

Fish as climate change mitigators – A modelling approach to quantify the contribution of western Baltic fish stocks to carbon ecosystem fluxes under different management scenarios

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Summary

Fish has ever since been an irreplaceable resource for the human society but our knowledge on their ecological role remains incomplete. Yet, we continue to deplete global fish stocks without being fully aware of the consequences. One aspect that has so far found too little recognition in fisheries management is the involvement of fish in ocean carbon fluxes, which is particularly urgent against the background of climate change. Since fish are central components in the biological carbon pump, fisheries should not only alter stock biomass but consequently also the magnitude of fish-related carbon fluxes, hence impacting the ocean's CO₂ uptake capability.

To address this data gap, an existing ecosystem model of the western Baltic Sea (WBS) was used to quantify changes in carbon flows attributed to fisheries in the ICES subdivisions (SD) 22 and 24. The base model is a mass-balanced snapshot of the WBS in 1994 and includes 17 trophic groups and detritus as well as four fisheries-related compartments exerting pressure in the study area. Focus was laid on changes in standing stock biomass, the flow of carbon to detritus and respiration for Atlantic cod (*Gadus morhua*), Atlantic herring (*Clupea harengus*) and a pooled flatfish group. After validating the model's accuracy to compute physiologically reasonable egestion and respiration fluxes by comparing the output against a manually-calculated reconstruction dataset using historical ICES stock data and literature values on fish bioenergetics, a set of short-, mid- and long-term forecast scenarios spanning the entire 21st century was simulated. These projections investigated the impact of five different fisheries management strategies on fish-related carbon fluxes, in particular a continuation of the present average fishing pressure (Business as Usual - BAU) and a more considerate, ecosystem-based fisheries management strategy (EBFM) relying on principles of fisheries science and ecology. Also, the effect of ocean warming and changes in phytoplankton biomass were included in the analysis.

The simulations revealed that the study species react differently to new management strategies. Upon the implementation of EBFM, the currently depleted stocks of both cod and herring increased in biomass by $\geq 100\%$ towards the mid-21st-century, while flatfish decreased (-25%). BAU instead mostly had detrimental effects, especially on herring, causing a further decrease in stock biomass for all three species combined (-10%). While changes in the carbon flux to detritus followed the ones of the underlying stock biomass, they were even more pronounced for cod and herring. Overall, it was estimated that by the mid-21st century, BAU as compared to EBFM would withhold 41-43,000 tonnes of carbon being contributed to the detritus compartment annually in SD 22 and 24 and thereby being available to carbon sequestration processes. Including the additional environmental stressors mostly had detrimental effects on cod and herring but first and foremost increased data scatter and thereby distorted the forecast certainty. They further constrained the leverage of fisheries management by reducing the benefits conferred by EBFM towards BAU, incentivising to approach fisheries management on multiple levels instead of only relying on fishing pressure as an ultimate management tool.

Zusammenfassung

Fische sind seit jeher eine unersetzliche Ressource für den Menschen, doch unser Wissen über ihre ökologische Bedeutung ist unvollständig. Trotzdem dezimieren wir weltweit weiter die Bestände ohne uns der Konsequenzen vollends bewusst zu sein. Vom Fischerei-Management bisher wenig beachtet ist ihre Rolle im marinen Kohlenstoffkreislauf, welcher gerade im Hinblick auf den Klimawandel von hoher Bedeutung ist. Fischerei sollte nicht nur die Bestände, sondern in der Folge auch den Beitrag von Fischen zur biologischen Kohlenstoffpumpe wesentlich beeinflussen, mit wichtigen Implikationen für die CO₂-Aufnahmekapazität des Ozeans.

Um diese Wissenslücke zu füllen, wurde ein bestehendes Ökosystem-Modell der westlichen Ostsee verwendet, um durch Fischerei veränderte Kohlenstoffflüsse in den ICES Arealen 22 und 24 zu quantifizieren. Dem Modell liegt eine Momentaufnahme des Ökosystems von 1994 zugrunde und es setzt sich aus 17 trophischen Gruppen, Detritus sowie vier Fischerei-Komponenten zusammen. Im Fokus stehen die Bestandsbiomasse, der Beitrag von Kohlenstoff zum Detritus und veratmeter Kohlenstoff vom Atlantischen Dorsch (*Gadus morhua*), Atlantischen Hering (*Clupea harengus*) und Plattfischen. Die Exaktheit des Modells hinsichtlich der Berechnung physiologischer Ausscheidungs- und Atmungsprozesse wurde durch einen Abgleich mit anhand von ICES Bestandsdaten und Bioenergetik-Literaturwerten manuell rekonstruierten Ergebnissen validiert. Anschließend wurden über das 21. Jahrhundert verteilte kurz-, mittel- und langfristige Prognosen modelliert, welche den Einfluss von verschiedenen Management-Strategien, besonders einer Fortsetzung der aktuellen durchschnittlichen Fischereiintensität (Business as Usual - BAU) und einer ökologisch grundierten Strategie (Ecosystem-Based Fisheries Management - EBFM), simulieren. Außerdem wurden die zusätzlichen Auswirkungen von Ozeanerwärmung und Veränderungen in der Phytoplanktonbiomasse untersucht.

Die Ergebnisse zeigen, dass die untersuchten Arten unterschiedlich auf neue Management-Strategien reagieren. Unter EBFM nehmen die aktuell stark verminderten Dorsch- und Hering-Bestände bis Mitte des 21. Jahrhunderts um $\geq 100\%$ an Biomasse zu, während Plattfische abnehmen (-25%). BAU ist meist nachteilig, besonders gegenüber Hering, und die Gesamtbiomasse an Fisch nimmt weiter ab (-10%). Während Trends in den Kohlenstoffflüssen zum Detritus denen der zugrundeliegenden Biomasse folgen, ist der Zuwachs für Dorsch und Hering sogar noch ausgeprägter. Zusammengenommen wurde für die Mitte des 21. Jahrhunderts berechnet, dass BAU gegenüber EBFM dem Detritus jährlich 41-43.000 Tonnen Kohlenstoff in der untersuchten Region vorenthält, welche anderenfalls langfristigen Speicherungsprozessen zur Verfügung stehen würden. Die zusätzlichen Umweltstressoren zeigen größtenteils negative Auswirkungen auf Dorsch und Hering, erhöhen jedoch vor allem die Datenstreuung und schwächen so die Vorhersagefähigkeit. Desweiteren vermindern sie die Handlungsfähigkeit von Fischerei-Management durch eine Reduzierung der durch EBFM gegenüber BAU hervorgerufenen Vorteile und verstärken so die Notwendigkeit, Management zukünftig auf mehreren Ebenen anzugehen anstatt sich auf Fangquoten als wesentliches Handlungsinstrument zu verlassen.

1 Introduction

1.1 Fish - Much More Than a Dish

No other organism in the marine realm is as closely tied to humans as fish. Relicts from many of the first known permanent settlements and isotopes from early skeletal remains, like that of the so-called Tianyuan man, tell a story of more than 40,000 years of shared history (Hu et al., 2009), long before the Agricultural Revolution (ca. 12,000 BP). Since then, fish has remained a valuable component of our diet and, even in the modern era of expansive terrestrial livestock farming, it still makes up more than 16% of the global population's animal protein intake (Tacon & Metian, 2013). This existential importance of fish has, apart from the dietary link, also led to a cultural adoption, and Pisces, Nemo, the Hindu god Vishnu or "bacalhau", the national symbol of Portugal, are only a few examples of how fish has found its way into almost every facet of our everyday life. Its role as an essential supplier of protein and omega-3 fatty acids however remains the most crucial.

Nevertheless, the fact that fish has always constituted a fundamental part of our menu and traditions is needed to comprehend how global fish populations have ended up in today's poor and despoiled state. While traditional techniques, mostly serving the purpose of subsistence, can still be found in some parts of the world (Tyedmers, 2004), they are rather a remnant from the past. Technological advances such as the advent of the first steam-powered boats and near exponential world population growth have in recent centuries instead equipped us with increasingly effective tools to exploit the world's oceans and catapulted global landings to new and still increasing highs (FAO, 2022). While at the beginning of this marine gold rush, fish was commonly believed to be an infinite resource, the collapse of Atlantic cod fisheries on the Grand Banks or the boom-bust dynamics of anchovy in the Pacific tell a completely different story. However, monetary incentives continue to outweigh early warning signs and ecological advice, leaving global fisheries in an unprecedented crisis.

1.2 The Overfishing Crisis

Aquatic resource management in the past decades and centuries predominantly lacked integrated, large-scale management strategies, which has in many cases led to an extreme depletion of the fish stocks. Today, more than 35% of all stocks are considered overfished, while more than 57% are fished to a maximally sustainable level (FAO, 2022). In fact, as of 2019, only 7% could still be seen as underfished. Plentiful scientific evidence published over the recent decades hints at the large majority of global fish stocks being in increasingly depleted shape (Palomares et al., 2020). Nonetheless, marine landings remain at an ecologically detrimental level. From 1950 to 2018, catches increased from 20 to 84 million tons per year and are expected to reach 96 million tons by 2030 to satisfy the growing demand for aquatic foods, which has multiplied fivefold since 1960 (FAO, 2022). At first glance, increasing catches despite pro-

gressively declining stocks seems counter-intuitive and in fact, it is indeed only feasible owing to perpetual advances in fishing technology (Jackson et al., 2001). Nevertheless, this period of growth is finite as the decline of stocks will inevitably lead to limit its productivity. Also, having to increase the input effort to maintain or even increase the catch numbers in times of decline substantially decreases profitability. Therefore, global fisheries today receive subsidies in the billions, further fuelling the over-capitalization of the sector (Khan et al., 2006; Sala et al., 2018). These subsidies are a primary reason for global fisheries still being a distortedly profitable industry, generating USD 141 billion in 2020 alone (FAO, 2022).

It is therefore safe to conclude that modern-day fisheries have become far from sustainable, the consequences of which become more and more apparent. A study by Pauly et al. (1998) has shown a decline in the mean trophic level of marine landings, indicating a shift from long-lived, piscivorous to short-lived, planktivorous fish, hinting at presently unsustainable exploitation patterns. Furthermore, over-exploitation by fisheries does not only impact the fish stocks as such but also causes cascading effects reaching far into marine ecosystems. It has for instance been demonstrated that overfishing can heavily impact food web dynamics by singling out essential functional groups and hence altering existing top-down or bottom-up processes leading to a shift in species composition (Jackson et al., 2001; Casini et al., 2009), which makes much-needed improvements in fisheries management even more urgent.

The degree of precariousness for global fish stocks has in fact been up for debate, as the denial of a "fisheries crisis" by, among others, the fisheries industry itself, as well as political stakeholders, is still an ongoing challenge (Pauly, 2008). Additional stressors such as ocean warming and acidification complicate the picture by further impacting the resilience of stocks and have been shown to have detrimental effects on e.g. the reproductive success of fish (Polte et al., 2021; Möllmann et al., 2021), obscuring the contribution of fisheries to the documented decline or even collapse of many fish stocks. However, this neglects the fact that this susceptibility of fish to additional environmental stressors often derives from stocks being depleted in the first place and while climate change and shifting environmental conditions can potentially amplify the rate of decline, fisheries management has still been pointed to as a primary cause as e.g. shown for cod (*Gadus morhua*) and herring (*Clupea harengus*) in the western Baltic Sea (WBS) (Froese et al., 2022). This is both a blessing and a curse since it illustrates that we in fact are in a position enabling us to make a change by implementing better management strategies while at the same time holding us responsible for the emergence of the problem in the first place. Additionally, transforming fisheries to increase sustainability most often entails a reduction of fishing effort and quotas, in the short term leading to an elimination of jobs (Worm et al., 2009), which further complicates the feasibility of essential measures. Prospective decision-making has to be both ecologically farsighted as well as socioeconomically indulgent to overcome the undeniable crisis that global fisheries are currently in. Failing to do so would result in stagnating or decreasing marine landings and increasing fishing effort, generating long-term economic losses, as well as

depleted ecosystems and expanding stock collapses (Pauly et al., 2003; Worm et al., 2009), a scenario which to avoid should be in everyone's interest.

1.3 Gear Wheel in Ocean Carbon Fluxes

Traditionally, fish has simply been treated as a (partly) renewable resource with little thought spared about their ecological importance. The idea of conservation, rooted in the recognition that continuously depleting an ecosystem has far-reaching effects on biodiversity, is still comparatively new and has now slowly found its more or less extensive implementation into global management frameworks. Another aspect of living fish, namely the involvement in ocean carbon fluxes, and the impact of fisheries on the latter are instead still generally excluded. This omission ignores the numerous pathways through which fish are contributing to global carbon fluxes, as illustrated in Figure 1 adapted from Saba et al. (2021), who estimated that fish are responsible for ~16% of all carbon exported out of the euphotic zone.

Figure 1 summarises the processes through which fish affect the biological carbon pump, namely respiration, egestion (defecation), excretion and the sinking of fish carcasses. In the case of certain species, diel vertical migration further constitutes a mechanism allocating substantial amounts of carbon into deeper waters (Saba et al., 2021). Although important, this process is not within the scope of the thesis.

Apart from the biological carbon pump, which is of direct interest to climate-related studies, fish also contribute to the cycling of nitrogen and phosphorus, indirectly supporting the pump mechanism by fuelling bacteria and phytoplankton productivity (Saba et al., 2021), as well as

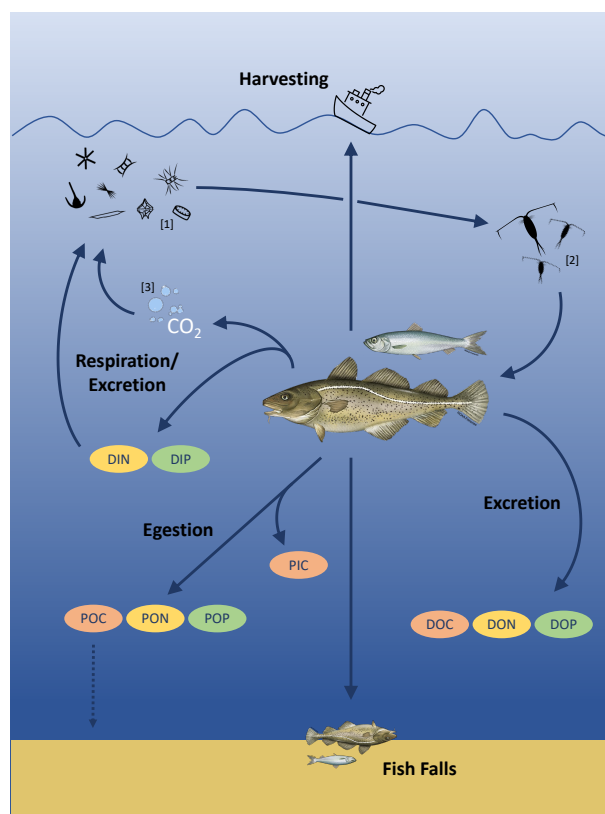


Fig. 1: Fish-related nutrient fluxes. Depicted here are the three groups of fish (represented by cod and herring), phytoplankton and zooplankton, their trophic relations as well as the fluxes of nutrients released in the course of fish-related physiological processes, namely carbon, nitrogen and phosphorus in their respective dissolved inorganic (CO_2 released via gills and DIN/DIP released via gills and kidney), dissolved organic (DOC/DON/DOP released via gut fluids), particulate inorganic (PIC released as bicarbonate precipitates in faeces) and particulate organic forms (POC/PON/POP released as faeces); image adapted from Saba et al. (2021).

