<td>Fishing variance : Temperature</td>
<td></td>
<td></td>
<td>-0.797***</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(0.272)</td>
</tr>
<tr>
<td>Constant</td>
<td>-34.181***</td>
<td>-59.707***</td>
<td>-68.974***</td>
</tr>
<tr>
<td></td>
<td>(3.165)</td>
<td>(7.998)</td>
<td>(9.762)</td>
</tr>
</tbody>
</table>

Observations 1,500 1,500 1,500
Log Likelihood -117.553 -57.485 -52.439
Akaike Inf. Crit. 245.105 126.970 118.879
Residual Deviance 235.105 114.970 104.879
Null Deviance (df = 1499) 1,927.059 1,927.059 1,927.059

Note: *p<0.1; **p<0.05; ***p<0.01

Probability of recovery

From the 3000 cases, 2066 cases fell below the Allee effect threshold. From these 2066 cases, we randomly selected 1500 trajectories. 655 of these 1500 cases had recovered. The best fit (AIC, log likelihood) logistic model for the probability of recovery includes one interaction terms between the Allee effect and management delay (model (2), Table S2). See the results
section in the main text for interpretation of the coefficients and interaction term of the fitted models.

Table S2: Generalized linear regression models for probability of recovery (log odds). The two nested and best fit models with increasing complexity are shown below. ßs from equation 5 in main text are the coefficients for Allee effect (ß₁), temperature (ß₂), fishing (ß₃), management delay (ß₆), residual fishing pressure during the moratorium (ß₇) and the constant (ß₀). Temperature variance and fishing variance were found to be not significant (ß₄ = 0, ß₅ = 0).

<table>
<thead>
<tr>
<th></th>
<th>Recovery</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(1)</td>
<td>(2)</td>
</tr>
<tr>
<td>Allee effect</td>
<td>−9.400*** (0.601)</td>
<td>−6.281*** (0.696)</td>
</tr>
<tr>
<td>Temperature</td>
<td>−2.317*** (0.191)</td>
<td>−2.676*** (0.224)</td>
</tr>
<tr>
<td>Fishing</td>
<td>−0.212*** (0.053)</td>
<td>−0.204*** (0.055)</td>
</tr>
<tr>
<td>Mgmt. delay</td>
<td>−0.110*** (0.015)</td>
<td>−0.038** (0.018)</td>
</tr>
<tr>
<td>Fishing during moratorium</td>
<td>−2.591*** (0.246)</td>
<td>−3.067*** (0.285)</td>
</tr>
<tr>
<td>Allee effect : Mgmt. delay</td>
<td></td>
<td>−0.413*** (0.062)</td>
</tr>
<tr>
<td>Constant</td>
<td>15.223*** (1.134)</td>
<td>15.740*** (1.252)</td>
</tr>
</tbody>
</table>

| Observations         | 1,500            | 1,500    |
| Log Likelihood       | −260.134         | −220.489 |
| Akaike Inf. Crit.    | 532.268          | 454.978  |
| Residual Deviance    | 520.268 (df 1494)| 440.978 (df 1493) |
| Null Deviance (df = 1499) | 2,055.310       | 2,055.310 |

* p<0.1; ** p<0.05; *** p<0.01
Table S3: The two best fitted generalized linear regression models for probability of collapse and recovery (log odds).

<table>
<thead>
<tr>
<th></th>
<th>Collapse</th>
<th>Recovery</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allee effect</td>
<td>5.609***</td>
<td>-6.281***</td>
</tr>
<tr>
<td></td>
<td>(0.963)</td>
<td>(0.696)</td>
</tr>
<tr>
<td>Temperature</td>
<td>13.309***</td>
<td>-2.676***</td>
</tr>
<tr>
<td></td>
<td>(1.967)</td>
<td>(0.224)</td>
</tr>
<tr>
<td>Fishing</td>
<td>7.701***</td>
<td>-0.204***</td>
</tr>
<tr>
<td></td>
<td>(1.100)</td>
<td>(0.055)</td>
</tr>
<tr>
<td>Fishing variance</td>
<td>2.568***</td>
<td>-0.038***</td>
</tr>
<tr>
<td></td>
<td>(0.704)</td>
<td>(0.018)</td>
</tr>
<tr>
<td>Mgmt. delay</td>
<td></td>
<td>-3.067***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.285)</td>
</tr>
<tr>
<td>Fishing during moratorium</td>
<td>-0.797***</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.272)</td>
<td></td>
</tr>
<tr>
<td>Fishing : Temperature</td>
<td>1.549***</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.240)</td>
<td></td>
</tr>
<tr>
<td>Fishing variance : Temperature</td>
<td>-0.413***</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.062)</td>
<td></td>
</tr>
<tr>
<td>Allee effect : Mgmt. delay</td>
<td>-0.413***</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.062)</td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>-68.974***</td>
<td>15.740***</td>
</tr>
<tr>
<td></td>
<td>(9.762)</td>
<td>(1.252)</td>
</tr>
<tr>
<td>Observations</td>
<td>1,500</td>
<td>1,500</td>
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<tr>
<td>Log Likelihood</td>
<td>-52.439</td>
<td>-220.489</td>
</tr>
<tr>
<td>Akaike Inf. Crit.</td>
<td>118.879</td>
<td>454.978</td>
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<tr>
<td>Residual Deviance (df = 1493)</td>
<td>104.879</td>
<td>440.978</td>
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<tr>
<td>Null Deviance (df = 1499)</td>
<td>1,927.059</td>
<td>2,055.310</td>
</tr>
<tr>
<td>Average marginal effect</td>
<td>5.66</td>
<td>-76.58</td>
</tr>
</tbody>
</table>

Note: *p<0.1; **p<0.05; ***p<0.01

The marginal effects associated with the Allee effect were calculated in the “margins” package in R (Leeper 2017). The average marginal effect is the average of all marginal effects calculated for every value of the predictors in the logistic regression model. The average marginal effect was estimated for each of the parameters, considering and excluding the Allee effect (Table S4).
Table S4: Average marginal effect of the Allee effect and average marginal effects of each of the parameters considered in the logistic regression model, estimated separately without Allee effect (noA.E.) and with the Allee effect (A.E.). In brackets are the variances of the average marginal effects.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Collapse</th>
<th>Recovery</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>noA.E.</td>
<td>A.E.</td>
</tr>
<tr>
<td>Allee effect</td>
<td>5.66</td>
<td>-76.576</td>
</tr>
<tr>
<td></td>
<td>(0.003)</td>
<td>(0.013)</td>
</tr>
<tr>
<td>Temperature</td>
<td>16.56</td>
<td>21.497</td>
</tr>
<tr>
<td></td>
<td>(0.003)</td>
<td>(0.003)</td>
</tr>
<tr>
<td></td>
<td>(0.003)</td>
<td>(0.004)</td>
</tr>
<tr>
<td>Fishing</td>
<td>9.737</td>
<td>13.428</td>
</tr>
<tr>
<td></td>
<td>(0.001)</td>
<td>(0.001)</td>
</tr>
<tr>
<td></td>
<td>(0.001)</td>
<td>(0.001)</td>
</tr>
<tr>
<td>Fishing variance</td>
<td>0.833</td>
<td>1.1</td>
</tr>
<tr>
<td></td>
<td>(0.001)</td>
<td>(0.001)</td>
</tr>
<tr>
<td>Mgmt. delay</td>
<td>-0.261</td>
<td>-1.019</td>
</tr>
<tr>
<td></td>
<td>(0.0)</td>
<td>(0.0)</td>
</tr>
<tr>
<td>Fishing during moratorium</td>
<td>-20.851</td>
<td>-6.929</td>
</tr>
<tr>
<td></td>
<td>(0.007)</td>
<td>(0.007)</td>
</tr>
</tbody>
</table>
References


Metadata S1: Computer code (R language) to simulate population dynamics

Implications of Allee effects for fisheries management in a changing climate: evidence from Atlantic cod

*Ecological Applications*

Anna-Marie Winter¹, Andries Richter¹,², Anne Maria Eikeset¹

¹Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, N-0316 Oslo, Norway

²Environmental Economics and Natural Resources Group, Sub-Department of Economics, Wageningen University, 6700 EW Wageningen, The Netherland
Metadata S1: Computer code (R language) to simulate population dynamics

The attached computer code (Data S1) simulates population collapse and recovery. An example for a Monte Carlo draw is given. To initialize the simulations, population dynamics were first simulated for 500 years under baseline conditions (no SST change, no fishing pressure and no Allee effect), until average population size reached equilibrium. For population collapse, mean SST and fishing pressure was gradually increased (Fig. 3a, b, Fig. 6a, b).