¹ <https://vecta.io/symbols/303/flora-microalgae/28/mixed-phytoplankton-community-coloured>

² <https://w7.pngwing.com/pngs/492/796/png-transparent-zooplankton-jellyfish-phytoplankton-plankton-leaf-monochrome-jellyfish-thumbnail.png>

³ https://www.nicepng.com/ourpic/u2q8a9w7u2r5q8e6_how-to-set-use-bubbles-svg-vector/

inorganic carbon (Wilson et al., 2009; Salter et al., 2017). The latter is continuously released in the gut in the form of carbonate, produced as an osmoregulatory by-product, and is estimated to make up 3 to 15% of the total global carbonate production (Wilson et al., 2009). These carbonate crystals further add ballast to faecal pellets, potentially accelerating the downward flux of organic carbon into deeper layers, and thereby indirectly stimulating the biological carbon pump (Saba et al., 2021).

With regards to the long-term sequestration of carbon, fish could be of particular interest. Fish faecal pellets have been shown to exhibit faster average sinking rates than those of zooplankton, representing a potentially effective downward flux of particulate carbon into deeper waters with greater sequestration times and support for pelagic-benthic coupling (Saba & Steinberg, 2012; Saba et al., 2021). Lastly, fish carcasses are hypothesised to contribute substantially to the export of carbon from the pelagic to the deep sea (Mariani et al., 2020).

1.4 The Underestimated Role of Fisheries in Blue Carbon Budgets

It is needless to say that fishes, like the vast majority of living organisms, have not been left untouched by climate change and the impact it is having on ocean ecosystems. Ocean warming, acidification and eutrophication have been shown to increase the fragility of stocks (Polte et al., 2021; Möllmann et al., 2021) and, apart from fisheries, add yet another level of stress that fish stocks worldwide are increasingly exposed to. But fish are not passive components suffering under climate change scenarios, they actively take part as an important blue carbon storage and driver of the biological carbon pump (Mariani et al., 2020; Saba et al., 2021). Thereby, fishes contribute to the buffer capacity of the world's oceans and potentially mitigate the consequences of climate change. So far, this aspect has however found little to no recognition in the way fish stocks are managed, both due to a lack of awareness about the role of fish in carbon ecosystem fluxes as well as due to a lack of quantifiable data.

The term "blue carbon" was first officially used in a report by Nelleman et al. (2009) on the role of oceans in large-scale oceanic carbon sequestration processes and refers to organic carbon being captured and stored in ocean ecosystems as an aquatic counterpart to "green carbon" in terrestrial systems (Macreadie et al., 2019). While originally a metaphor, it has led to an intensified interest beyond the scientific community, and over the past decade, the importance of blue carbon and ocean systems for climate change mitigation has become increasingly apparent. However, the oceans are still given less attention in the ongoing development of improved global climate strategies. While two-thirds of the signatories of the Paris Agreement committed to implementing so-called nature-based solutions in their climate pledges, today's focus is mostly on terrestrial or coastal primary producers, in particular afforestation (Seddon et al., 2019). The relevance of fish stock management for blue carbon is still neglected, even though recent studies show that the contribution to climate change of fisheries alone, direct or indirect, is substantial. According to Mariani et al. (2020), global fisheries have prevented the sequestration of ~22

million metric tons of carbon (MtC) between 1950 and 2014. CO₂ emissions of global fishing fleets during that time span were even higher, with more than 165 MtC of carbon being emitted into the atmosphere due to fossil fuel burning and a further considerable amount of emissions caused by consumption and processing. However, these values do not include all commercially exploited fish species, and do not consider other dynamic processes associated with living fish like respiration and the production of faecal pellets, which further impact ocean carbon fluxes (Saba et al., 2021; Bianchi et al., 2021). This implies that the real amount of non-sequestered carbon due to fisheries most likely exceeds the estimates by Mariani et al. (2020).

1.5 Less Fish Equals More Emissions

While traditional fishing methods can still be found to persist in many parts of the world, industrial fisheries have long been accounting for the majority of landings worldwide (Tyedmers, 2004). In fact, the magnitude of landings nowadays would be impossible without the use of motorised vessels, which facilitate most of today's fishing methods in the first place, trawling in particular. The dependency on the combustion of fossil fuels, however, heavily increases the amount of input energy and hence of emitted CO₂ per weight unit of landed fish. While subsistence fisheries are dependent on the nutritional value of the catch exceeding the amount of human physical input energy, industrialised fisheries can operate independently of that equation (Tyedmers, 2004). However, when looking at the total energy input of industrialised fisheries, also including the energy release from fuel combustion, it becomes apparent that it exceeds the nutritional energy embodied in the catch by at least one order of magnitude (Tyedmers, 2004).

The term "fishing effort" is generally a measure of the intensity of fishery activity and describes the total effective area being fished during a number of unit operations (Sanders & Morgan, 1976). While the effort alone does not provide any information on the amount of fish being caught during a given time, it is still a key parameter to understand the carbon footprint of global fisheries, since it is closely linked to CO₂ emissions. If we assumed that the fish density (number of fish per unit area) remained constant, maintaining the same fishing effort over time would also yield the same amount of landings. However, global fish stocks are strongly regressive. To even maintain the same number of annually landed fish, the fishing effort in turn has to be increased and so do the carbon emissions (Martin et al., 2022). At present, landings are not only held at a constant level but are in a continuous surge (FAO, 2022). This results in an even steeper increase in emitted CO₂ per weight unit of landed fish. While technological advances, such as the catch efficiency of gears, mitigate this trend to at least some extent, there is no doubt that the carbon footprint of wild-caught fish continues to expand.

This issue once more illustrates how complex the crisis is that global fisheries are currently in. Not only are they far from sustainable with regard to biodiversity, but they also constitute a non-negligible component in driving climate change. Against the backdrop of increasing demands for aquatic foods worldwide (FAO, 2022), the upward pointing trend of the sector's CO₂ emis-

sions seems contradictory to the 1.5 °C goal that the 195 signatories of the Paris Agreement committed to, and highlights the importance of approaching fisheries management also from a climate point of view instead of focusing on conservation only.

1.6 Towards a More Holistic Management of Fisheries

This thesis introduces a modelling approach to quantify the contribution of western Baltic fish stocks to carbon ecosystem fluxes under different management scenarios with the aim to raise awareness of the multi-faceted complexity of fisheries, hinting at the fact that the impact of fisheries reaches beyond the extraction of biomass alone.

In recent times, there has for example been an increase in awareness of the climate impact of fisheries. Quantifiable data are urgently needed since the focus of fisheries science has traditionally been on conservation, both of the stocks themselves as well as that of large marine predators and mammals in direct competition with fishermen. Therefore, this extensive knowledge gap now has to be filled to adjust ongoing management frameworks and transform the economic sector of fisheries towards a reduction in climate impact.

To generate such data, this work applies an existing ecosystem model of the western Baltic Sea (Scotti et al., 2022), encompassing the ICES (International Council for the Exploration of the Sea) subdivisions (SD) 22 and 24. The model allows quantifying stock biomasses and carbon fluxes depending on fish, especially those towards the detritus compartment. Results from the period 1994-2019 will be used to make predictions about the future evolution of carbon ecosystem fluxes at different time points in the 21st century under different fisheries management strategies. These forecasts serve as estimates of the potential of carbon sequestration in the western Baltic Sea and its dynamics under alternative management scenarios. To gain a broader understanding of the total amount of blue carbon stored in commercially exploited fish, both the stock biomass and the amount of respired carbon will also be incorporated in the analysis in addition to egested carbon alone.

To verify the reliability of the forecasted scenarios, model results for the period 1994-2019 will be compared against calculations based on empirical stock data from ICES for the same time span in combination with literature data on fish physiology. By identifying the statistical relationship between the model and empirical calculations, realistically expected values could then later be derived from the model outcome for future predictions.

The thesis will follow two leading questions, which are as follows:

1. How do stock biomasses and fish-related ecosystem carbon fluxes change under different fisheries management strategies?
2. What additional impact do perturbations like ocean warming and changes in phytoplankton biomass concentration have on the fish stocks and what does that imply for future management frameworks?

1.7 The Baltic Sea: An Ideal Model Region

The Baltic Sea (Figure 2) provides ideal conditions for a study aiming at quantifying the impact of fisheries on ecosystem carbon fluxes, starting with an exceptional data availability. Efforts in monitoring both biotic and abiotic variables have, in some cases, been made for more than 100 years, much longer than in many other regions worldwide and hence, the availability of data for fish stock assessments is generally very good (Reusch et al., 2018).

Furthermore, the Baltic Sea at present is already exposed to multiple stressors such as warming, eutrophication, acidification and an increase in oxygen minimum zones, making it a highly perturbed sea (Snoeijs-Leijonmalm et al., 2017). Its susceptibility to these pressures, often of anthropogenic origin, derives from several factors, including a shallow average water depth, its young evolutionary age, a limited exchange with marine waters as well as as it being enclosed by nine industrialized countries (Reusch et al., 2018). All of these factors accelerate the effects of perturbations compared to many other regions, making it a suitable model area for predictions on the future state of the ocean.

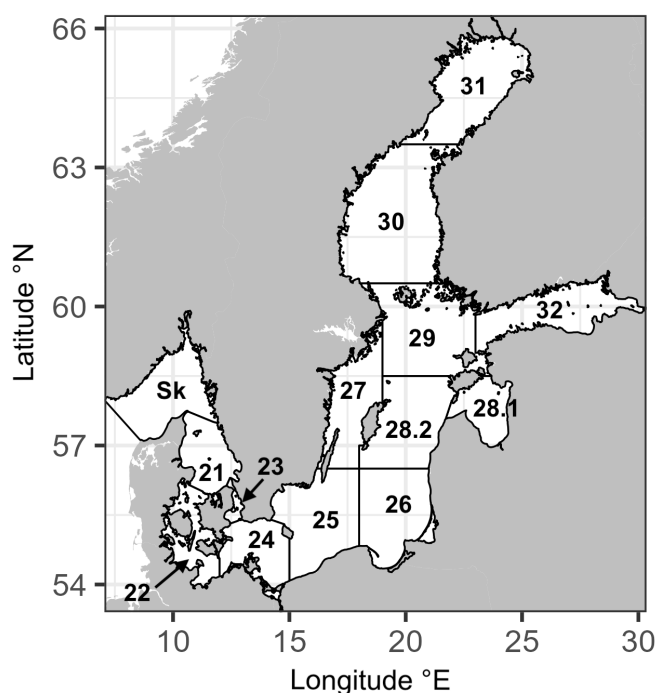


Fig. 2: Map of the Baltic Sea. Areas numbered 21 to 32 indicate the ICES subdivisions, while "Sk" stands for Skagerrak; map produced by Liam MacNeil.

Lastly, the Baltic Sea represents an area of long-lasting, intense fishing effort that, combined with detailed catch documentation, allows for the direct investigation of the fisheries' impact on stocks and cascading ecosystem effects. The decline of several stocks is well documented, such as cod and herring over the past decades, as a consequence of management authorities knowingly exceeding sustainable quotas (Aps & Lassen, 2010), which in turn has in some cases even caused a shift in ecosystem functioning by altering the direction and strength of trophic links within the system (Casini et al., 2009). The region is thus of particular interest for fisheries science, to investigate both the historical impact of fish exploitation and to forecast future developments on the basis of modelling approaches.

The western Baltic Sea is well-suited for a study aiming at the blue carbon potential of fish. Firstly, the region is home to two commercially important stocks, the western Baltic cod (WBC) and the western Baltic spring-spawning herring (WBSSH). Both stocks are relatively constrained to this area, meaning that studies in this region encompass both stocks as a whole

instead of requiring to fraction them due to non-congruent study areas and biological boundaries. Secondly, this region matches ICES subdivisions 22 and 24 (Figure 2), which eases data retrieval and knowledge transfer for the development and application of management strategies. Lastly, the western Baltic Sea shows homogeneous ecological features compared to the surrounding ICES subdivisions, such as a very even distribution of sandy to muddy sediments (Al-Hamdani et al., 2007).

1.8 Fisheries in the Western Baltic Sea

Fishing fleets from four different nations are currently operating in SD 22 and 24, namely Denmark, Germany, Poland and Sweden (ICES, 2023a). Their targeted species of commercial interest are, most notably, Atlantic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus*), as well as sprat (*Sprattus sprattus*) and several flatfish species such as flounder (*Platichthys flesus*), plaice (*Pleuronectes platessa*), dab (*Limanda limanda*), turbot (*Scophthalmus maximus*) and brill (*Scophthalmus rhombus*). As already hinted, fisheries in the Baltic Sea have predominantly been unsustainable, which particularly applies to cod and herring, both of which play crucial roles in the Baltic ecosystem (Snoeijs-Leijonmalm et al., 2017). Subpopulations of both species have been documented to inhabit the ICES subdivisions 22 and 24, the western Baltic cod (Bagge & Thurow, 1994) and the western Baltic spring-spawning herring (Jørgensen et al., 2005), and have in the last decades been exposed to immense fishing pressure (Table 1). Apart from flatfish, sprat is the third fish species of pronounced commercial interest in Baltic fisheries. However, it is not subject to this thesis due to the limited availability of data on the species' physiology, which was required to validate the model.

Table 1: Fisheries Biology Terms

F	fishing mortality/pressure = yearly fraction of a fish population extracted by fisheries
B_{MSY}	stock biomass at maximum sustainable yield, meaning the largest yield that can be extracted from a stock without causing its long-term decrease
B_{PA}	stock biomass at precautionary fisheries approach, which considers prediction uncertainties of the MSY approach and keeps a buffer zone to the latter to guarantee that the biomass does not fall below the B _{MSY} threshold (Berveridge et al., 2013)
B_{LIM}	limit stock biomass at which the number of offspring no longer reaches the carrying capacity (Berveridge et al., 2013)
F_{MSY}	fishing mortality/pressure corresponding to B _{MSY}
F_{PA}	fishing mortality/pressure corresponding to B _{PA}
F_{LIM}	fishing mortality/pressure corresponding to B _{LIM}

1.8.1 Cod (*Gadus morhua*)

The western Baltic cod stock is relatively small compared to the eastern stock, and despite ample mechanical mixing of the two in the Arkona Basin (SD 24), hybridization has shown to be very low (Hemmer-Hansen et al., 2019; ICES, 2022a). Offshore, it has traditionally been actively targeted by bottom trawls while coastal fisheries mainly use passive gears such as gill-nets, longlines and fishtraps to catch both cod and flatfish (ICES, 2023a). Western Baltic cod is further targeted by recreational fisheries, an activity which substantially contributes to impair the stock as it was responsible for more than 25% of the total landings in 2015 (Radford et al., 2018).