For population recovery, fishing pressure was restricted once SSB fell below the Allee effect threshold. We investigated the impact of the fishing moratorium being implemented with different management delays and the impact of a less consequent moratorium with a residual fishing pressure (Fig. 3c, d, Fig. 6c, d).

In the Monte Carlo simulations, all parameters were drawn from uniform distributions, and variance of SST and fishing pressure was additionally altered. A description of the parameter values and simulated scenarios is found in the main text.

To run the computer code, only the file Data S1: run_dynamics.R needs to be run, it will automatically read in all necessary files. The location of the remaining files should be the same as the working directory or the Data S1: run_dynamics.R file.

A description of each computer code is given below.

Data S1: population_data.R:

The data file contains the averaged life history traits (W = weight, pmat = probability of maturation, M = natural mortality; data from ICES) and parameters \((a – d)\) and residuals error; equation 1 in main text) for the stock-recruitment function. Further, the initial population abundance (N_init), SSB (SSB_init) and total biomass (TB_init) based on the most recent data
year (of the RAM database; year 2005) is given. The standard deviation for the yearly fishing pressure (F\_sd) and sea surface warming (SST\_sd) is given, while the mean fishing pressure and SST is set in Data S1: run\_dynamics.R. At the end of the code, the stock-recruitment function is defined. In Data S1: run\_dynamics.R, this file is read in and all parameters needed and the stock-recruitment function is automatically saved and can be used for the simulation.

Data S1: population\_dynamics.R

This code simulates the basic population dynamics with annual time steps for 500 years (“simtime” defined in Data S1: population\_data.R). For each year sea change in sea surface temperature, SST, is drawn from a distribution (its mean is set in Data S1: run\_dynamics.R). Recruitment is produced based on the stock-recruitment function with or without an Allee effect (set in Data S1: run\_dynamics.R) and on the year’s SST increase. SSB is constituted by the mature individuals which survive from natural and fishing mortality at the end of the year. The year’s fishing pressure is drawn from a lognormal distribution (mean is set in Data S1: run\_dynamics.R). Individuals are exposed to natural and fishing mortality, but one year olds are spared from fishing. At the end of the year the number of caught individuals are registered as “Catch” and surviving individuals are registered for SSB and the total biomass, TB. SSB is the mass of mature individuals, while TB is the mass of all individuals. The population dynamics loop is saved as a function, which is read and run in the Data S1: run\_dynamics.R.

Data S1: population\_recovery.R

This code simulates the population dynamics similar to Data S1: population\_dynamics.R on an annual basis for 500 years (“simtime” defined in Data S1: population\_data.R), with the
difference of initializing fishing restriction once biomass falls below the Allee effect threshold (Allee effect threshold = “AT * MAX”). Once biomass falls below the Allee effect threshold, years below the Allee effect threshold are counted. If SSB is below the threshold for at least 2 consecutive years and the delay in management has passed (“mlag”, defined in Data S1: run_dynamics.R), fishing is restricted. Fishing can be restricted to zero or a residual fishing pressure remains. The actual remaining fishing pressure is drawn from a lognormal distribution with a mean set in Data S1: run_dynamics.R (“F_res” = 0 $y^{-1}$ for a full moratorium or $F_{res} > = y^{-1}$ for a remaining residual fishing pressure). As in Data S1: population_dynamics.R, at the end of the year individuals surviving from natural and the (residual) fishing pressure are registered as SSB and TB and the catch is estimated. The population dynamics loop is saved as a function, which is read and run in the Data S1: run_dynamics.R.

Data S1: run_dynamics.R

This code takes the previously defined functions for data and population dynamics (“source”) to run the actual simulations. The location of the other files needs to be the same as the working directory/the Data S1: run_dynamics.R file. Otherwise the full path needs to be added when sourcing (e.g. source (“the full path name/population_data.R”)) For the scenarios, the Allee effect strength (parameter $c$ in main text: 0 = no Allee effect, 69.91 = strong Allee effect, but one could also use other parameter values see e.g. Appendix S1: Table S7), the increase in sea surface temperature, SST (here as an example 2.5 °C) and the fishing pressure (here as an example 0.31 $y^{-1}$) have to be chosen. The code generates a plot of the SSB trajectory with and without an Allee effect. Horizontal lines show the threshold for population collapse and the Allee effect threshold. For the simulated probability of collapse (Fig. 3 a, b) this code was used with increasing values of SST and fishing pressure.
For the predicted probability of collapse (Fig. 6 a, b), SST, fishing pressure and their variance levels were drawn from normal distributions (Monte Carlo Analysis) and a logistic regression model was fitted to the population status (collapsed, not collapsed). The given example for the Monte Carlo run is slightly simplified and only the values for the Allee effect (no Allee effect or strong Allee effect), SST increase (random draw from uniform distribution with a minimum of 0 °C and a maximum of 4.5 °C) and fishing pressure (random draw from uniform distribution with a minimum of 0 $y^{-1}$ and a maximum of 1 $y^{-1}$) are drawn. The code also plots the trajectory of SSB. For the logistic regression models, the population status at the end of the simulation is registered and used as the dependent variable (equation 4 in main text).

The simulated and predicted probability of recovery is estimated with the function defined for the recovery dynamics. The difference to the collapse dynamics is that fishing pressure is restricted once SSB falls below the Allee effect threshold and after a given delay in management (here called “lag”). In addition once can choose whether fishing pressure is fully restricted (“fishing_res” = 0 $y^{-1}$ or not: fishing_res > 0 $y^{-1}$). As an example, we show here the effect of a 0.1 $y^{-1}$ residual fishing pressure (as in Fig. 3 c, d). The code generates a plot of the SSB trajectory showing in addition to the Allee effect threshold and collapse threshold, the time when fishing pressure is restricted (vertical line).

In the Monte Carlo analysis for the predicted probability of recovery, in addition to the values for the Allee effect, SST increase and fishing pressure, also the management delay (drawn from uniform distribution with a minimum of 0 years and a maximum of 30 years) and the residual fishing pressure (drawn from a uniform distribution with a minimum of 0 $y^{-1}$ and a maximum of 0.2 $y^{-1}$) are drawn. The code plots the trajectory of SSB. For the logistic regression models, the population status at the end of the simulation is registered and used as the dependent variable (equation 5 in main text).
PAPER II

Spawner weight and ocean temperature drive Allee effect dynamics in Atlantic cod, *Gadus Morhua*: inherent and emergent density regulation

Anna-Marie Winter, Nadezda Vasilyeva, Artem Vladimirov

Highlights

- Presence of an Allee effect in Atlantic cod is common, highly dynamic and environment dependent.
- Ocean warming can strengthen and weaken the Allee effect.
- Reduced spawner weight e.g., through age-size truncation, can induce an Allee effect.
- Future environmental conditions can “unmask” Allee effects that had been counteracted by favorable conditions in the past.
- Allee effect presence correlates with prolonged recovery.
End-century projections of Atlantic cod (*Gadus Morhua*) under simultaneous ocean acidification and ocean warming from experimental data and time series

Martina Stiasny, Anna-Marie Winter

Highlights
- Climate change impacts can substantially differ within the same (fish) species.
- With nonlinear ocean warming and ocean acidification not all fish may be saved with the global target of 1.5 °C.
- Fisheries management needs to consider magnitude and pace of ocean warming and ocean acidification.
- Managing fishing mortality and selectivity can mitigate the impact of climate change.
Impediments to Fisheries Recovery in Canada: Policy and Institutional Constraints on Developing Management Practices Compliant with the Precautionary Approach

Anna-Marie Winter, Jeffrey A. Hutchings

Highlights

- The Precautionary Approach aids decision-making under uncertainty and risk.
- Science based and science determined decision processes are identified.
- Canada’s policy and institutional set-up obfuscate the role of science.
- Accountability and credibility of the decision-making is weaker than in the EU.
- Structured decision-making and guidelines for uncertainty management are suggested.
- The need for a clear definition of the science responsibility is emphasized.
Impediments to fisheries recovery in Canada: Policy and institutional constraints on developing management practices compliant with the precautionary approach