Historically, the western Baltic cod stock has been drastically overfished, with F exceeding F_{MSY} (Table 1) by often more than fourfold since the mid 1980s (ICES, 2022b). While the stock still seemed to recover in the early 1990s, the spawning stock biomass (SSB), a measure for the recruitment capability, has been in a pronounced decline since 1997 and has fallen further below B_{MSY} (Table 1) since 2008 (ICES, 2022b). As a consequence, recruitment has become highly variable, so that the most recent year class dominating today's catches dates to 2016 (ICES, 2022a; Froese et al., 2022). Since catch quotas are reassessed annually and are guided by the respective SSB at the time, the historical catch records follow the same pattern as the stock biomass, with a clear peak in 1996 and continuous decrease subsequently. It is however important to mention that the appointed catch quotas do not necessarily mirror the underlying scientific advice. On the contrary, the agreed total allowable catch (TAC) has been exceeding the advice in almost all years of the past two decades (ICES, 2022b), underlining overexploitation as an explanation for the collapse of the stock. This has led to historically low catch recommendations in 2022 and 2023, with the more recent TAC not exceeding 943 t for commercial and recreational fisheries combined. For the latter, additional seasonal closures and a so-called bag limit of one cod per angler and day are in place as further protective measures.

Even though the targeted exploitation of western Baltic cod by fisheries has been decreasing in the past years, bycatch still poses a threat to the stock. Especially in demersal trawl fisheries, which formerly fished cod and flatfish combined, a reduction in cod bycatch has still to be achieved, and despite gears suitable to reduce the latter already being available (Santos et al., 2022), its implementation is still pending (ICES, 2022b).

1.8.2 Herring (*Clupea harengus*)

Western Baltic spring-spawning herring inhabiting SD 20-24 is seasonally isolated from herring in the central and northern Baltic Sea due to an earlier spawning period in spring, whereas the latter spawn towards late spring/early summer (Jørgensen et al., 2005). Despite some overlap, they are therefore treated as separate management units and consequently fished as such, using both active (pelagic trawls) and passive (gill- and trapnets) gears (ICES, 2023a). The main fish-

ing season of WBSS herring is during the spawning period in March/April. During that time, they form large aggregates at the inlets to shallow inshore spawning grounds, where they are targeted by both commercial trawl and artisanal gillnet fisheries (Polte et al., 2021).

Compared to western Baltic cod, herring fisheries in SD 22 and 24 are in an even more severe state. Since 2018, the scientific catch advice has been a total closure of herring fisheries (ICES, 2022g) and since 2022, any directed commercial herring fisheries activity has officially been prohibited to facilitate stock recovery (Council Regulation (EU) 2021/1888). The 2022 and 2023 TAC of 788 t is now exclusively restricted to bycatch, which is particularly pronounced in mixed sprat fisheries where a herring bycatch rate of at least 5% still poses a risk to the already depleted WBSS herring stock (ICES, 2023a). While the recommendation for 2024 is still a zero-catch strategy, the fishing pressure has at least fallen below F_{MSY} and as a consequence, the stock biomass has experienced a slight increase again in recent years, however, is still far below B_{MSY} (ICES, 2023b).

The decline of the stock has been continuous since the early 1990s due to the fishing pressure surpassing the F_{MSY} of ~ 0.3 in almost all years preceding 2019 (ICES, 2022g). As a consequence of the agreed TAC routinely exceeding the scientific advice, the SSB fell below the sustainable threshold already in the mid-1990s and has since then decreased even further. Owing to the lasting overexploitation, it has now long been below B_{LIM} (ICES, 2022g), meaning that the number of yearly recruits lags behind the capacity the ecosystem could theoretically sustain (Beveridge et al., 2013). The limit biomass further constitutes the minimum threshold, below which a fish stock should not be further exploited (Snoeijs-Leijonmalm et al., 2017). Nevertheless, the exploitation of the WBSS herring stock has continued for 15 years after the SSB first fell below this threshold.

Alongside the stock biomass, landings experienced a substantial decline. From $\sim 200,000$ tonnes at the beginning of the 1990s, they dropped to less than 15,000 tonnes in 2021 (ICES, 2022g). Despite the herring fisheries closure, the SSB is still expected to remain below B_{LIM} for 2024 (ICES, 2022g). It is therefore indeterminate when the WBSS herring stock will be opened to fisheries again. A further factor of uncertainty for the stock recovery is the fact that the distribution area of the WBSS herring stretches into the North Sea where it mixes with the North Sea autumn-spawning (NSAS) herring and is still exposed to fishing (ICES, 2022g). It is therefore assumed that more than 6,000 t of WBSS herring will end up as bycatch in the North Sea fleet targeting the NSAS herring (ICES, 2022c). Despite the efforts undertaken in the western Baltic Sea, it can therefore not be ruled out that the stock will be further depleted and thereby hindered from reestablishing a viable size.

1.8.3 Flatfish

Flatfish species of commercial interest in the Baltic Sea encompass European plaice (*Pleuronectes platessa*), European flounder (*Platichthys flesus*), common dab (*Limanda limanda*),

brill (*Scophthalmus rhombus*), turbot (*Scophthalmus maximus*) and common sole (*Solea solea*) (Florin, 2005), which are targeted using both active (demersal/bottom trawls) and passive (e.g. gillnets) gear types (ICES, 2023a).

In total numbers, plaice and flounder are the most commercially important flatfish species in the western Baltic Sea with relatively stable landings since the early 2000s in SD 22 and 24 combined (ICES, 2022d,e,h,i). It is important to mention that the management units of both species are not congruent with the ICES subdivisions 22 and 24 but instead exceed them. Despite constant landings, both species show a pronounced increase in their respective stock size, which might be explained by the combined effect of fishing pressure in both cases being below F_{MSY} , meaning that the stocks are fished at a sustainable level, and a competitive release from the overfished cod stock, hence an increase in benthic food availability and a decrease in predation pressure. As a consequence, the two species show stock biomasses above the B_{MSY} threshold. While plaice is directly targeted and is currently managed using an MSY approach with a defined TAC, no such management strategy is in place for flounder for which catches are mainly taken as bycatch in mixed bottom trawl fisheries often also targeting cod (ICES, 2022d,e,h,i, 2023a).

Dab is treated as one Baltic stock encompassing the ICES subdivisions 22 to 32, even though it is currently not actively managed. As such, fisheries-related data restricted to SD 22 and 24 alone is difficult to resolve. The total landings in the entire Baltic Sea combined since the year 2000 have however been lower than those of plaice and flounder in the western Baltic Sea alone (ICES, 2020). While Baltic International Trawl Survey (BITS) data indicates an increase in stock biomass over the past 20 years, the real stock size remains unknown. However, the fishing pressure is, as of 2020, below both F_{MSY} and F_{PA} (ICES, 2020). The precautionary approach has been introduced to minimise the risk of a stock falling below B_{MSY} , especially when the available knowledge on the stock size is uncertain or unreliable (Berveridge et al., 2013).

Even though turbot is actively targeted in Swedish fisheries using gillnets (ICES, 2023a), no data on its stock status or that of the closely related brill (Florin, 2005) are available for the western Baltic Sea. The stock in the adjacent Kattegat, however, shows a highly stable biomass since the 1980s and has been exploited at a more or less sustainable level for the past 40 years (ICES, 2022j). Whether or not these findings can also be transferred also to the western Baltic Sea can only be hypothesised.

2 Materials & Methods

2.1 Study Area

The thesis focuses on the western Baltic Sea (SD 22 and 24), which corresponds to the geographical regions of the Belt Sea (Great Belt, Little Belt, Kiel Bay, Mecklenburg Bay) and the Arkona Basin until west of the Bornholm Basin. Together, SD 22 and 24 comprise an area of approximately 42,224 km² (Opitz & Froese, 2019), which shows an average yearly water temperature of around 10 °C (Gräwe et al., 2013). The water depth is generally shallow, with average values ranging between 14 and 46 m in the entailed regions (Leppäranta & Myrberg, 2009). But bathymetric variability is common in the WBS with the deepest channels in the Belt Sea reaching up to 60 m depth (Leppäranta & Myrberg, 2009). The inflow of oxygenated, salty marine water masses from the North into the Baltic Sea necessarily channels through the western Baltic Sea. In the context of this process, the most important topographic feature is the Darss Sill in SD 24 between Darsser Ort and the Gedser Peninsula, where the water only reaches 18 m depth (Leppäranta & Myrberg, 2009). It thereby poses a geographical barrier to the horizontal transport of water masses, which is of particular importance considering that more than 70% of the water exchange between the two seas takes place via that sill (Lemke et al., 1994). Behind the Darss Sill, the water depth increases towards the centre of the Arkona Basin in SD 24 west of Bornholm, which reaches 53 m at its deepest point (Snoeijs-Leijonmalm et al., 2017).

Due to the semi-enclosed location, salinity in the Baltic Sea

follows a clear gradient, which is negatively correlated to the geographical distance from the North Sea as the only supplier of saltwater masses. Towards the Baltic Proper and the northern Baltic Sea, the amount of freshwater discharge increases, mostly due to a higher number of adjacent rivers, causing a unique gradient from temperate marine to almost limnic and subarctic environmental conditions (Snoeijs-Leijonmalm et al., 2017). In the Belt Sea, which together with the Kattegat forms the transition zone between the Baltic and the North Sea (HELCOM, 1986), salinity shows pronounced fluctuations between 9.6 and 22.9 PSU due to the strong in-

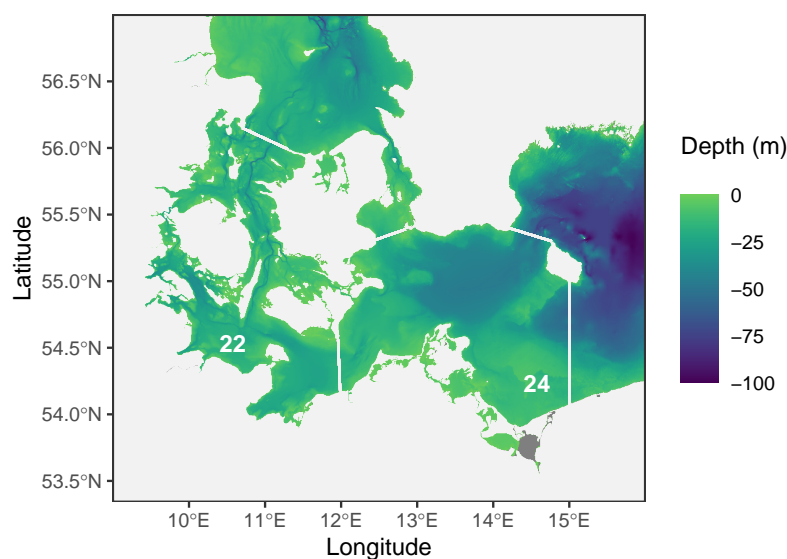


Fig. 3: Map of the study region. Located in the western Baltic Sea, it encompasses the ICES subdivisions 22 and 24. Produced using data BSBC (2013) and the ICES Metadata Catalogue.

fluence of marine water inflow from the Skagerrak (Andersen et al., 2017; Snoeijs-Leijonmalm et al., 2017). In the Arkona Basin and the Bornholm Sea, which are part of the Baltic Proper, salinity reaches values of 7.6-11.3 and 4.3-8.1 PSU, respectively.

While the exchange of water between the North and the Baltic Sea is driven by differences in water density and sea level due to riverine runoff and precipitation/evaporation, as well as the direction and strength of prevailing winds (Lass & Matthäus, 2008), the exchange within the Baltic Sea between the sub-basins is mainly governed by the sills separating them from each other (Leppäranta & Myrberg, 2009). When looking at the amounts of saltwater entering and those of freshwater leaving the Baltic Sea, an annual net outflow can be seen (Snoeijs-Leijonmalm et al., 2017). The density difference between these two water masses leads to a pronounced pycnocline, with lighter fresh and brackish water forming a layer on top of the heavier salt water from the North Sea. The depth of this pycnocline changes with total water depth with 2-10 m in the Belt Sea and the coastal areas, and 20-40, in some parts even 60 m in the Arkona Basin and the southeastern Bornholm basin (Alanen et al., 2007). The Darss Sill thereby marks a clear barrier, where heavier North Sea water dams up under a relatively shallow pycnocline, while the latter remarkably drops in depth once the salt water masses overflow the sill into the deeper adjacent Arkona Basin (Stigebrandt, 1987).

In SD 22 and 24, the sea floor is mostly comprised of sandy and muddy sediments with some exceptions of hard clay and hard bottom around the Danish islands of Lolland, Falster and Møn, outside of Ystad at the southern tip of Sweden as well as south of Bornholm (Al-Hamdani et al., 2007). These features are important to understand the benthic community assembly.

2.2 Ecosystem Model of the Western Baltic Sea

For the aim of this thesis, changes in carbon flows attributed to fisheries will be quantified using an existing ecosystem model of the western Baltic Sea, which was built by Scotti et al. (2022) starting from an earlier version by Opitz & Froese (2019). The model was constructed using Ecopath with Ecosim (EwE), a software program initially conceived by Jeffrey Polovina at the NOAA (Polovina, 1984) and further developed by other fisheries scientists such as Daniel Pauly, Villy Christensen and Carl Walters (Pauly et al., 2000).

The base model is a mass-balanced snapshot of the WBS ecosystem in 1994, covering the ICES subdivisions 22 and 24, and is comprised of biomass compartments connected through trophic interactions (Scotti et al., 2022). The currency used to quantify the standing stocks is weight of carbon per area (gC m^{-2}), which are modelled as yearly averages, while fluxes are expressed as $\text{gC m}^{-2} \text{yr}^{-1}$. The model includes 18 compartments, some of which describe single species or even separate ontogenetic stages, as well as larger functional groups comprised of several species and a non-living node. They are as follows: harbour porpoise (*Phocoena phocoena*), seals (comprised of harbour seal - *Phoca vitulina* and grey seal - *Halichoerus gry-*

pus), seabirds, juvenile and adult cod (*Gadus morhua*), flatfish (comprised of European plaice - *Pleuronectes platessa*, European flounder - *Platichthys flesus*, common dab - *Limanda limanda*, brill - *Scophthalmus rhombus* and turbot - *Scophthalmus maximus*), herring (*Clupea harengus*), sprat (*Sprattus sprattus*), other demersal fish, other pelagic fish, pelagic macrofauna, benthic macrofauna, benthic meiofauna, zooplankton, bacteria/microorganisms, phytoplankton, benthic producers and detritus/DOM.

This thesis lays its focus on the commercially exploited fish stocks of cod, herring and flatfish as well as their respective organic carbon fluxes to detritus/DOM and fisheries. Since many of the other groups included in the model are comprised of an extensive number of individual species and are not further involved in this work, it is referred to the original paper by Scotti et al. (2022) for a detailed description of the group compositions and the origin of the data.

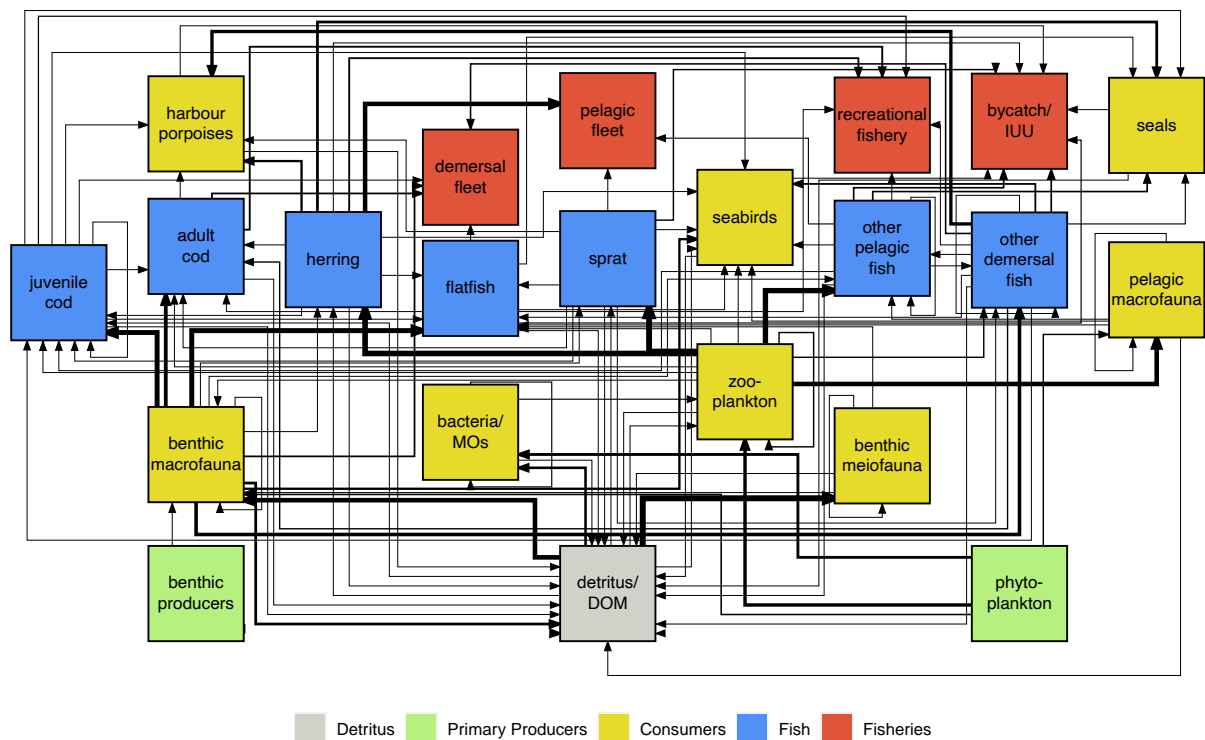


Fig. 4: WBS Model Structure in 1994. The black, arrowheaded links depict the carbon flow between the compartments with the thickness being proportional to the percentage of the respective flux in the total carbon import of the receiving compartment. The vertical positioning of each compartment is proportional to its effective trophic level (Scotti et al., 2006), reaching between 1 and ~4.5. IUU, MOs and DOM here stand for "illegal, unreported and unregulated fisheries", "microorganisms" and "dissolved organic matter".

The Ecopath model is mainly based on two master equations for each group, which have to be satisfied and describe the biomass production (1) and the conservation of matter (2), while a third equation describes the amount of carbon flowing to the detritus compartment (3) (Opitz & Froese, 2019).

$$\text{Production} = \text{Catch} + \text{Predation} + \text{Biomass Accumulation} + \text{Net Migration} + \text{Other Mortality} - \text{Import} \quad (1)$$

$$\text{Consumption} = \text{Production} + \text{Respiration} + \text{Unassimilated Food} \quad (2)$$

$$\text{Flow to Detritus} = \text{Other Mortality} + \text{Unassimilated Food} \quad (3)$$

Further, a set of parameters has to be set for every group, including biomass (B), the production/biomass ratio (P/B) or total mortality (Z), the consumption/biomass ratio (Q/B) and the ecotrophic efficiency (EE). The latter expresses the proportion of a group's total production that is transferred further to other living or non-living compartments in the system, either through predation/grazing or fisheries (Heymans et al., 2016). These parameters are needed to calculate unknown values in order to establish mass balance (Scotti et al., 2022).

The WBS reference model was validated using ICES catch and stock biomass data of western Baltic cod, WBSS herring, sprat and flatfish in SD 22 and 24 between 1994 and 2019. Then, the model was applied to project future stock biomass and catch levels under four different fisheries management scenarios and a "No Fishing" scenario assuming a total absence of fishing activity.

1. ***Business as Usual (BAU)*** meaning a continuation of the average fishing pressure between 2015 and 2019.
2. ***Ecosystem-Based Fisheries Management (EBFM)*** corresponding to $F = 0$ for juvenile cod, $0.5 F_{\text{MSY}}$ for herring and sprat and $0.8 F_{\text{MSY}}$ for adult cod and flatfish.
3. ***Maximum Sustainable Yield (MSY)*** with $F = F_{\text{MSY}}$.
4. ***Half Maximum Sustainable Yield*** with $F = 0.5 F_{\text{MSY}}$.
5. ***No Fishing*** equalling $F = 0$, which serves the purpose of a reference scenario to investigate stock changes in the absence of human interference, at least with regard to direct fishing pressure.

While a complete stop of fishing activities until the end of the century would be politically and economically unrealistic, a combination of catch quotas and strategically placed fishing closures has been suggested as a very effective management tool when trying to rebuild depleted stocks (Worm et al., 2006; 2009). Furthermore, the ecosystem state and the status of the stocks in the absence of fisheries are of central importance as a reference when evaluating whether a certain management strategy is sustainable or not.

In addition to these five base scenarios, the WBS model provides the possibility of also including potential changes in ocean temperature and phytoplankton biomass. These two additional stressors, presumably having an impact on the selected fish species either indirectly through trophic cascades in the food web or directly on the physiological tolerance of the species, add new layers of complexity to the model. Multi-stressor scenarios were considered for BAU and EBFM only.

The projected increase in ocean temperature is included in the model in three distinct steps, of +1, +2 and +3 °C; temperature is embedded in terms of its direct effects on cod, herring and sprat recruitment. Changes in phytoplankton are represented by either a 25% increase or decrease in its biomass. While both temperature and phytoplankton shifts can act on the system in isolation, the model also allows for a fully factorial design, resulting in 22 different scenarios for BAU and EBFM combined.

2.3 Model Validation

The WBS ecosystem model lays the focus on the biomass of the functional groups (Scotti et al., 2022). Therefore, the validation of the accuracy of associated processes like egestion/flow to detritus or respiration was not yet thoroughly conducted. The way they are calculated by EwE is as follows:

- Flow to detritus is equal to the amount of non-assimilated (= egested) food + the fraction of a group which dies of age, diseases, etc., summarized as 'other mortality'. The latter is calculated as $1 - EE$ (ecotrophic efficiency).
- Respiration is equal to the carbon dissipated by a living compartment, which corresponds to the amount not used in any of the other modelled processes. Since the model always aims at maintaining mass balance, respiration is solely used to achieve that by balancing the budget of flows of each compartment. In the construction of the model, it is thus not possible to set physiological respiration parameters for the individual groups.

Since models depict a simplified representation of the real world, they can only serve as an approximate approach to the latter. The first step was therefore to compare the model quality with regards to egestion and respiration against manual calculations based on empirical stock data for the years 1994-2019 in combination with physiological parameters taken from literature. By quantifying potential deviations between modelled and manually calculated data, it is then possible to later derive realistic values from the model output using generalized linear models (GLMs) even for forecasted ecosystem scenarios.

The WBS model calculates both egestion and respiration by applying a fixed ratio to the total stock biomass (TSB). While this is totally reasonable for such a big model with many species/functional groups, it still does not recognize the fact that each fish stock is comprised of several different age classes, for which these allometric ratios might vary. Since the amount of carbon egested or respired per unit of biomass changes with the age of a fish, taking only the total stock biomass for the calculation of physiological parameters results in a reduced resolution and thereby potentially in reduced accuracy. To evaluate the impact of this limitation, manual calculations were performed per age class. If the data obtained from these two different and independent approaches more or less coincide, the level of certainty that the model output falls into a realistic range is substantially increased.

2.3.1 Data Sources

The data needed for the model verification step were taken from numerous sources, which are listed per species and application in Table 2. The latter are grouped into four main categories. Note that the types and amount of information used to derive the data needed for this analysis vary between species. This is because the underlying stock data taken from the ICES reports differed in their informative content, which is why extra calculation steps were sometimes necessary to achieve the desired output. A detailed description of the individual calculations can be found in section 2.3.2.

Table 2: Literature Data Sources used for the manual model validation of stock biomass (B), consumption (Q), egestion (E) and respiration (R)

	Stock Data	Q/B	E/Q	R/B
Cod	ICES (2022a)	FishBase	Hansson et al. (1996)	FishBase
Herring	ICES (2022f)	Arrhenius & Hansson (1993)	Rudstam (1988)	Rudstam (1988)
Flatfish (Plaice)	ICES (2022a); BITS data	Mackinson & Daskalov (2007)	Mackinson & Daskalov (2007)	Fonds et al. (1992)

2.3.2 Calculations

2.3.2.1 Cod

SSB

All the information needed to calculate the spawning stock biomass for cod was taken from the ICES (2022a) report, which provided the number of individuals (n), the mean weight (W) and the fraction of adult individuals (a) per year and age class (age; 0 to 7+). Using these parameters, the SSB was calculated for each year and age class between 1994 and 2019 as follows:

$$SSB_{age} \left(\frac{gC}{age} \right) = \left[n_{age} \left(\frac{Ind}{age} \right) * W_{age} \left(\frac{gWW}{Ind} \right) * a_{age} \right] * 0.1 \left(\frac{gC}{gWW} \right) \quad (4)$$

The multiplication by 0.1 converts the wet weight biomass (WW) into grams of carbon (C) using the conversion factor of $10 \text{ gWW} = 1 \text{ gC}$ valid for fish biomass (Czamanski et al., 2011). Since grams of carbon is the currency used by the model, it was also used in the manual verification step. The same was done for herring, sprat and flatfish. The subscript "age" indicates the age-class resolution of the validation approach, since egestion and respiration were, whenever possible, calculated for each age class separately before being summed up to attain the stock's total estimate.

Egestion

For estimating the egestion, the amount of consumed carbon was needed first. In the case of cod, that was quantified using all 27 entries on daily ration (in % of biomass) per weight class available on FishBase. Body weight was plotted against ration and a power trendline fitted to the data, which uses the equation $y = cx^b$ with c and b being constants and y and x being daily ration and body weight, respectively. The equation of the trendline, $y = 0.112x^{-0.364}$ ($R^2 = 0.910$), was then applied to calculate the total yearly consumption Q of the stock as follows:

$$Q \left(\frac{gC}{yr} \right) = \sum_{age=0}^7 SSB_{age} \left(\frac{gC}{age} \right) * \left[0.112 W_{age}^{-0.364} \right] \left(\frac{1}{d} \right) * 365 \left(\frac{d}{yr} \right) \quad (5)$$

Yearly egestion E of carbon was then derived by applying a conversion factor of $E = 0.17Q$ found in the literature (Hansson et al., 1996).

Respiration

The respiration of cod was again calculated using data from FishBase, in this case directly from the respiration table. It contained 151 entries on oxygen consumption in mg/kg/h derived from a collection of studies and further detailed information on the respective experimental conditions, meaning the weight of the fish, water temperature, salinity, activity status and additional stressors. The FishBase data were subset so that entries from respiration measurements under hypercapnia (elevated CO₂ concentration in the blood) were excluded. The remaining O₂ consumption data (139 entries) were plotted against biomass and a power trendline was fitted to the data. The equation of the trendline, $y = 326.4x^{-0.237}$ ($R^2 = 0.650$), includes y and x to represent oxygen consumption and body weight, respectively. Such equation was applied to calculate the total yearly respiration R (in gC) of the stock as follows:

$$R \left(\frac{gC}{yr} \right) = \sum_{age=0}^7 \left(\frac{[326.4 W_{age}^{-0.237}] \left(\frac{mg}{kgWW h} \right) * W_{age} \left(\frac{kgWW}{Ind} \right) * 24 \left(\frac{h}{d} \right) * 365 \left(\frac{d}{yr} \right)}{1,000 \left(\frac{mg}{gWW} \right) * 10 \left(\frac{gWW}{gC} \right)} \right) * n_{age} \left(\frac{Ind}{age} \right) \quad (6)$$

2.3.2.2 Herring

SSB

The SSB of herring was calculated for each year and age class between 1994 and 2019 following Eqn. 4, with the only difference that the required information here was taken from ICES (2022g) and that the number of age classes ranges from 0 to 8 instead of 7+.

Egestion

The yearly egestion of the herring stock was calculated from the yearly consumption. To obtain the latter, several steps were needed using the previously derived SSB per age class and year as well as literature data on the conversion efficiencies from Arrhenius & Hansson (1993), which is a measure of the amount of biomass increase per weight unit of consumed food and was applied per age class. For the calculation of the consumption, both the conversion efficiencies and the biomass increase between age classes were therefore needed. The growth was obtained by averaging the mean weight per age class over all years and then calculating the difference between two consequent classes. However, that way only the average growth for the age classes 0 to 7 could be derived. For a8, the growth values for a0 to a7 were plotted against age and a linear trend line was fit to the data ($R^2 = 0.877$). The equation expressing growth (y) as a function of age (x), $y = -4.806x + 44.053$, was used to infer the mean growth of eight-year-old individuals.

Using the conversion efficiency (CE) and the average growth ($\overline{\Delta W}$) per age class, the consumption and hence the Q/B ratio (QB) could then be calculated as follows:

$$QB_{age} \left(\frac{1}{yr} \right) = \frac{\overline{\Delta W}_{age} \left(\frac{gWW}{age \ yr} \right)}{CE_{age} * \overline{W}_{age} \left(\frac{gWW}{age} \right)} \quad (7)$$

By applying the Q/B ratio per age class to the stock data, the yearly organic carbon consumption of the herring stock could be derived as follows:

$$Q \left(\frac{gC}{yr} \right) = \sum_{age=0}^8 SSB_{age} \left(\frac{gC}{age} \right) * QB_{age} \left(\frac{1}{yr} \right) \quad (8)$$

From this equation, the stock's yearly egestion E of carbon was derived by applying the conversion factor of $E = 0.17Q$ (Rudstam, 1988).