Anna-Marie Winter, Jeffrey A. Hutchings

Department of Biosciences, Centre for Ecological and Evolutionary Synthesis, University of Oslo, Oslo, N-0316, Norway
Environmental Economics and Natural Resources Group, Sub-Department of Economics, Wageningen University, Wageningen, 6700 EW, The Netherlands
Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, NS B3H4R2, Canada
Institute of Marine Research, VÅlerenga Marine Research Station, N-4817, Hils, Norway
Centre for Coastal Research, Department of Natural Sciences, University of Agder, N-4604, Kristiansand, Norway

ARTICLE INFO

Keywords:
Precautionary approach
Sustainable fisheries framework
Common fisheries policy
Science advice
Fisheries management
Scientific credibility

ABSTRACT

The status of many Canadian fisheries is poor, a consequence of inadequate implementation of sustainable fishery policy within the context of the Precautionary Approach (PA). A key component of implementation lies with the provision of science advice. Scientists are responsible for advising on options likely to meet policy intent and objectives. Here, we examine PA-compliance in the role of science in Canada’s fisheries management decision-making. We distinguish science-based from science-determined decisions and processes. Science-based decisions emerge from consultation processes involving stakeholders; science need not always have a clear and accountable role that can be transparently separable from other inputs. Science-determined decisions result from impartial, publicly available, peer-reviewed scientific determinations clearly distinguishable from other inputs. Our findings are consolidated with a comparison to the European Union (EU), which is legally bound to PA implementation, but which differs in its institutional organization and decision-making process. Compared to the EU, Canada’s science advisory process is less structured and transparent, scientific advice is not always clearly distinguishable, and policy formulation is not explicit in affording science a responsibility compliant with the PA. The institutional structure and policy framework in Canada has potential to obfuscate the role of science, leading to an erosion of credibility and accountability of fisheries management decisions. We emphasize the strengths of a structured and transparent decision-making process, the existence of a coherent system for categorizing uncertainty with respective rules for decision-making, and unambiguous definitions of the responsibility of science in sustainable fisheries policy.

1. Introduction

One of the focal areas of marine policy relates to the sustainability of marine fisheries. The high degree of uncertainty and natural variability involved, the slow reversibility of population changes, and the (nearly) open-access nature of many fisheries makes the Precautionary Approach (PA) the guiding principle in fisheries management [1,2]. The purpose of the precautionary approach is the protection of the environment (such as a fish stock) and limitation of risks (such as a fish stock collapse) by taking preventive action in response to threats of environmental harm at an early stage, including situations of scientific uncertainty. The PA recognizes that the absence of full scientific certainty shall not be used as a reason for postponing decisions where there is a chance of serious or irreversible harm (Article 6.2 in Ref. [3]). Thus, the PA tries to establish a bridge between scientific uncertainty and policy decision-making to improve society’s ability to identify and act in response to environmental risks [4], while implying a societal responsibility to protect the environment. The PA lays the burden proof on the resource user, whereby the protections can only be relaxed if further scientific findings emerge that provide sound evidence that no harm will result.

Application of the PA to maritime affairs is embedded in numerous international documents, with the 1995 UN Agreement on Straddling and Highly Migratory Fish Stocks (UN Fish Stocks Agreement (UNFA) [3]) and the FAO Code of Conduct for Responsible Fisheries [5] being
the most relevant international agreements for fisheries management. The UNFA stipulates that when implementing the PA, States shall determine stock-specific target (or management) and limit (or conservation) reference points for harvested fish stocks and shall identify the actions to be taken if limit reference points are exceeded. In addition, the FAO Guidelines [6] recommend the establishment of (i) reference points for fishing mortality (to identify overfishing) and stock size (to determine if stocks are in an overfished state), (ii) rebuilding plans, and (iii) harvest control rules.

Although these policy frameworks are clear in the necessity of having reference points and harvest control rules, they do not specify the role of science in defining them. Since the collapse of numerous groundfish fisheries across the North Atlantic in the late 1980s and early 1990s, the role of science in sustainable fisheries policies has evolved at considerably different rates across jurisdictions. (By ‘science’, it is here referred specifically to the natural sciences, although it is likely that the incorporation of social science in the implementation of sustainable fisheries policies shares a similar degree of divergence.) The role of science in the PA can be summarized in the following key principles: 1) definition of quantifiable criteria (reference points) for scientific judgment of management objectives (e.g., total allowable catch), an analysis of attendant risks, and 2) evaluation of what respective actions (harvest rules) will meet the objectives. Besides following scientific standards (objective, verifiable and potentially replicable), this implies 4) a peer-review process to ensure the usage of the best available evidence and 5) a transparent science advisory process.

Data-limited evidence, provided that it is recognized as the best available at that time, can be used in designing conservation and management measures. However, implementation of the PA requires reliable information consistent with the scientific standards of assessing stock status (functions of data availability, model complexities, quality of jurisdictional peer review, scientific excellence) in light of different fishing mortalities and at a level of detail that makes operationalization of target and limit reference points possible [7]. For stocks with uncertain status, annex II of UNFA provides for provisional reference points, which may be established by analogy to similar and better known stocks until improved information becomes available.

To ensure that the available evidence is always the best at the time, the PA demands regular independent, objective and in-depth peer-review of the scientific standards, periodic re-evaluation of the data, and a process for scientific assessment and analysis that is transparent [6]. This implies an institutional organization and political framework that allows for a defined, transparent, and independent role of science that has the scientific capacity that allows for regular provision of the necessary information.

The role of science in Canada’s fisheries management practices has been controversial [8], with Newfoundland’s northern cod (Gadus morhua) collapse being one of the most defining moments [8-10]. Since the collapse, two major policy decisions were taken: participatory decision-making with stakeholder inclusion is promoted by a ‘shared stewardship’ management strategy; and, with the agreement to UNFA and the FAO Code of Conduct for Responsible Fisheries, the PA was introduced. This brought considerable attention to the development of a PA framework that would provide a more structured science-focused approach to managing fisheries [11]. Of the 110 of Canada’s stocks for which health status under the PA framework has been ascertained (thus, excluding those with unknown status), biomass estimates of 30% (33 stocks) are in the Critical Zone, meaning that stock biomass is less than the limit reference point ($B_{lm}$) [12]. As of 2020, all Canadian Atlantic cod stocks are in the Critical Zone (DFO webpage [13]).

Canada has an exceptionally long-standing fishing history and deep cultural appreciation for fish, which is considered a common property resource to be managed for the benefit of all Canadians [14]. The government recognizes fishing as a public right. The diminished success of Canada’s fisheries management stands in contrast to the level of governmental support to the fisheries sector ($675,526$ million USD per year — almost double the annual landings value; Table 1) and the high economic ($1.74$ billion USD per year added to Canada’s GDP from fisheries alone; Table 1) and public (3 workers per 1000 are occupied in the fishing sector; Table 1) importance of fisheries.

Serial failures of governmental management to prevent the depletion of fish stocks have generated a significant amount of literature on the causes and consequences of these deficiencies. Most literature focuses on the ecological constraints on recovery (for example [15-21]) rather than the essential governance mechanisms that might be required to achieve sustainability, such as implementation of a fisheries policy fully compliant with the PA [2,22]. There is a general consensus that scientifically informed policies promote recovery and, consistent with the poor state of many of Canada’s fish stocks, the role of science and implementation of the PA in Canada requires strengthening [8,11].

In the present study, we address the question: Does the role of science in Canada’s fisheries management practice meet the requirements of the PA? We examine (i) the role of science in setting reference points, harvest control rules, and total allowable catches (PA key principle 1 + 3; Table 2), (ii) the role of science in handling uncertainty and data limitations (PA key principle 2), (iii) the peer-review process for evaluating scientific evidence (PA key principle 4), and (iv) the transparency of the science advisory process (PA key principle 5). We then compare Canada’s fisheries management practice to that in the European Union (EU), which is also legally bound to the obligations of implementing the Precautionary Approach, but which differs profoundly in its institutional structure. In the EU, science is provided by an independent intergovernmental council (International Council for the Exploration of the Sea or ICES), consisting of 20 member states, while in Canada, the Department of Fisheries and Oceans (DFO) communicates its science advice through its in-house Canadian Science Advisory Secretariat (CSAS). Canada’s fisheries management process allows for a flexible, arguably adaptive management approach rather than being bound to strict legislative constraints [23]. It should be noted, however, that there is no requirement that management decisions be evidence-based, as in the EU. While in the EU authority over fisheries is delegated to the different EU states, in Canada control is retained by the federal Minister of Fisheries, Oceans and the Canadian Coast Guard. Here, we focus on two guiding fisheries management approaches: the Sustainable Fisheries Framework in Canada and the Common Fisheries Policy in the EU.

### 2. Implementation of a PA-compliant harvest strategy in Canada

The seeds for present-day support for the Sustainable Fisheries Framework in Canada, which have been detailed elsewhere [24,25], were arguably sown in 1976 when the national Fisheries Act (1868) was revised to explicitly include strong and effective protection of fish habitat. Further, encouraged by the subsequent Policy for the Management of Fish Habitat (1986), which strived to ensure a net gain of habitat for Canadian fisheries resources, the stage was set for government support of the two main international agreements incorporating the PA: the UN Agreement on Straddling and Highly Migratory Fish Stocks (UNFA) [3] and the establishment of the FAO Code of Conduct for Responsible Fisheries [5]. In support of a national implementation of the FAO Code of Conduct, Canada adopted a Canadian Code of Conduct for Responsible Fishing Operations (1998), setting out fundamental principles for commercial harvesters that included a commitment to pursue the ecological sustainability of Canadian fisheries.

In 2001, Canada began to incorporate the PA across all ocean and freshwater resource management strategies [26,27]. This included A Policy Framework for the Management of Fisheries on Canada’s Atlantic Coast [26], which defined conservation as “sustainable use that safeguards ecological processes and genetic diversity for present and future generations” [28] and incorporated the general principles of the PA. As in the Fisheries Act itself, neither the role of science nor the responsibility of science for implementing the PA was clearly articulated.
Table 1
Main fisheries statistics and indicators for Canada and the European Union. The data are mainly from 2015 to 2018.

<table>
<thead>
<tr>
<th>Access to the sea</th>
<th>Canada</th>
<th>European Union</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coastline [km²]</td>
<td>202,080</td>
<td>78,634</td>
</tr>
<tr>
<td>Coastal population [% of total]</td>
<td>22%</td>
<td>49%</td>
</tr>
<tr>
<td>Exclusive Economic Zone [mil km²]</td>
<td>3.01</td>
<td>17.17</td>
</tr>
<tr>
<td>Territorial Sea [mil km²]</td>
<td>2.69</td>
<td>1.04</td>
</tr>
<tr>
<td>Cultural and financial value</td>
<td>17,703</td>
<td>65,400</td>
</tr>
</tbody>
</table>

| Employment fishing vessel¹ | 75,541 (3.1 per 1000 workers) | 221,024 (0.67 per 1000 workers) |
| Number of motorized fishing vessels | 5,634 | 5,427 |
| Total marine landing value [000 USD]¹ | 395,165 | 6,019,338 |
| % landing value comprising Atlantic Cod¹ | 5.6% | 5.4% |
| Export Atlantic Cod [000 USD]¹ | 13,322 (3.4% of total landing value) | 827,142 (13.74% of total landing value) |
| Import Atlantic Cod [000 USD]¹ | 3,858 (0.98% of total landing value) | 3,327,422 (55.28% of total landing value) |
| Gross Value Added [billion USD]¹ | 1738 (0.122% of total GVA) | 11,773 (0.11% of total GVA) |
| Fish protein [% total proteins]¹ | 5.4 | 6.3 |
| Assessed stocks | 194 (179 yearly) | 247 (65–71 yearly) |
| Stocks with unknown status | 74 (38% of assessed stocks) | 105 (43% of assessed stocks) |
| Number of stocks in critical zone (Canada) outside safe biological limits (EU) | 17 (14% of assessed stocks) | 17 (25% of assessed stocks) |
| MSC stocks (no. of certified fisheries) | 19 (0 Atlantic cod fisheries) | 125 (14 Atlantic cod fisheries) |
| Stocks with F > FMSY | not estimated | 29 (12% of total assessed stocks) |
| Fisheries support to fisheries sector | 675,526 (171% of landing value) | 525,865 (10% of landing value) |
| % for management of resources¹ | 54% | 46% |

¹ Data from 2017 and from The FAO’s the fisheries global information system [74]. The data describe import and export of fresh, chilled, frozen Atlantic cod (as meat, fillets, minced, in portions or as stocks), salted and/or dried Atlantic cod (klipfish, stockfish), smoked Atlantic cod and Atlantic cod in brine. In the EU estimate, data from Cyprus are missing and the export quantity from Malta is missing. For the EU the export estimate is missing.

² Data from 2016. The gross value added (GVA) reflects the value generated by the fisheries sector (fishing fleet, fish processing and packaging) and is measured as the value of output minus the value of intermediate consumption. The GVA was extracted from the STECF report on the EU fishing fleet [83] and fish processing sector [84], with the estimate for the EU fish processing sector from 2015. The GVA of Canada is from the DFO and is missing for the EU. The data given in the Canadian Economic statistics and includes besides fishing also hunting and trapping. Canada’s real GVA by the fisheries sector is therefore lower. The GVA is also given as a percentage of the total gross value added, which was for each entity extracted from the National Accounts of OECD Countries report [81]. Estimates were converted into USD.

³ Data from 2013 and from the FAO year book [76]. For the EU, the median of the Member State’s estimates was taken.

⁴ Data from 2019 and from Oceanma Canada’s third annual Fishery Audit [78]. At least all 179 major stocks are assessed yearly.

⁵ Data from 2019 from the Scientific, Technical and Economic Committee for Fisheries report on the performance of the Common Fisheries Policy [85]. For the EU, stocks with unknown status are stocks without estimates of fishing mortality, biomass and/or trends (ICES category 4–6). Data for the number of stocks for which overfishing is occurring (F > FMSY) are from 2017.

⁶ Current (August 2019) MSC status according to the Marine Stewardship Council’s website [77]. For each certified fishery fishing in the according EEZ, each stock was counted separately (e.g., the MSC labelled GVO North Sea fishery fishing European plaice (Pleuronectes platessa), Sole (Solea solea) counts as two stocks for the EU). Inland waters are excluded and only fully certified stocks included.

⁷ Data from 2017 and from the OECD Fisheries Support Estimate (FSE) database [82]. Data for non-OECD countries, Austria, Czech Republic, Finland, Hungary, Poland, Slovenia and the US are missing. The FSE reflects the Canadian vision of support, or the level of effort made by governments, as implied by their fisheries policies. It does not directly measure policy impacts on harvest, incomes, consumption, trade or environment. The FSE value is budgetary, which implies direct payments to fishers, or to support the sector in general through management, harbours, and other infrastructure. Data for non-OECD countries are missing; the estimates from Ireland are from 2016. The research and development estimate of Lithuania is from 2016, from Greece and Spain from 2015. The management estimate from Greece is also from 2015. In 2017, Denmark imposed cost recovery charges for management, research, and enforcement of 19 million USD and 0.8 million USD, respectively. Thus, the FSE estimates of Denmark for management is a gross estimate.

The role of science became clearer in the subsequent A harvest strategy compliant with the precautionary approach [29]. It called for the categorization of fish stocks into three status zones – healthy, cautious, and critical – and the setting of harvesting removal rates within each status zone [29]; Fig. 1). These status zones were intended to conform with UNFA recommendations that Parties to UNFA determine stock-specific Target Reference Points (e.g., the biomass allowing for maximum sustainable yield, BMSY) and Limit Reference Points (e.g., the biomass limit reference point, BLim) and the actions that must be taken if the reference point thresholds are crossed, e.g., a Harvest Control Rule. The DFO’s decision-making framework for incorporating the PA uses somewhat different terminology than that used by UNFA. DFO identifies an Upper Stock Reference (USR), which in practice can either be equivalent to, or less than, the Target Reference Point. The USR is the stock level threshold below which removals must be progressively reduced to avoid reaching the Limit Reference Point, BMSY. Thus, the USR is somewhat analogous to the biomass precautionary approach reference point (BPA) used by ICES. From a science perspective, determination of the USR is not purely a function of the stock’s biology (as in the ICES framework), but determined by the objectives for the fishery, which include biological, social and economic factors [29].