Respiration

The yearly respiration of the herring stock was obtained using the bioenergetics model of Rudstam (1988), which expresses daily respiration (in $g \ g^{-1} \ d^{-1}$) as a function of fish weight (W), temperature (T) and swimming speed (U), where α , β , ρ and ν are constants equal to 0.003, -0.227, 0.055 and 0.030, respectively:

$$R = \alpha * W^{\beta} * e^{\rho * T} * e^{\nu * U} \quad (9)$$

The temperature T was set to 8.6 °C, in accordance with the average yearly water temperature in the western Baltic Sea and adjacent North Sea from 1994 to 2019 and between 0 and 200 m, the preferred depth distribution of herring (Whitehead et al., 1985). The observational temperature data was obtained from the SHARKweb database of the Swedish Meteorological and

Hydrological Institute (SMHI). Applying that temperature resulted in the swimming speed U being calculated as follows:

$$U = 3.9 W^{0.130} * e^{1.281} \quad \text{for } T < 9^{\circ}\text{C} \quad (10)$$

By combining these two equations, the stock yearly respiration across all age groups could then be derived:

$$R \left(\frac{\text{gC}}{\text{yr}} \right) = \sum_{age=0}^8 [0.003 W_{age}^{-0.227} * e^{0.471} * e^U] \left(\frac{\text{g}}{\text{gWWd}} \right) * W_{age} \left(\frac{\text{gWW}}{\text{age}} \right) * 365 \left(\frac{\text{d}}{\text{yr}} \right) * 0.1 \left(\frac{\text{gC}}{\text{g}} \right) \quad (11)$$

2.3.2.3 Flatfish / Plaice

While the flatfish group in the WBS model consists of five different species, namely European plaice (*Pleuronectes platessa*), European flounder (*Platichthys flesus*), common dab (*Limanda limanda*), brill (*Scophthalmus rhombus*) and turbot (*Scophthalmus maximus*), only the European plaice was used for model validation. This choice was made due to an insufficient ICES stock data availability for the other four species. Nevertheless, European plaice, alongside European flounder and common dab, have been shown to be the most important flatfish species, both ecologically and commercially as well as in abundance (Rau et al., 2019). Hence, the choice of focusing on plaice is a suitable base for the model validation with regard to the flatfish.

SSB

The SSB of plaice was calculated based on the stock data available in ICES (2022a). Unlike for cod and herring, these data were however not available for SD 22 and 24 alone but pooled for SD 21-23 and SD 24-32. For the latter, the SSB was already summarised across all age classes, thereby lacking age-specific data and was unavailable before 2002, so only the total SSB for the entire stock could be obtained for the period 2002-2019. In the case of flatfish, the years 1994-2001 had to be excluded from the model validation step for all three parameters, since the calculation of both egestion and respiration build upon SSB as an underlying variable. For SD 21-23, the SSB was calculated per age class, here ranging from 1 to 7, and year using Eqn. 4. Age-class SSBs were afterwards summed to obtain the total SSB per year, equal to that available for SD 24-32.

In order to derive the yearly SSB for SD 22 and 24 alone, the total SSB for SD 21-32 was subset according to the fraction of the Baltic plaice stock assumed to occupy these two regions. The calculation of those yearly fractions (f) was conducted with the help of Liam McNeil from the Ecosystem Modelling Group at the GEOMAR Helmholtz Centre for Ocean Research Kiel using a cleaned BITS data set (Baltic International Trawl Surveys). The latter contains CPUE (catch per unit effort) data in kg km^{-2} from yearly surveys between 2001-2020, conducted in

Q1 (Feb-Mar) and Q4 (Oct-Dec), where the swept area is calculated using the geometry of the used gear and the haul duration. Depending on the vessel sizes, two different standardised gears were used, TVS (530 meshes) and TVL (930 meshes), at a standard towing speed of 3 knots. For further information on the sampling methodology, it is referred to the BITS manual (ICES, 2017). The data set was cleaned by removing all values with geographical uncertainty (missing longitude or latitude) and values from surveys longer than 90 or shorter than 15 min. After that, the data were individually subset to the SD 22 and 24 using a polygon (Figure 5). For both subdivisions, a yearly ratio was then calculated, expressing the fraction of the total Baltic plaice stock occupying each of these regions.

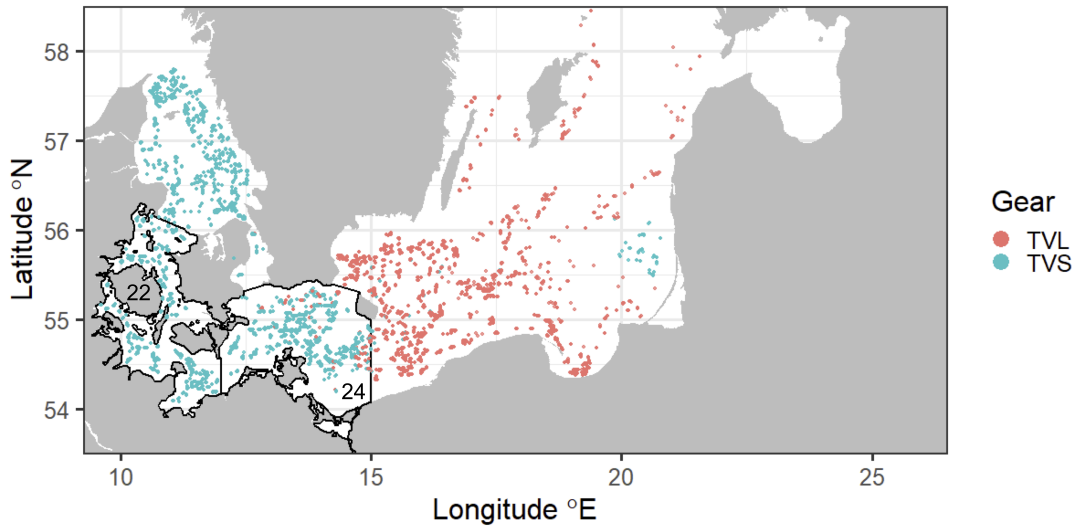


Fig. 5: Map of BITS data entries for European plaice. Each dot represents one observation in the period 2001-2020 in kg km^{-2} derived from yearly surveys in Q1 and Q4, using the gear types TVS (520 meshes) and TVL (930 meshes); map produced by Liam MacNeil.

By applying the yearly ratios for SD 22 (f_{22}) and SD 24 (f_{24}), the yearly spawning stock biomass in both subdivisions combined could then be calculated as follows:

$$SSB_{21-23} (gC) = \sum_{age=1}^7 \left[n_{age} \left(\frac{Ind}{age} \right) * W_{age} \left(\frac{gWW}{Ind} \right) * a_{age} \right] * 0.1 \left(\frac{gC}{gWW} \right) \quad (12)$$

$$SSB_{21-32} (gC) = SSB_{21-23} (gC) + SSB_{24-32} (gC) \quad (13)$$

$$SSB_{22+24} (gC) = SSB_{21-32} (gC) * f_{22} + SSB_{21-32} (gC) * f_{24} \quad (14)$$

Egestion

Since the SSB for plaice was not calculated per age class but for the total stock, calculating the yearly egestion of organic carbon was kept rather straightforward. First, the consumption was derived as $Q = 3.42 SSB$, from which the egestion could be calculated as $E = 0.2 Q$ (Mackinson & Daskalov, 2007).

Respiration

The respiration of plaice was obtained using the linear regression of oxygen consumption R (mg h^{-1}) being plotted against fish weight W (g), taken from a study by Fonds et al. (1992). The regression follows the equation $R = A * W^B$, where A is equal to the oxygen consumption of a fish of 1 g and B is the metabolic weight exponent. In their study, Fonds et al. conducted experiments under different temperatures and with both fasting and well-fed fish of varying body weights. Before applying the equation for model validation, the parameters A and B were averaged across all experimental conditions, which resulted in $A = 0.280$ and $B = 0.791$. Since information specific to age classes was only available for the ICES subdivisions 21 to 23, these were taken as a proxy for the age structure of the entire Baltic stock to calculate a total R/B ratio per year:

$$RB \left(\frac{1}{\text{yr}} \right) = \left[\sum_{age=1}^7 \frac{[0.28 W_{age}^{0.791}] \left(\frac{\text{mg}}{\text{h Ind}} \right) * n_{age} \left(\frac{\text{Ind}}{\text{age}} \right) * 24 \left(\frac{\text{h}}{\text{d}} \right) * 365 \left(\frac{\text{d}}{\text{yr}} \right)}{1000 \left(\frac{\text{mg}}{\text{gWW}} \right) * 10 \left(\frac{\text{gWW}}{\text{gC}} \right)} \right] / SSB_{21-23} \text{ (gC)} \quad (15)$$

These yearly ratios could then be applied to the previously calculated SSB in SD 22 and 24 to obtain the amount of respired organic carbon per year for the period 2002-2019:

$$R \left(\frac{\text{gC}}{\text{yr}} \right) = SSB_{22+24} \text{ (gC)} * RB \left(\frac{1}{\text{yr}} \right) \quad (16)$$

2.4 Modelling of Ecosystem States using Ecopath with Ecosim

2.4.1 Time Periods

To investigate the progression of the western Baltic fish stocks throughout the 21st century, three different time periods were selected, namely 2020-2025, 2050-2060 and 2090-2100. They were chosen to provide good coverage of the entire century as well as a short- (tactical), mid- and long-term (strategic) forecast of the impact of different fisheries management strategies on cod, herring and flatfish.

2.4.2 Fisheries Management and Multi-Stressor Scenarios

A total of 27 different scenarios were investigated. These include the five main fisheries strategies (BAU, EBFM, MSY, 50% MSY, "No Fishing"). In addition to the base scenarios, 11 multi-stressor scenarios were run for each BAU and EBFM, modelling the ecosystem state against the backdrop of environmental changes, here expressed as an increase in water temperature (+1, +2 or +3 °C) and shifts in phytoplankton biomass ($\pm 25\%$). Both stressors were investigated separately from each other and adopting a fully factorial design resulting in 22 multi-stressor scenarios for BAU and EBFM combined.

2.4.3 Ecological Parameters

A number of response variables were selected to quantify the impacts that fisheries management, increasing water temperatures and shifts in phytoplankton biomass have on fish-related carbon ecosystem fluxes. The first one is the organic carbon biomass of the stocks, which was included for two main reasons. Firstly, all physiological processes are heavily dependent on biomass as an underlying driver. The amount of living biomass in a stock determines the quantity of carbon entering and leaving the stock. Secondly, stock biomass itself represents a substantial carbon storage. The larger the stock, the higher the capacity to fixate carbon on a long-term basis. Stock biomass thereby takes on both a passive and an active role in marine carbon biogeochemistry, as a storage unit as well as a driver.

The second parameter included in the analysis is the flow of organic carbon to detritus. In EwE, this flow is comprised of two variables, the amount of egested carbon and the amount of sinking dead biomass/fish carcasses. The latter is defined as the fraction of biomass leaving the stock that is not associated with fisheries catches, predation or migration. This flow is of particular interest for the aim of this thesis, since it represents the fraction of fish-related carbon being available to carbon sequestration processes, meaning the medium- to long-term retention of carbon. It is hence of importance against the background of climate change, since sequestered carbon is refrained from being released back into the atmosphere in the form of CO₂.

Lastly, the amount of carbon respired and released by the fish as CO₂ was modelled. While this flow does not contribute to the detritus compartment and thereby to the potentially sequestered

carbon, it still is an important parameter in the carbon balance of the investigated fish stocks. CO₂ further provides the basis for primary production and thereby completes the cycling of carbon within the food web.

2.4.4 Data Generation Using Monte Carlo Simulations

Since a biological system displays a high level of stochasticity, trying to forecast its state over a period of several decades based on a limited set of biological parameters creates a level of uncertainty in the resulting output. Therefore, EwE provides the option to run Monte Carlo simulations, making it possible to define non-parametric confidence intervals based on varying levels of input data uncertainty. The latter were set for the biomass, consumption/biomass ratio and production/biomass ratio prior to running the model, according to the coefficients of variation (CV) cited in the supplementary material of Scotti et al. (2022). Monte Carlo simulations are used whenever the object of investigation is analytically intractable, meaning that using experimental approaches to solve it would be either impractical or even impossible (Harrison, 2010). Essentially, what the method does is to introduce an element of randomness and use it to solve problems probabilistically, which in principle are deterministic, meaning non-random. Without such computational algorithms, investigating systems as complex as marine food webs would not be feasible.

For the purpose of this thesis, 100 Monte Carlo simulations were performed per scenario and year in the effort to obtain statistical certainty in the generated data while still maintaining the running of the model at a computationally feasible level. The model output data were generated using the EwE plugin "Ecopath model from Ecosim", which saves one new file of the format .ewemdb per Monte Carlo simulation.

2.4.5 Data Extraction

EwE output files are specially-formatted Microsoft Access database files that can not be easily read by R or any other commonly used data processing software tool. To avoid manually copying the required data from the 75,600 model output files, a custom Python script was used. The underlying code, which made accessing the files possible, was provided by Tushith Islam of the Center for Policy Exploration, Analysis and Simulation. The code was modified and built upon, so that all .ewemdb files of the selected scenario and years can be automatically accessed one after the other, and data on the required variables (biomass, egestion, other mortality, flow to detritus, respiration) are extracted and saved to one .csv file each.

Except for biomass, these data were not directly accessible but had to be calculated in the process of extraction with the help of the exact equations and parameters used by the software program. The reliability of these post hoc calculations was verified by comparing the results against the data set covering the years 1994-2019, which was generated for the model validation

step. The script used for the data extraction can be found on the GitHub repository¹.

2.4.6 Data Cleaning & Processing

To analyse the model output data, some pre-processing steps were executed exclusively using R. For adult cod (> 35 cm), the model's calculation of respiration was flawed, since the majority of values were negative, the reason for which is discussed later on. This issue was corrected by multiplying the simulated stock size by the mean R/B ratio for adult cod. This ratio was calculated with the ICES SSB data and respiration rates used for model validation for the years 1994-2019:

$$\overline{R/B} \left(\frac{1}{yr} \right) = \frac{\sum_{year=1994}^{2019} \left(\sum_{age=3}^7 \frac{SSB_{age_year} \left(\frac{gC}{age} \right)}{R_{age_year} \left(\frac{gC}{age\ yr} \right)} \right)}{\quad} \quad (17)$$

Only the age classes 3 to 7 were included, since these were considered to be equivalent to the definition of adult cod used in the model (individuals of body length > 35 cm). Using the average weight per age class (ICES, 2022a) and the length-weight calculation tool for Atlantic cod (FishBase), the weight threshold was identified to lie between age group 2 and 3. For further analysis, juvenile and adult cod were grouped and the respective values summed for all modelled parameters.

¹<https://github.com/smorsbach/carbonfish>

3 Results

The results of the model validation form the basis for the interpretation of the core findings, namely the quantification of fisheries-induced changes in carbon ecosystem fluxes, and are therefore shown first. The subsequent sections thereby build upon each other and are ordered in a way that ensures coherence.

3.1 Model Validation

3.1.1 Egestion

The manual reconstruction of the yearly amount of egested carbon produced values strongly correlated with the output computed by the EwE model of the WBS for all three trophic groups (Figure 6). For cod and herring, the manual approach emulates the downward trend generated by the model, which coincides with the documented decline in stock numbers and biomass in the past decades as an underlying variable for egestion. For flatfish, both approaches result in an upward trend, most noticeable in the model output since 2009. Nevertheless, the corresponding Pearson correlation was weakest amongst the three ($\rho = 0.818$, $p < 0.001$).