The Harvest Control Rule identified by UNFA has been interpreted as...
Table 2
Comparison of the role of science and stakeholders as well as the transparency of science advice in determining reference points, harvest control rules and total allowable catch.

<table>
<thead>
<tr>
<th>Role of science</th>
<th>Canada</th>
<th>European Union</th>
</tr>
</thead>
<tbody>
<tr>
<td>Limit reference point</td>
<td>Established by science, although the Minister can alter it, based on cultural and socio-economic factors. Upper reference points are precautionary reference levels.</td>
<td>Formally recommended by science (Council regulation), de facto defined by science.</td>
</tr>
<tr>
<td>Role of stakeholders</td>
<td>No formal role.</td>
<td>No explicitly defined role.</td>
</tr>
<tr>
<td>Transparency of science advice</td>
<td>Science advice is the result of a peer-reviewed process that can include stakeholders. Reports are publicly available (<a href="http://www.dfo-mpo.gc.ca">www.dfo-mpo.gc.ca</a>).</td>
<td>Publicly available in ICES stock assessment report (<a href="http://www.ices.dk">www.ices.dk</a>).</td>
</tr>
<tr>
<td>Target reference point</td>
<td>Advisory; secondary to role of fishery managers and their consultations with fishery and other interests.</td>
<td>Formally unclear (Council regulation), de facto defined by science.</td>
</tr>
<tr>
<td>Role of stakeholders</td>
<td>Explicitly defined, primary role.</td>
<td>No explicitly defined role.</td>
</tr>
<tr>
<td>Transparency of science advice</td>
<td>Clarity of science advice varies among fisheries. If present, not always distinguishable from advice from non-science sources. Stock assessment process involves stakeholders to greater or lesser degrees. Reports publicly available (<a href="http://www.dfo-mpo.gc.ca">www.dfo-mpo.gc.ca</a>).</td>
<td>Publicly available in ICES stock assessment report (<a href="http://www.ices.dk">www.ices.dk</a>).</td>
</tr>
<tr>
<td>Harvest Control Rule (HCR)</td>
<td>Management responsibility. HCRs developed with stakeholders. Science plays advisory role subordinate to others, including Ministerial discretion.</td>
<td>Unclear in Council regulation; de facto defined by science.</td>
</tr>
<tr>
<td>Role of stakeholders</td>
<td>Considerable influence. HCRs often prepared by stakeholders (e.g., 3Ps Atlantic cod).</td>
<td>No explicitly defined role.</td>
</tr>
<tr>
<td>Transparency of science advice</td>
<td>Clarity of science advice varies among fisheries. HCRs can be developed in the absence of science advice (e.g., 3Ps cod).</td>
<td>Publicly available in ICES stock assessment report (<a href="http://www.ices.dk">www.ices.dk</a>).</td>
</tr>
<tr>
<td>Removal reference</td>
<td>Although unclearly articulated in policy, the removal reference is a management responsibility. Science plays subordinate advisory role.</td>
<td>Determined by science.</td>
</tr>
<tr>
<td>Role of stakeholders</td>
<td>Decisive role.</td>
<td>No explicitly defined role.</td>
</tr>
<tr>
<td>Total Allowable Catch (TAC)</td>
<td>Advisory and not binding. It is the responsibility of science to communicate scientific uncertainty involved in the management advice, while the Minister weighs the level of uncertainty.</td>
<td>Forms basis for Council decision.</td>
</tr>
<tr>
<td>Role of stakeholders</td>
<td>Cultural and socio-economic factors considered.</td>
<td>Invited by Commission for consultation on ICES advice, socio-economic stability considered.</td>
</tr>
</tbody>
</table>

Table 2 (continued)

<table>
<thead>
<tr>
<th>Canada</th>
<th>European Union</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transparency of science advice</td>
<td>Science may provide recommendations on TAC. Decision ultimately subject to Ministerial discretion. TACs are publicly available. In matters of high public interest, a high-level summary of a peer review is shared with media.</td>
</tr>
<tr>
<td>Scientific advice (<a href="http://www.ices.dk">www.ices.dk</a>), stakeholder consultation (Advisory Council’s webpage or Eur-Lex) and decided TAC (Eur-Lex) are publicly available.</td>
<td></td>
</tr>
</tbody>
</table>

Stock Status

Fig. 1. DFO’s Reference Points and Stock Status Zones. The stock status zones are created by defining the Limit Reference Point (1) at the Critical: Cautious zone boundary, and an Upper Stock Reference Point (2; USR) at the Cautious: Healthy zone boundary and the Removal Reference (3) for each of the three zones. If a Target Reference Point (4) is set, it is at least as high as the Upper Stock Reference Point. It is determined by productivity objectives for the stock and/or socio-economic objectives for the fishery.

being analogous to DFO’s ‘Removal Reference’, which is defined for each of the three status zones. In many respects, DFO’s harvest strategy conforms with the UNFA. For example, under UNFA, the removal rate associated with MSY (the maximum sustainable yield) is a minimum standard for a PA fishing mortality limit reference. Within DFO’s PA harvest strategy, the removal rate is the maximum acceptable fishing mortality (removal) rate for the stock and is understood to be a limit rate; a harvest control rule under DFO policy specifies a target fishing rate which ensures that the limit is avoided [24]. There are, however, areas in which DFO’s policy diverges from UNFA. For example, UNFA’s guidance stipulates that to prevent a stock from falling below a Limit Reference Point, action to stop directed fishing should be initiated when abundance drops below some level above (rather than at) the Limit Reference Point (Fig. 1), a point noted by VanderZwaag, Hutchings [25].

Biomass references, removal references, and stock status are to be determined by the best available science, an objective that is PA-compliant and agrees with UNFA (“determine, on the basis of the best scientific information available, stock-specific reference points and the action to be taken if they are exceeded”). This fundamental role of science was underscored one year later in the form of a recommendation that target and limit reference points be identified in accordance with the 2006 PA harvest strategy [29], thus “ensuring that they have a sound biological basis”, and that limit reference points are based on “best available scientific evidence” [30].

3. The subordinate role of science in Canada’s Sustainable Fisheries Framework

While DFO initially seemed intent on implementing the PA with science taking a key role, the succeeding and current Fishery Decision-Making Framework Incorporating the Precautionary Approach [31], a policy developed as part of the Sustainable Fisheries Framework [32], does
not reflect the advice published by DFO a few years earlier. Rather than have science establish target reference points and harvest controls independently of fisheries management and fishing industry interests, science is limited to an advisory role subservient to other components of the decision-making process.

Building upon previous work [25], we use a conceptual framework to distinguish science-based decisions from science-determined decisions in the setting of reference points, harvest control rules, and total allowable catch (TAC; Table 2). Science-based decisions are the result of a consultation process involving input from stakeholders [25]. The term stakeholder refers to various non-science interest groups with keen interest in some aspect of fisheries (such as unions, individual fish-harvesters, seafood processors, conservation organizations). Science is involved in the decision-making process, but its role is not always clearly defined and accountable. Often, such as in the setting of a potential target (e.g. Upper Stock Reference), a public record of the policy decisions that clearly distinguishes science from non-science inputs is not available. Science advice uninfluenced by non-science factors often cannot be identified as the starting point of a decision consultation. In contrast, science-determined decisions are those resulting from determinations made solely by scientists, using evidence analyzed by scientific models that are also applied elsewhere in the world [25]. Science-determined advice is transparent (accountable) and forms the basis for the decision consultation (horizontal process in which science advice is taken up, such as the stakeholders counsel, based on science advice, in the EU) (Fig. 2a).

With respect to limit reference points, Canada’s Sustainable Fisheries Framework remains clear: the limit reference point is “based on biological criteria and established by science through a peer reviewed process”. By contrast, the USR (a ‘target’) is developed by “fishery managers informed by consultations with the fishery and other interests, with advice and input from science” (Table 2). While the function of the USR in guiding management of the risk of approaching the Limit Reference Point has to be maintained, the policy framework states explicitly that socio-economic factors may influence the location of the USR. This subordinate role of science is contrary to the earlier stipulation by DFO that all reference points be determined by the best available science [29].

It is important to note that target reference points do not need to be only biology based and determined by MSY (even though UNFA only considers MSY). MSY as a target does not guarantee sustainability and there is no evidence that the maximum economic yield is less sustainable than MSY, considering for example that the stock size associated with the maximum economic yield is, in most cases, larger than at MSY [33, 34]. While the Target Reference Point should consider ecological criteria, there are no objections to the incorporation of socio-economic factors per se, but an obfuscation of the role of science is troubling; the Sustainable Fisheries Framework and the decision-making policy [31] in particular, as written, allows for considerable breadth of interpretation regarding the scientific basis of USRs and the process by which they are developed.