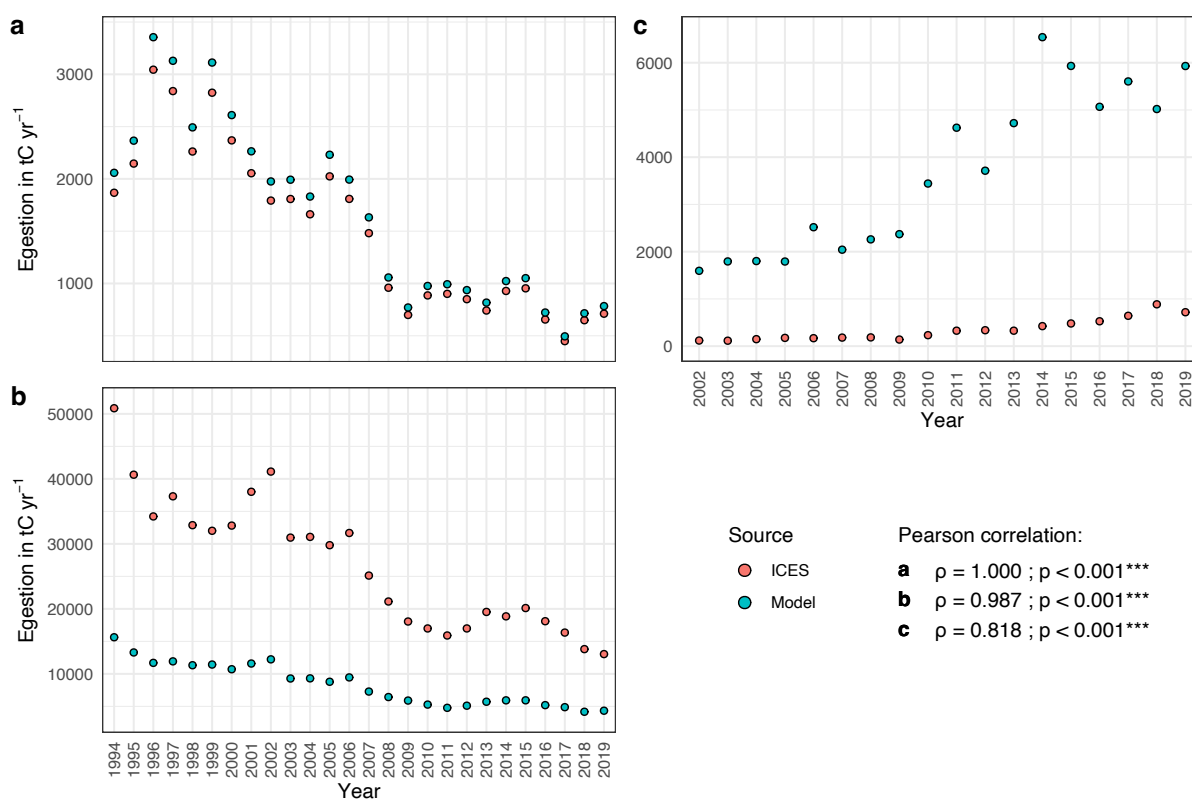


Fig. 6: Validation of modelled egestion flows. Amount of yearly egested total carbon by **a**) cod (*Gadus morhua*) and **b**) herring (*Clupea harengus*) in tC yr^{-1} for the years 1994 to 2019, as well as by **c**) flatfish (brill (*Scophthalmus rhombus*), common dab (*Limanda limanda*), European flounder (*Platichthys flesus*), European plaice (*Pleuronectes platessa*) and turbot (*Scophthalmus maximus*) for the years 2002 to 2019. Simulated trends were obtained from the western Baltic Sea EwE model and manual calculations were based on historical ICES stock biomass time series and physiological literature data; Pearson correlation coefficients (ρ) and the respective p-values are visualized.

With regard to the order of magnitude, cod stands out against herring and flatfish as for the first, the modelled and ICES-derived values show a strong correlation ($\rho = 1.000$, $p < 0.001$) and are congruent for the entire time series. While overall relative changes for herring over the years are nearly identical when comparing model and manual calculations, the model values are lower, on average by a factor of ~ 3.2 . In the case of flatfish, the opposite can be seen, with the manually-calculated values falling in a lower range than those computed by the model. It is however important to keep in mind that the manual validation only focused on the European plaice while the model groups five different species into one large flatfish group.

3.1.2 Respiration

The two approaches to calculating the amount of respired carbon in SD 22 and 24 showed good Pearson correlations for both cod and herring (Figure 7). In both cases, manual and model computations resulted in an overall downward trend since 1994 and produced values falling in the same order of magnitude. However, the absolute deviation between the methods is inconsistent over time, which can for example be seen for herring between the years 1999 to 2011. Overall, model values for cod tend to be higher than those obtained from the manual reconstruction, while the opposite can be seen for herring.

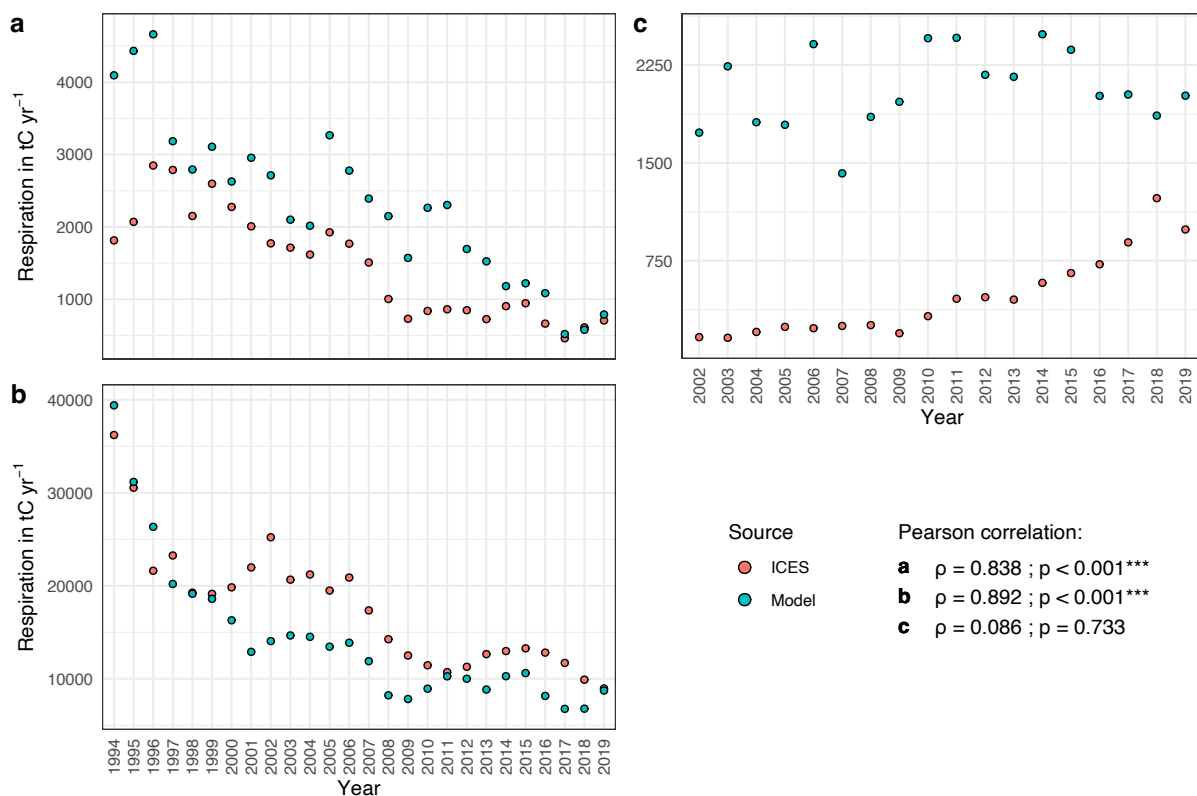


Fig. 7: Validation of modelled respiration flows. Amount of respired total organic carbon in SD 22 and 24 by **a**) cod and **b**) herring for the years 1994 to 2019, as well as by **c**) flatfish in tC yr⁻¹ for the years 2002 to 2019. Simulated trends were obtained from the western Baltic Sea EwE model and manual calculations were based on historical ICES stock biomass time series and physiological literature data; Pearson correlation coefficients (ρ) and the respective p-values are visualized.

The model validation for the flatfish group resulted in uncorrelated values ($\rho = 0.086$, $p = 0.733$). While the manual calculations show a steady upward trend until 2018, the model output underlies pronounced interannual fluctuations without a distinct long-term trend. Furthermore, the manually calculated values fall in a lower range than those computed by the model (note again the different number of included species), especially in the first years. This relative deviation decreases however towards the year 2018.

3.2 Model Results

3.2.1 Biomass

3.2.1.1 Base Scenarios

When looking at the biomass of cod, herring and flatfish, it becomes apparent that the most pronounced changes take place between 2020-2025 and 2050-2060, while the values obtained for the years 2090-2100 resemble those from the previous period (Figure 8).



Fig. 8: Modelled average organic carbon biomass. Charts show biomass values (gC m^{-2}) obtained from 100 Monte Carlo simulations for cod, herring and flatfish under four different management strategies and a reference “No Fishing” scenario for the time periods 2020-2025, 2050-2060, and 2090-2100. Values were calculated as yearly means from 100 Monte Carlo simulations each and averaged per species and scenario for all years in respective period; outliers were not plotted for reasons of clarity and comprehensibility.

Both cod and herring show an increase in stock biomass upon the switch from BAU to any of the other selected management strategies as well as the "No Fishing" reference scenario. This increase can already be seen in 2020-2025, but becomes even more pronounced in 2050-2060, where the divergence between the biomass under EBFM, MSY, 50% MSY and "No Fishing" as compared to BAU reaches its maximum. A continuation of the latter scenario results in the stagnation of the cod stock biomass when compared to the period 2020-2025, while for herring it decreases even further despite an already low starting value of $\sim 0.1 \text{ gC m}^{-2}$. Furthermore, for all fishing scenarios except BAU the relative distances amongst each other are maintained over time, meaning the stock biomass under these four scenarios follows the same progression.

In the case of flatfish, the stock biomass does not show a large variability, neither among fishing scenarios nor over time. Nevertheless, the average biomass decreases by ~ 23 to 25% for EBFM, MSY and 50% MSY and by $\sim 15\%$ in the absence of fishing between 2020-2025 and 2050-2060 (Figure 13), while no noticeable change in biomass can be seen under BAU. Overall, flatfish biomass tends to be highest under BAU followed by the reference "No Fishing" scenario, while the other three management strategies result in even lower biomasses.

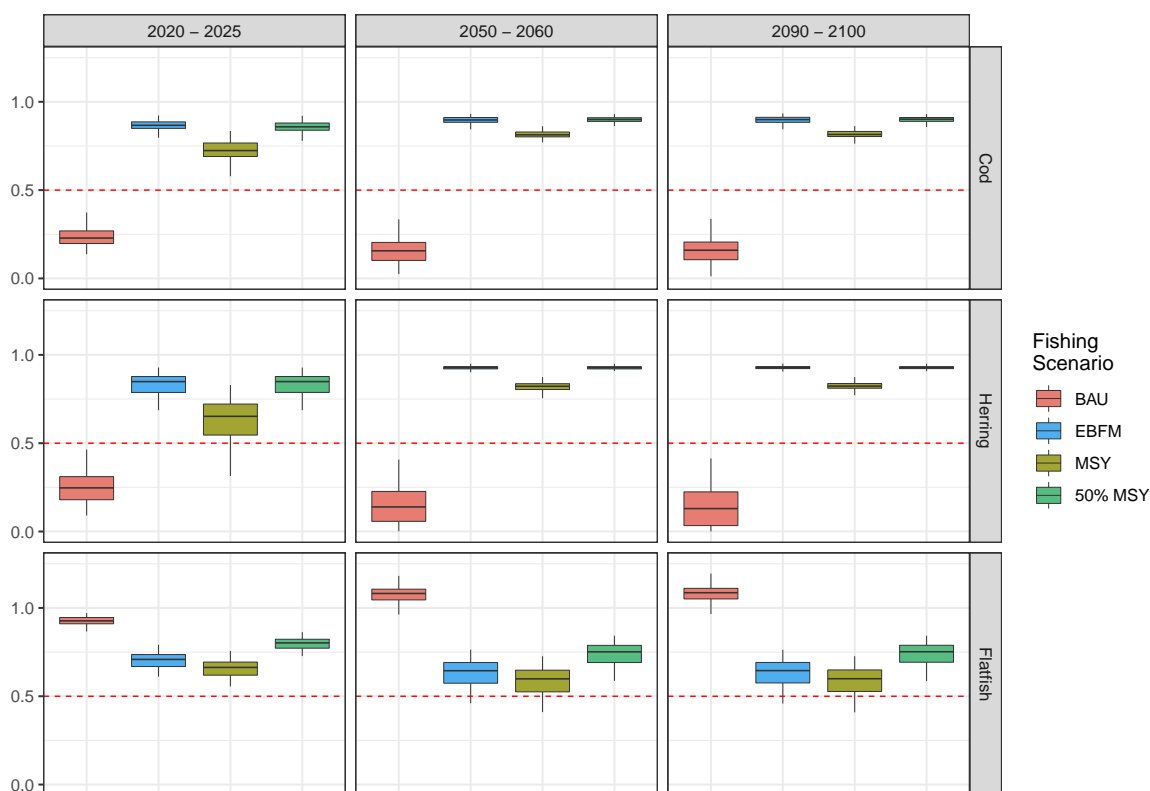


Fig. 9: Status of cod, herring and flatfish stocks under different management strategies. Sustainability was assessed by calculating the ratio between the modelled average carbon biomass (gC m^{-2}) under alternative fisheries management scenarios (BAU, EBFM, MSY, and 50% MSY) and the average carbon biomass with "No Fishing". For all scenarios, biomass values were obtained from 100 Monte Carlo simulations for the time periods 2020-2025, 2050-2060 and 2090-2100. The dotted red line at $y = 0.5$ indicates the threshold ratio above which stocks are considered to be sustainably fished; outliers were not plotted for reasons of clarity and comprehensibility.

To further investigate whether or not the three selected fish stocks are sustainably managed, the ratio between the biomass under a selected fishing strategy and the biomass resulting from the absence of fishing can be used as a proxy (Figure 9). Sustainable fisheries are defined as a ratio ≥ 0.5 . This ratio was set according to the following principle: In the absence of fishing, stocks can grow until they reach the maximum carrying capacity. This threshold is defined by various factors, for example a limited availability of food or spawning sites (Beveridge et al., 2013). At half the maximum carrying capacity, which is equal to B_{MSY} , reproduction reaches its maximum rate and stocks exhibit a surplus in produced offspring which can then be harvested (Maunder, 2008).

For cod and herring, a continuation of the current fisheries management (BAU) corresponds to an unsustainable exploitation of the two stocks in all of the investigated time periods. The remaining three strategies result in ratios >0.5 and are thereby classified as sustainable fisheries. The only exception here is the MSY strategy for herring in the years 2020-2025, when some of the 100 Monte Carlo simulations resulted in ratios <0.5 . However, the first three quartiles of the boxplot still fall above the threshold, meaning that the majority of simulations resulted in MSY being classified as "sustainable".

When looking at the flatfish, the majority of simulations across all strategies resulted in ratios exceeding the threshold. In all three time periods, BAU reaches the highest ratios, even surpassing 1.0 in 2050-2060 and 2090-2100. Only in the case of EBFM and MSY in the mid- and long-term simulation periods, a number of Monte Carlo runs generated ratios below the threshold. In both cases however, the three upper quartiles remain >0.5 .

3.2.1.2 Multi-Stressor Scenarios

To account for potential environmental changes apart from fishing pressure, a set of multi-stressor scenarios was run for the years 2050-2060 as a mid-term forecast, including changes in average yearly water temperature and phytoplankton biomass. The resultant biomasses for cod, herring and flatfish under BAU and EBFM can be seen in Figure 10.

In the case of EBFM, stock biomass for both cod and herring slightly decreases with increasing water temperatures while for BAU the temperature increase mainly resulted in a larger scatter of the different Monte Carlo simulations, especially for herring. Here, the temperature increase from ± 0 to $+1$ °C even resulted in an initial stock biomass increase, after which it stagnates with warmer temperatures.

A decline in fish stock biomass can be seen under both BAU and EBFM in presence of decreasing phytoplankton biomass while a 25% increase of phytoplankton biomass did not result in noticeable stock biomass changes but instead increased the data scatter.

The stock biomass of cod and herring changes differently under BAU and EBFM in the multi-

stressor scenarios, which leads to variations in the biomass ratio between the two management strategies. Here, the relative biomass increase under EBFM as compared to BAU is shown in % for each environmental scenario (Figure 10). The relative change has also been plotted separately using normalised percentages for better visualization (Figure 11). These values do not refer to changes in biomass itself but only to the relative difference between the two management scenarios. For both cod and herring, this difference is largest when the current water temperature remains stable and phytoplankton decreases and it shrinks with an increase in phytoplankton. With regards to the impact of water temperature, cod shows an initial decrease between ± 0 °C and +1 °C, which is then followed by a slight increase towards +3 °C (Figure 10a). For herring, a continuous decrease from ± 0 °C to +3 °C can be seen, which is most pronounced between ± 0 °C and +1 °C (Figure 10b).

In the case of flatfish (Figure 10c), both temperature changes and shifts in phytoplankton biomass do not have a noticeable impact on the stock biomass neither under BAU nor EBFM. This response results in a near to consistent ratio between the two management strategies and hence the relative change of stock biomass under EBFM as compared to BAU, which falls between -40% and -46%. This means that, as opposed to cod and herring, the flatfish stock generally decreases under EBFM and benefits from a continuation of the current fisheries management strategy (BAU); environmental fluctuations do not alter the degree of change. Due to the consistent ratios, flatfish was excluded from Figure 11.

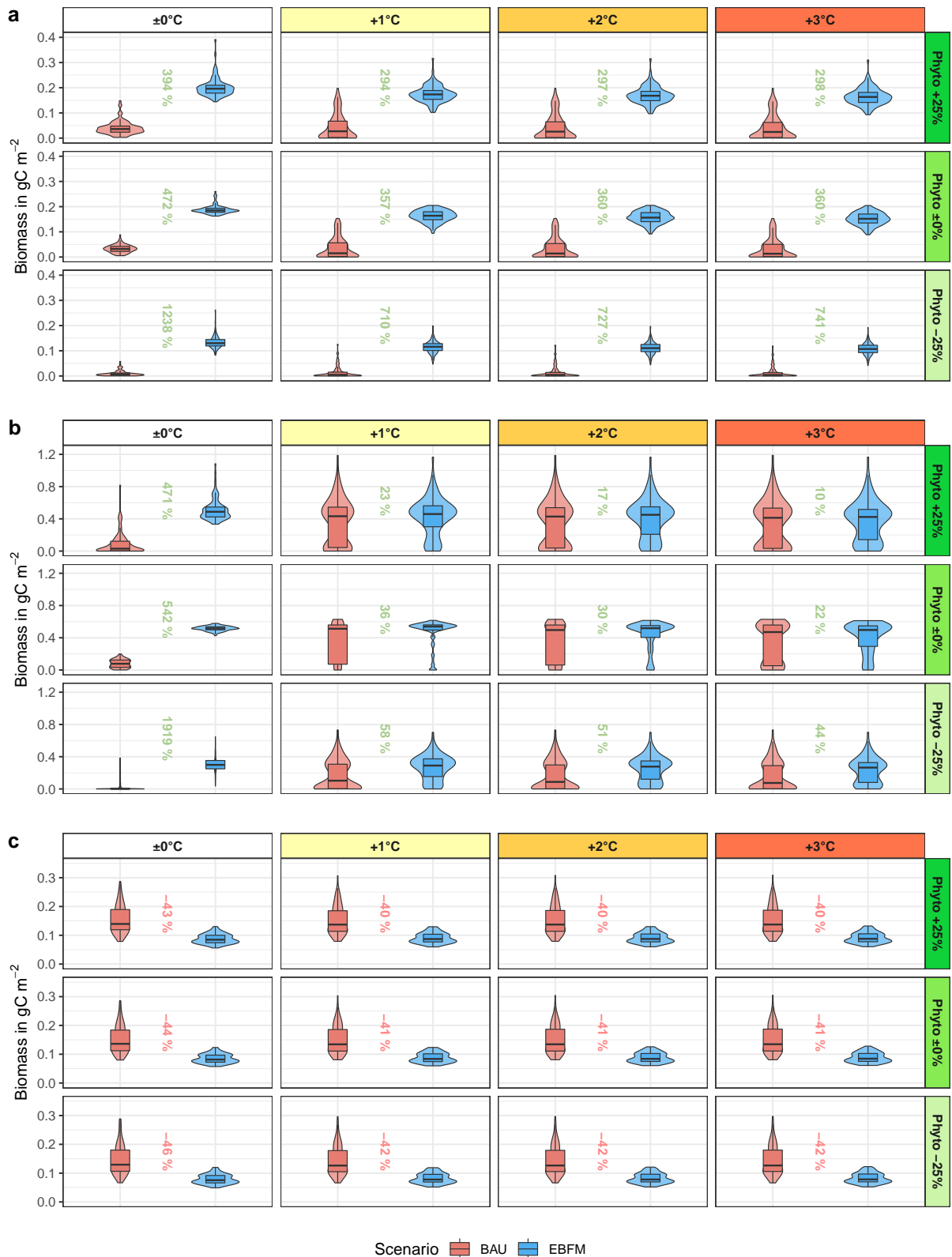


Fig. 10: Modelled average organic carbon biomass in multi-stressor scenarios. Stock biomass (gC m^{-2}) under BAU and EBFM for 12 scenarios incorporating changes in both ocean temperature and primary productivity (phytoplankton biomass). For all scenarios, biomass values were obtained from 100 Monte Carlo simulations for **a**) cod, **b**) herring, and **c**) flatfish in 2050–2060. The percental change in mean biomass under EBFM as compared to BAU is annotated in each plot with red and green, indicating whether the respective species benefits from the implementation of an EBFM strategy or not; outliers were not plotted for reasons of clarity and comprehensibility.

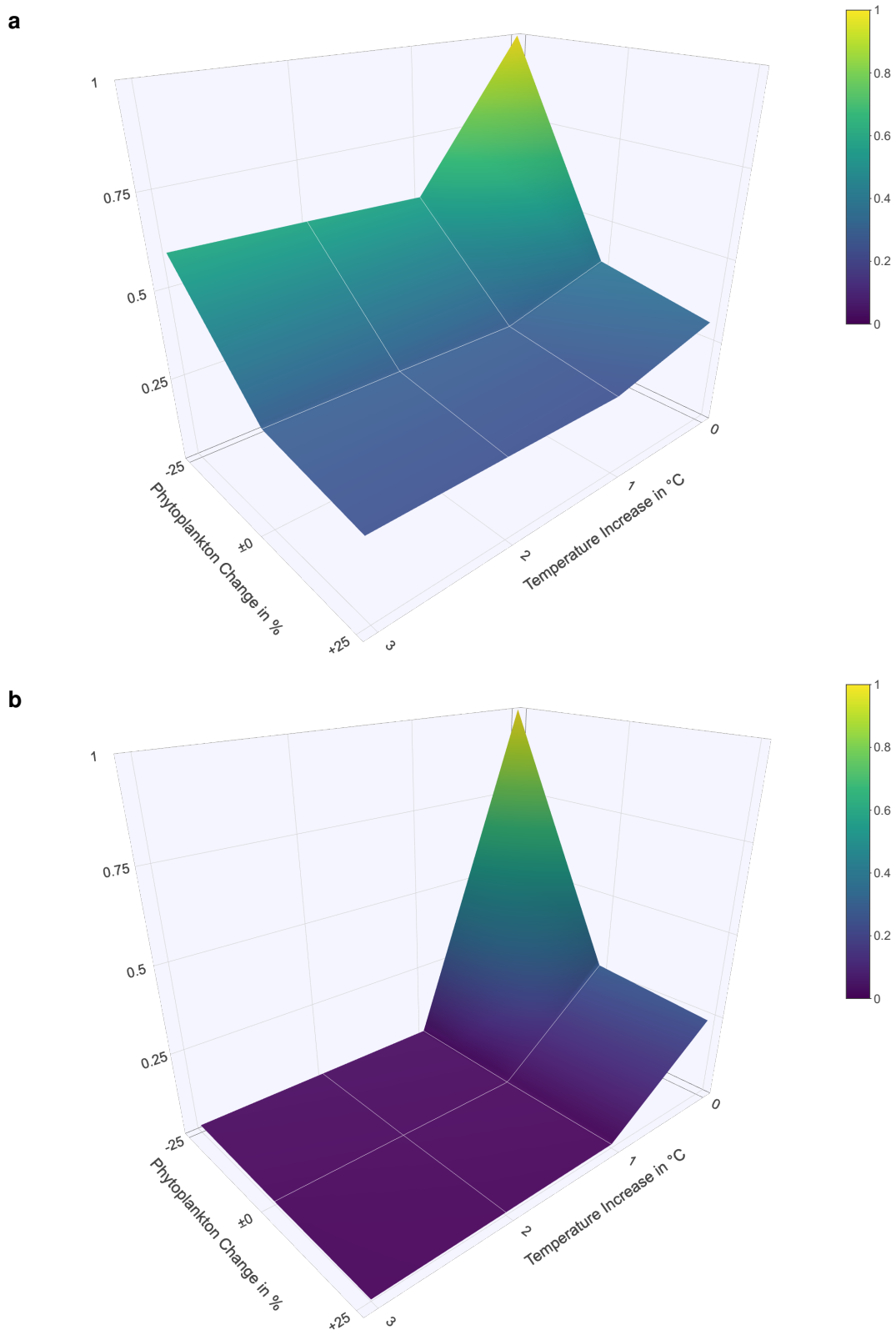


Fig. 11: Climate change mitigation potential. Variations in the average carbon biomass under EBFM as compared to BAU in 2050-2060 for 12 multi-stressor scenarios incorporating ocean warming and changes in primary productivity (phytoplankton biomass). For all scenarios, comparisons were carried out using 100 Monte Carlo simulations for **a)** cod and **b)** herring. Discrete temperature values ranged from ± 0 °C to +3 °C and phytoplankton biomass was increased/decreased by 25% compared to reference values. The magnitude of biomass change has been normalized for comparability, with the maximum value equal to 1 (for absolute % changes see Figure 10a,b).

3.2.2 Flow to Detritus

3.2.2.1 Base Scenarios

To investigate the amount of organic carbon flowing from the three selected fish stocks to the detritus, the years 2050-2060 were chosen as a mid-term forecasting period. Since this flow is directly dependent on biomass as an underlying controlling variable, the patterns do not substantially deviate from those seen in section 3.2.1 (Figure 12). The carbon flow from cod and herring to detritus is substantially higher under EBFM, MSY, 50% MSY and with "No Fishing" as opposed to a continuation of the current fishing strategy (BAU), while for flatfish, all scenarios result in a similar range. The disparity between all three trophic groups is therefore lowest for BAU, while all other fishing scenarios result in a much higher divergence.

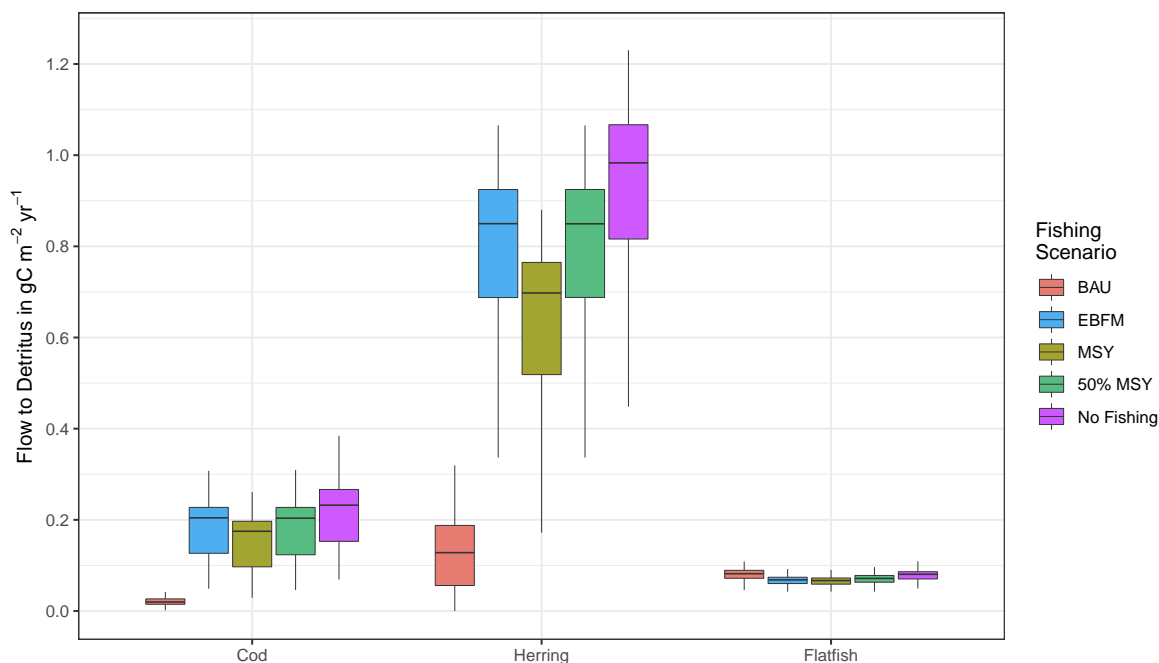


Fig. 12: Modelled average carbon flow to detritus. Magnitude of these flows ($\text{gC m}^{-2} \text{yr}^{-1}$) were obtained from 100 Monte Carlo simulations for cod, herring, and flatfish in 2050-2060, under four different management strategies and a reference "No Fishing" scenario.