Regarding harvest decision or harvest control rules, the decision-making policy states, “the development of decision rules is a management responsibility and science’s role is to provide advice in support of the development”. In this case, it seems clear that the decision-making role in establishing harvest control rules (the removal reference) is management’s with science acting in a secondary, advisory capacity in “support of their development” (Table 2).

The unintended negative consequences of such a framework are evident in the HCR established for the south-coast Newfoundland fishery of cod in Division 3Ps, a fishery that had its 2016 certification by the Marine Stewardship Council suspended in 2017 because of deteriorating stock status. The subsidiary role of science is evident from the fact that fishery managers accepted a HCR and determined it to be PA-compliant, despite scientists making it clear that the HCR could not be quantitatively evaluated through simulation [35]. Simple inspection of one of its
most important elements renders clear the ambiguities of the 3Ps cod
HCR: “If the 3-year average SSB [spawning stock biomass] is below \(B_{\text{lim}}\),
consideration may be given to whether directed fishing will be permitted
at some level. Decision-making should be guided by the recent and ex-
pected SSB trajectories, and the extent of the decline below \(B_{\text{lim}}\). Directed fishing
should not be approved if the decline below \(B_{\text{lim}}\) is
substantial, and occurs within a reasonable timeline” [36], [italics added].
The HCR is not in line with the Sustainable Policy Framework’s zero
tolerance towards preventable stock decline and the prescription that a
rebuilding plan has to be in place as soon as the stock falls into the
critical zone. This HCR leaves enormous room for interpretation, making
it difficult if not impossible to enforce, while opening opportunities for
industry and fishery managers to set higher fishing rates than optimal for
rebuilding.

The final management decision is taken by the federal Minister of
Fisheries, Oceans and the Canadian Coast Guard, who, despite amend-
ments to the Fisheries Act in 2019, enjoys broad discretionary authority.
For example, the Minister may (rather than ‘should’ or ‘will’) consider
the application of a precautionary approach and scientific information
Section 2.5 (a, c) [37] in their decisions. The 2019 amendments
identified a requirement to rebuild stocks if they fall below \(B_{\text{lim}}\). But if
the Minister is of the opinion that the rebuilding measures could have
adverse socio-economic or cultural impacts, the Minister can set her/his
own limit reference point (section 6.1(2)) and may amend the rebuilding
plan (Section 6.2(2)).

One consequence of allocating science an unclearly defined and
subsidiary role, especially when coupled with the primary role afforded
to vested interests, is a potential weakening of the ability to implement
the policy consistently across all fisheries. A lack of consistency is
afforded by the Ministerial discretion permitted by the Fisheries Act
which provides industry with an opportunity to obtain ministerial de-
cisions regarding harvesting that align with industry’s interests at the
cost of weakening the decision’s underlying scientific credibility [38].
Evidence of inconsistent application of the PA across fisheries is illus-
trated by the fact that, since 2009, directed fisheries have been
permissible for some Atlantic cod stocks that are below \(B_{\text{lim}}\) (e.g.
northern cod) but not others (e.g. Southern Gulf cod) [39].

Stock assessments and science advice is published by the Canadian
Science Advisory Secretariat. The reports document peer-reviewed sci-
centific advice achieved through the consensus of participants at Cana-
dian Science Advisory Secretariat peer-review meetings [40,41]. The
peer review is intended to adhere to standards that ensure that all
findings, analyses, and recommendations of science advisors go through
a “rigorous internal and external review and assessment” (Principle III:
Sound Science and Science Advice [41]). A regular, transparent
peer-review process, involving at least one reviewer external to DFO, is
important to meet the requirements of the PA and to always provide the
best available science according to scientific standards for
decision-making. The frequency of peer review is not always consistent
and there is no clear rule about how rapidly newly available data need to
be considered. Besides DFO’s peer-reviewing process itself, DFO’s
management practices have been criticized for announcing management
plans or Rapid Science Responses without a peer-review process [8].

Under the Principle of Inclusiveness (Principle II [41]), the govern-
ment promotes the consideration of experts from relevant non-scientific
disciplines (e.g., non-governmental organizations, industry representa-
tives, harvesters, Aboriginal representatives, DFO Resource Managers,
international experts) in the advice-making process (Fig. 2B). While this
accords with DFO’s shared stewardship strategy, and the inclusion of the
public, Aboriginal groups and stakeholders in the decision-making
process, it creates challenges for those wishing to ensure that the pub-
lished science advice is free of non-science considerations. While there is
a framework for how natural scientific (biological) factors and objec-
tives are to be considered, there is no agreed framework for practical
integration of social, economic, and institutional objectives in
decision-making [42]. The Canadian Science Advisory Secretariat pol-
cy, however, states that the consensus of the science advice is to be
science based, on the evidence given by the data and scientific analysis
[43].

Aiding decision-making in the presence of high uncertainty is a
fundamental goal of the PA. Quantification of the uncertainty involved
is, therefore, important. Canada’s Sustainable Fisheries Framework
recognizes the need to take into account uncertainty and risk when
developing reference points and decision-rules, and provides a catego-
ration of accepted risk level depending on the stock status zone. The
exact accepted risk level is a management decision. Quantification of the
uncertainty level involved in the scientific evidence and the manage-
ment decisions is desirable. However, in Canada’s Sustainable Fisheries
Framework it remains unclear how and by whom uncertainty should be
quantified and how uncertainty influences the decision-rules. There are
only vague guidelines for data-limited stocks, such as: “[...] precau-
tionary management actions should be based on the estimates of pro-
ductive potential and harvest that are the most appropriate for the stock
of concern and data available, with the objective of avoiding serious
harm to reproductive capacity of the stock”. In the absence of data on
biomass (necessary for estimation of the limit reference point) and
fishing mortality related to maximum sustainable yield (necessary for
estimation of the removal reference), the Sustainable Fisheries Frame-
work suggests options for estimation of provisional reference points.
However, there is no clear decision rule of when and whether to use
which provisional approach. Besides, these provisional options are only
suitable if there is a sufficient time-series of biomass and/or fishing
mortality, which is not the case for bycatch species or species not
considered by DFO to be a ‘major fish stock’. However, there are recent
developments towards a more detailed tiered-approach framework
which could aid in determining the most appropriate stock assessment
method and type of management advice depending upon data avail-
ability and quality [44].

The government gives decision makers the responsibility to properly
evaluate and weigh the scientific uncertainty in decisions [41], which in
turn requires that scientists appropriately communicate the uncertainty
of their assessments (Table 2). Leaving the quantification and interpr-
tation of uncertainty to decision makers has the potential to allow in-
dustrial lobbyists to influence the level of uncertainty or risk that the
decision makers are willing to take.

In conclusion, the reference levels and harvest rules are ultimately
based (PA key principle 1 + 3), resulting from a consultation
process where socio-economic factors and industry views are consid-
ered. While the limit reference point is formally determined by science
(an example of a science-determined decision), the Minister retains the
right to set it differently depending on cultural and socio-economic
factors. Reference points, scientific methods and data are regularly
peer-reviewed (PA key principle 4). A key strength of the review process
is the involvement of DFO scientists with expertise in stock-assessment
analyses. A potential drawback is the inclusion of relatively few non-
DFO scientists in some peer reviews, a situation that has been prob-
lematic in the past [45]. The science advice, thus, represents a consensus of
the scientists and non-scientists who are invited to attend the peer
review meeting, which can make it difficult to disentangle scientific
evidence from stakeholder input (PA key principle 5). How to deal with
data limitation and uncertainty is ultimately the responsibility of the
decision makers because the framework provides only vague guidelines
for data-deficient stocks and no rules for quantification of uncertainty
(PA key principle 2).

4. Subordination of science advice in rebuilding northern cod

In 2019, DFO managers recommended a quota increase for northern
cod [46], despite the stock’s biomass being well in the critical zone at
0.48 \(B_{\text{lim}}\) and the science advice that removals from all sources should be
at the lowest possible level [47]. The Minister’s decision to permit an
increase in directed catch reflects a subordinate role of science in decision-making and the prerogative of ministerial discretion to over-ride science advice. Paradoxically, the Minister rendered the decision in the same month that parliament passed legislative revisions to Canada’s Fisheries Act intended to clarify and strengthen the act’s provisions to rebuild depleted fish stocks. It is difficult to argue that quota-related decisions on northern cod have ever been consistent with Canada’s Sustainable Fisheries Framework. The biomass of northern cod has been less than $B_{lim}$ ($B_{lim}$ was formally established in 2010) since the early 1990s. Yet since then, DFO managers have regularly permitted commercial harvests (exclusive of recreational and non-Canadian catches). Between 1998 and 2002, the TAC ranged between 4000 and 9000 tonnes, resulting in estimates of the fishing mortality of 7–9 year old cod of 0.30–0.35 per year [48]; it is highly probable that this fishery stifled nascent signs of recovery [17]. From 2006 onwards, beginning with annual allocations to license holders, catches continued to increase, reaching 10,000 tonnes in 2016. In 2017, despite northern cod being at less than half of $B_{lim}$ [49], DFO management accepted a harvesting plan submitted by the fishing industry that might have resulted in catches of 19,000 tonnes. In June 2019, DFO managers permitted the 30% increase in the catch quota mentioned above [50].

Ministerial decisions to increase catches of northern cod since 2009 contravene DFO’s Sustainable Fisheries Framework condition that if population biomass falls below $B_{lim}$, “removals from all sources must be kept to the lowest possible level” until population biomass exceeds $B_{lim}$ [29]. What constitutes the “lowest possible level”? It is self-evident from a science perspective that achievement of the lowest possible level would involve restrictions on all sources of human-induced mortality. For most fisheries, these sources originate from directed and non-directed fisheries. From a science perspective, to comply with DFO’s decision-making framework [31], if a stock falls below $B_{lim}$ all directed fisheries should be closed and all non-directed fisheries which catch affected fish incidentally (e.g. as bycatch) should be kept at the lowest levels possible. However, a lack of policy clarity, particularly with respect to the role of science in this regard, allows for multiple interpretations as to what constitutes the lowest possible level of human-induced mortality.

5. The role of science in the European Union’s Common Fisheries Policy

The Common Fisheries Policy (CFP) has been claimed one of the most science dependent policies in the EU [51]. Since its 2002 reform, decision-making within the CFP has been based on “sound scientific advice and on the precautionary approach” [52].

Within the EU, fisheries policy decision-making and governance is performed at the EU level as a Community System for Fisheries and Aquaculture [53]. Fisheries management decisions are taken by the Council of Ministers (Council of the EU; legislative branch) in a co-decision process with the European Parliament (legislative branch). The Council considers proposals drawn up by the European Commission (executive branch; Directorate-General for Maritime Affairs and Fisheries, DG MARE), which either consults its own scientific advisers (Scientific, Technical and Economic Committee of Fisherss, STECF) or requests advice directly from the International Council for the Exploration of the Sea (ICES). STECF is responsible for providing “sound and timely evidence-based scientific advice for the implementation and monitoring of the EU Common Fisheries Policy” ([54] (6)) and provides its advice while taking account of the scientific work conducted by ICES. The European Commission’s Joint Research Centre also supports STECF with (mainly demand) scientific research, but its role is relatively small in comparison to ICES (only 8 employed scientists in Fisheries and Aquaculture, as of March 2018). While the advice of ICES is purely of a scientific nature, STECF also considers the economic and social impacts of implementing management decisions [52]. In contrast to Canada’s Sustainable Fisheries Framework, the CFP has the provision of sustainable economic, environmental and social conditions explicitly as one of its objectives [52].

ICES has been a contracting partner of the EU (through a Memorandum of Understanding) since 1987. As an independent science organization consisting of 20 Member States, ICES’ mission is to “improve its capacity to give unbiased, sound, reliable, and credible scientific advice on human activities affecting and affected by, marine ecosystems” (Copenhagen Declaration 2002 [55]). The most recent Memorandum of Understanding between DG MARE and ICES stresses the unbiased and transparent nature of ICES’ science advisory deliverables and the methods they are produced upon [56]. In addition to the provision of science advice on fishing opportunities, ICES reports on the effectiveness of management plans in relation to their respective objectives (e.g. MSY and PA-compliance) [57].

ICES reserves the science advisory role for itself, leaving the responsibility of weighing the social and economic implications of the advice to the European Commission and the governments (ICES webpage). Socio-economic information is considered via Advisory Councils (Fig. 2a) and their role has been strengthened since the CFP recent reform ([58], Article 3(10)). The reports of the Advisory Council’s recommendations on fishing opportunities are public, allowing for a clear and transparent distinction between science and stakeholder advice. The science advice is frequently picked up again during this sequential decision-making process and forms the basis for DG MARE’s proposal to the EU Council of Ministers (Fig. 2a).

6. How the Common Fisheries Policy fulfils requirements of the precautionary approach

Before the 2002 reform, sustainability measures were mainly advised by STECF (the European Commission’s in-house fisheries science advisors) and included only limits on exploitation rates and catches ([53], Article 4). In 2002, the stock categorization into ’safe biological limits’ was introduced and concomitant limit and conservation reference points (targets) were established together with management action plans. In contrast to DFO’s Decision-Making Framework [31], stocks within safe biological limits are not only characterized by a population size above $B_{lim}$ but also by a fishing mortality that is less than the limit fishing mortality reference ($F_{lim}$) ([58], Article 4 (18)). Following the Council regulations, stocks inside and at safe biological limits are to be managed under management plans, while stocks outside these limits are to be managed under recovery plans [52]. In reality, not every stock has an established plan, often because not all relevant management parties could agree on one.

Management and recovery plans are based on the PA and the role of science is explicitly defined for the limit reference points, which are “recommended by relevant scientific bodies” ([italics added] [52] Article 5.3 and 6.3; Table 2). The role of science in defining the removal rate (and the harvest control rule) was unclear in the 2002 reform. However, following the World Summit on Sustainable Development, the objective of achieving exploitation rates allowing for MSY by 2020 (although as a target, not a limit) became a priority of the newest CFP. Exploitation levels estimated to produce MSY are now determined by scientific information ([58]; Table 2). The Council’s decisions on fisheries management measures are based on the scientific, technical, and economic advice of STECF. However, de facto it is ICES which defines the lower and upper population reference levels and the advice rule for the fishing mortality in relation to it (i.e., the harvest control rule). Besides ensuring that reference points and harvest rules are determined solely by science, ICES complies with the PA by introducing precautionary reference levels for biomass and fishing pressure, based on a precautionary safety margin that incorporates uncertainty to limit the risk of impaired recruitment production [57]. Thus, while the Council regulation stipulates that recovery plans and rebuilding measures only apply once the stock is below the limit.
reference point (outside the safe biological limit) [52], ICES ensures that actions are taken already at the precautionary reference point above $B_{\text{lim}}$ at the precautionary approach reference point, $B_{\text{pa}}$.

The science advice is more conservative with respect to possible impacts on the marine ecosystem when stock information is limited or less certain [57]. Therefore, only comparatively data-rich stocks, for which a full stock assessment is possible, are given reference points. In contrast to DFO, ICES and the European Commission (DG MARE) have explicit rules for providing quantitative advice for data-limited stocks [57,58,60]. Depending on the knowledge available, ICES’ advice is either based on the MSY approach or a MSY proxy approach consistent with the PA. In a similar way, the European Council considers proxy parameters when scientific information is not available [58]: “Where targets […] cannot be determined, owing to insufficient data, the multiannual plans shall provide for measures based on the precautionary approach, ensuring at least a comparable degree of conservation of the relevant stocks” [italics added] (Article 9 (2) [58]). DFO policy lacks clear action rules that account for data limitation and uncertainty, which often leaves it to the managers to ultimately judge the uncertainty involved in a management decision.

ICES ensures the availability of best science and data with regular benchmark workshops, which are open to experts and stakeholders and are reviewed by external experts throughout the process. The science advising process ends when DG MARE makes management proposals to the EU Council. These proposals may include adjustments, intended to help secure the Council’s approval. However, these adjustments cannot be scientifically examined [61]. A recent DG MARES annual activity report concluded that the Council’s decisions on the total allowable catch (TAC), in general, remained compatible with achieving MSY and only in limited cases deviated from ICES’ science advice because of “considerations linked to the socioeconomic impact of the proposed fishing limits” [62]. With the intention of seeking relative socio-economic stability among EU countries, the CFP also considers the Member States’ historical fishing rights (relative stability concept) when distributing the TAC among Member States.

Thus, the final TAC decisions rendered by the EU Council can deviate from the science advice. However, in contrast to the decision-making process in Canada, deviations between science advice, stakeholder input, and the final management decision can be fully traced back through the separate decision-making steps. This has allowed scientists to identify discrepancies and to determine the step(s) in the process where they were made [63-67].

With reference levels and the harvest rules de facto defined by science and regular re-assessments of the standards of evidence, the role of science within the CFP is considered compliant with the PA. The role of science within the CFP is not flawless (e.g. Ref. [68]) and for several stocks the CFP has not lead to sustainable management practices. However, it does fulfill the requirements of the PA: reference levels are science determined (PA key principle 1), the uncertainty involved is quantified by science (PA key principle 2), and the applied assessment methodology and advice depends on the uncertainty level (PA key principle 3). There is a regular benchmarking with external experts (PA key principle 4) and a structured, transparent decision-making process that is publicly comprehensible (PA key principle 5). Because each step in the decision-making process is published separately, including the science advice and stakeholder consultations, final management decisions can be compared with the science advice, which strengthens the scientific credibility and increases the accountability within EU’s fisheries management practices.

7. Structural constraints on the development of a PA-compliant role of science in Canada’s sustainable fishery framework

Canada’s Sustainable Fisheries Framework has strengths that contribute positively to the attainment of desirable fishery-rebuilding and stock-recovery outcomes [69]. However, it also has structural weaknesses that contribute to lack of clarity and, as a consequence, an unclear and inexact role of science that can compromise PA compliance of the Sustainable Fisheries Framework.

Unlike the foremost decision-making institution in the EU, with its separation of powers between executive (European Commission, DG MARE) and legislative (Council of Ministers, European Parliament) branches, Canada has a parliamentary system in which the executive (government) and legislative (House of Commons and Senate) branches are interwoven; the executive branch is part of the legislative branch. As a consequence, rather than having detailed, written laws directing the actions of the executive branch, the acts of Canada’s parliament (such as the Fisheries Act) tend to be unhelpfully broad and general, authorizing the government to make the detailed decisions [23]. Those decisions are officially made by the federal Minister of Fisheries, Oceans and the Canadian Coast Guard but, in reality, many are delegated to DFO officials. This has allowed Canada to develop flexible, potentially adaptive fisheries management strategies [8], whereas the EU operates within the strict legislative constraints of the CFP. While authority over fisheries is delegated to the different EU states, in Canada control is retained by the federal Minister. The Fisheries Act gives the Minister, and hence her/his officials, almost unlimited discretion and authority.

The increased flexibility combined with ministerial discretion has allowed Canada’s fisheries management to react to continually changing social, economic, and political pressures, but this can hamper effective implementation of the PA [8]. It can weaken the role of science and scientific credibility by obfuscating the different decision-making steps, rendering it difficult to determine who holds the respective accountability. In addition, the government has its own in-house scientific body to deliver the science advice, a system that can challenge the independence and objectivity of the scientific institution when the political will to do so is sufficiently strong, as it was in Canada in the 1980s and early 1990s [45] and from 2011 to 2015 [13]. Unlike the EU, Canada does not have a legislated requirement to take a structured decision-making approach with respect to fisheries sustainability (Fig. 2).

The role of science in Canada’s fisheries management practice has been shaped by history, in particular by the groundfish collapses in the late 1980s/early 1990s and the closure of the northern cod fishery in 1992 [8,10]. Before the collapse, management decisions were unpredictable based on science advice that tended to be inadequately documented and lacking peer review from outside government. Motivated by a desire for a less solitary role of science and an increased inclusion of industry in the advisory process, the contemporary science advisory committee (Canadian Atlantic Fisheries Scientific Advisory Committee) and the industry advisory board on management (Atlantic Groundfish Advisory Committee) were dissolved in the early 1990s and the Fisheries Resource Conservation Council (FRCC; 1993–2011) was created as the formally designated advisory body to the Minister.

The FRCC, comprised of individuals with experience in industry and science (natural and social), assessed the (regional) science advice and consulted with harvesters and processors on management options, thus providing stakeholders a more direct voice in governance. While this allowed a more structured provision of industry input, the FRCC’s advisory process to the Minister was not publicly accessible and the link between FRCC advice and DFO scientific assessments was not always evident [8]. To better coordinate the science review and advisory processes and ensure the scientific credibility in the advisory process, the Canadian Stock Assessment Secretariat (now Canadian Science Advisory Secretariat or CSAS) was created. To avoid re-establishment of the somewhat secluded science advisory process that existed prior to the collapse, CSAS has a mandate to make the science advisory process fully inclusive (also in the science peer review, as mentioned above) of academic experts as well as of persons from the fishing industry and other stakeholders. Participatory decision-making with stakeholder inclusion is further promoted by DFO’s ‘shared stewardship’ management strategy.

While the inclusion of stakeholder input in the entire science
advisory process can promote dialogue between scientists, industry and managers, the science and stakeholder input are not always well distinguished (Fig. 2b), potentially reducing the transparency and accountability of the science advisory process.

8. Conclusion and a way ahead

We conclude that Canada’s decision-making framework for the management of sustainable fisheries offers insufficient compliance with all of the requirements of the PA, thereby weakening the accountability, transparency, and contributions of science compared to jurisdictions such as the EU. Target reference points and harvest control rules are only science based, to greater or lesser degrees. The role of science in some key PA-related decisions is often unclear, imprecisely articulated, or subordinate to input by stakeholders and managers (PA key principle 1 + 3, Table 2). Scientific evidence creates an essential means for the public to hold decision-makers to account and should always be available to the public [70]. The institutional and policy framework, however, often obfuscates or renders unclear the role of science, eroding accountability and credibility of Canada’s fisheries management decisions. As a consequence, the scientific basis for management decisions cannot always be evaluated and sustainable fisheries management practices, such as the implementation of the PA, evolve slowly.

To ensure decision-making is based on the best-available evidence, the PA demands reliable information consistent with scientific standards and a regular, objective peer review of the evidence (PA key principle 4). Participation of stakeholders in the entire science advisory process, including the peer-review of the scientific evidence, without clear separation of the science, has potential to constrain the building of a transparent, credible role of science consistent with the PA (PA key principle 5). While stakeholder involvement in the advisory process is anticipated, the science advice should still be clearly distinguishable and provide a foundational base for stakeholder discussion and management consideration (as in the EU, Fig. 2). Such a structured decision-making would increase transparency and credibility of the advice.

Given the high number of stocks in Canada with unknown status (Table 1), it is surprising that there are only vague rules for evaluating stocks with high uncertainty and/or data limitation (PA key principle 2). According to the PA, the absence of full scientific certainty shall not be used as a reason for postponing management decisions. In addition, the government gives the responsibility of judging any uncertainty involved in management decisions to the decision-makers. A coherent and transparent system of categorizing stocks according to their uncertainty and/or data availability would be less prone to misinterpretation and misrepresentation, and could aid in building precautionary management strategies.

The government is financially supportive of, and legislatively required to manage, Canada’s fisheries (Table 1) and there is the necessary scientific expertise, scientific methodology, and scientific engagement. Amendments to Canada’s Fisheries Act in 2019 might serve to strengthen Canada’s PA-compliance of the role of science and evidence-based decision making in fisheries management practices. Symbolically, the revised legislation identifies full implementation of the PA as an overarching objective. Importantly, the amended legislation also includes legal obligations to manage stocks at levels necessary to promote sustainability, avoid limit reference points (e.g. $B_{MSY}$), and/or institute plans to rebuild fish stocks [37]. A future role of science will presumably lie in advising decision-makers on rebuilding plans likely to meet the intent and objectives of the newly amended legislation and management’s sustainable fishery objectives.

There will always be potential for the PA to be misused by stakeholders intent on pursuing their own objectives to the exclusion of others. To reduce the probability of misuse and misinterpretation of the PA, we have argued that there is merit in ensuring that science advice is always publicly distinguishable from other sources of advice in the setting of reference points, harvest decision rules, and other fisheries management decisions [50].

Author statement

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Appendix A. Supplementary data

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References

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