Compared to 2020-2025, carbon contribution from cod to detritus increases between 100-150% for all scenarios except BAU. In the case of herring, this increase spans from 60 to 140%. Flatfish show no substantial changes for all fishing scenarios. When summarising all the three stocks, the image resembles that of cod and herring taken individually, with a pronounced increase under EBFM, MSY, 50% MSY and "No Fishing", while BAU results in a further decrease of carbon flowing to the detritus (Figure 13).

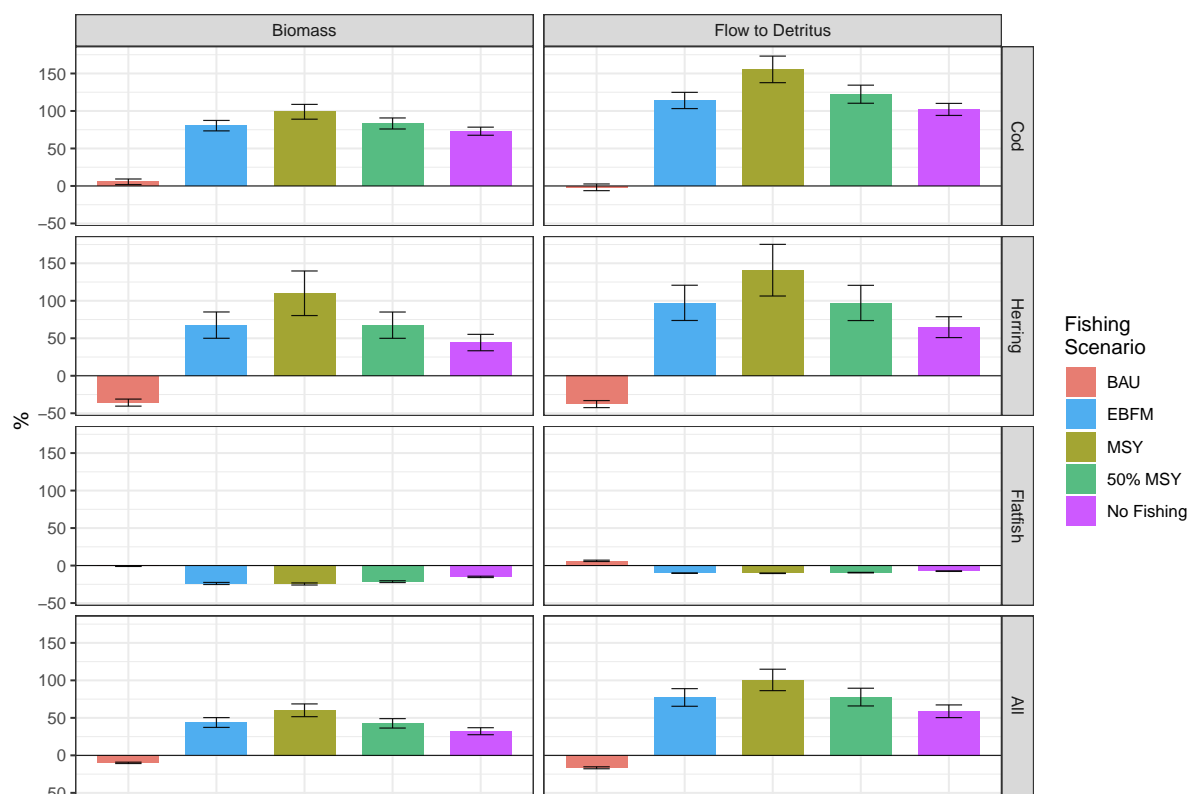


Fig. 13: Modelled percent change of average biomass and flow to detritus. Standing stock biomass (gC m^{-2}) and flow to detritus ($\text{gC m}^{-2} \text{yr}^{-1}$) were obtained from 100 Monte Carlo simulations for cod, herring, and flatfish in 2050-2060 vs. the period 2020-2025. Values were quantified under four different management strategies and the reference scenario with “No Fishing”. Error bars indicate the 95% confidence interval.

3.2.2.2 Multi-Stressor Scenarios

When considering temperature and phytoplankton changes as environmental stressors, the progression of carbon flowing from the three selected stocks to detritus (Figure 14) resembles that of biomass (see Figure 10).

A temperature increase under EBFM had a negative effect on the contribution of carbon to detritus by both cod and herring. The impact of phytoplankton changes was even more pronounced, with decreasing plankton biomass causing a clear decline in carbon fluxes under both BAU and EBFM. Looking at BAU alone, this strategy showed decreasing numbers with rising water temperatures in the case of cod, but first and foremost resulted in a larger data scatter in the case of herring, leading to an initial increase in the amount of carbon flowing to the detritus between ± 0 °C and $+1$ °C.

For flatfish, both an increase in water temperature as well as shifts in phytoplankton biomass did not have a noticeable impact on the respective carbon fluxes, neither for BAU nor for EBFM. This condition resulted in a consistent ratio between the strategies and hence the relative decrease from BAU to EBFM of 16-20% in the amount of carbon flowing from the flatfish stocks to detritus.

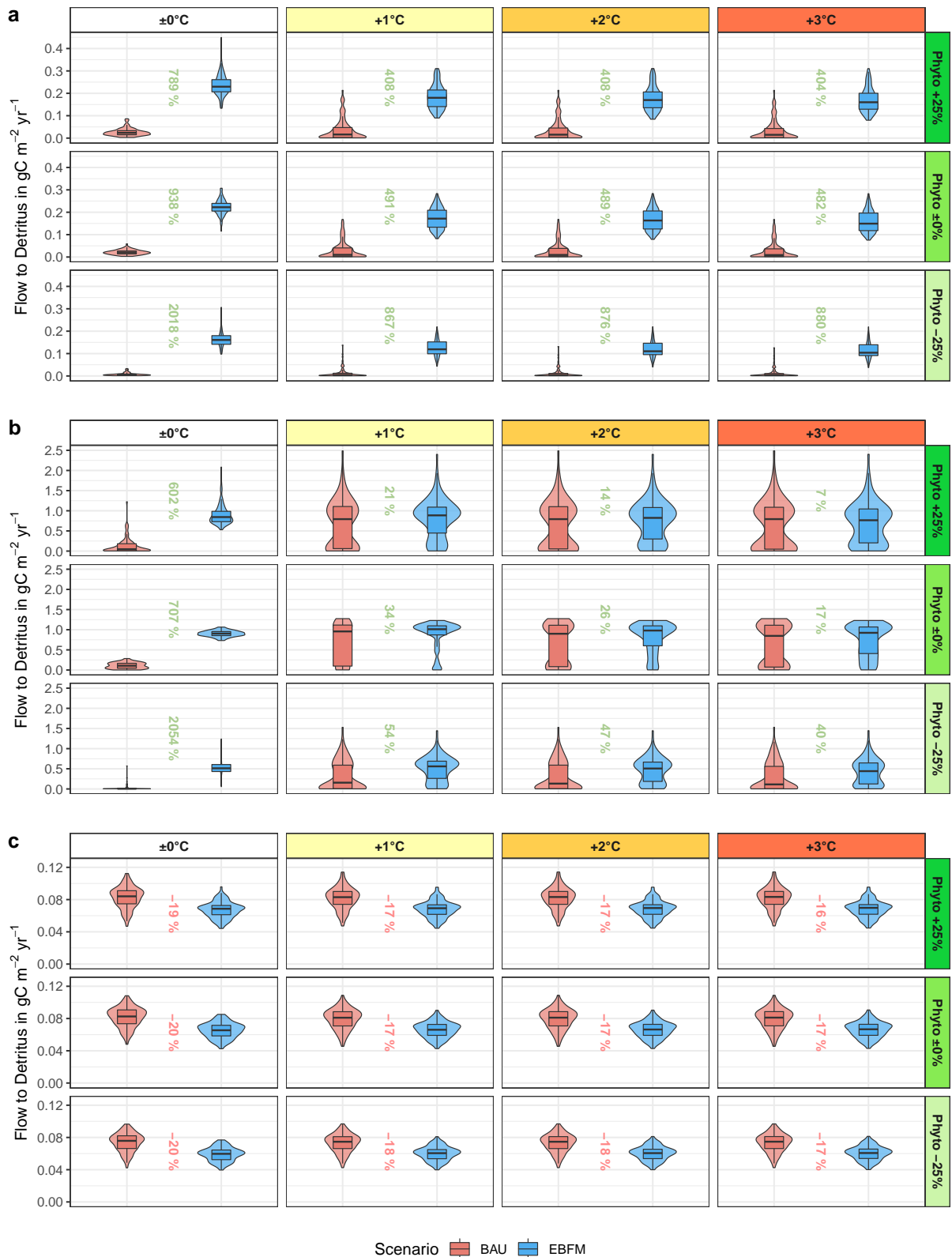


Fig. 14: Modelled average flow of organic carbon to detritus in multi-stressor scenarios. Carbon flows ($\text{gC m}^{-2} \text{yr}^{-1}$) under BAU and EBFM for 12 scenarios incorporating changes in both ocean temperature and primary productivity (phytoplankton biomass). Flows were quantified using 100 Monte Carlo simulations for **a**) cod, **b**) herring, and **c**) flatfish in 2050-2060. The percent change in mean flow magnitude under EBFM as compared to BAU is annotated in each plot with red and green, indicating whether the respective trophic groups benefit from the implementation of an EBFM strategy or not; outliers were not plotted for reasons of clarity and comprehensibility.

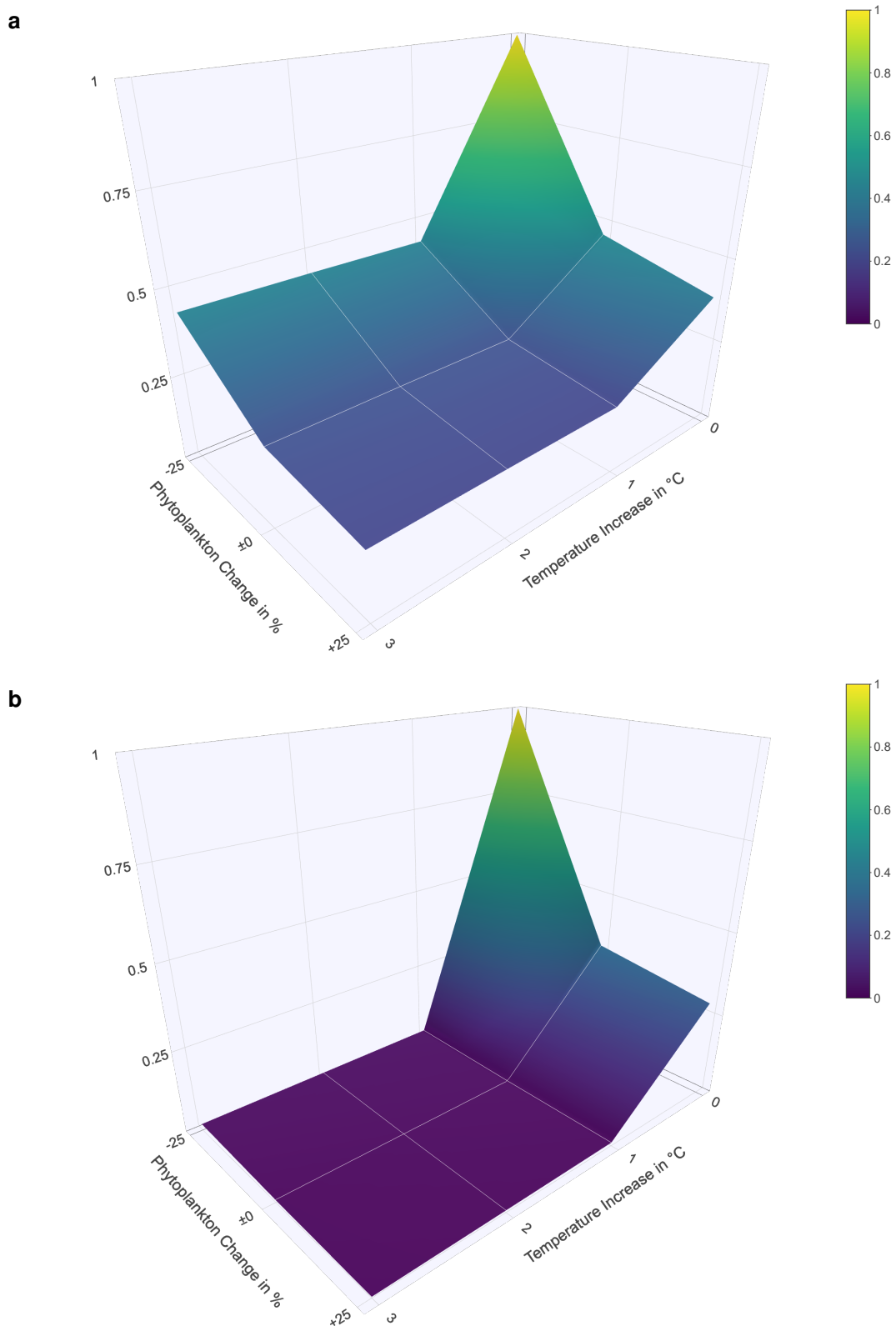


Fig. 15: Climate change mitigation potential. Variations in the average flow of carbon to detritus under EBFM as compared to BAU in 2050-2060 for 12 multi-stressor scenarios incorporating ocean warming and changes in primary productivity (phytoplankton biomass). Carbon flows were obtained from 100 Monte Carlo simulations for **a)** cod and **b)** herring, taking into account discrete steps of temperature increase, from ± 0 °C to +3 °C, and an increase/decrease of phytoplankton biomass of +25%. The magnitude of carbon flow change has been normalized for comparability, with the maximum value being equal to 1 (for absolute changes in % see Figure 14a, b).

3.2.3 Respiration

Like egestion, the process of respiration is closely coupled to the underlying stock biomass. Therefore, the patterns found for the midterm 2050-2060 resemble those already seen for biomass and carbon flow to detritus (Figure 16).

The amount of respired carbon for both cod and herring is higher under EBFM, MSY, 50% MSY and in the absence of fishing as opposed to a continuation of the current management strategy (BAU). For flatfish, however, all four strategies and the "No Fishing" scenario result in similar amounts, which are always $< 0.1 \text{ gC m}^{-2} \text{ yr}^{-1}$. In the case of flatfish, respiration attains the lowest values compared to cod and herring for all fisheries management strategies but BAU.

The 100 Monte Carlo simulations generated a comparatively scattered output for herring, with data points between Q_1 and Q_3 (50% of the data) for EBFM, MSY, 50% MSY and "No Fishing" spanning a range of $\sim 0.35 \text{ gC m}^{-2} \text{ yr}^{-1}$. Boxplots of all scenarios remain instead rather narrow for cod and flatfish with all data points (excluding outliers) falling in a similar range.

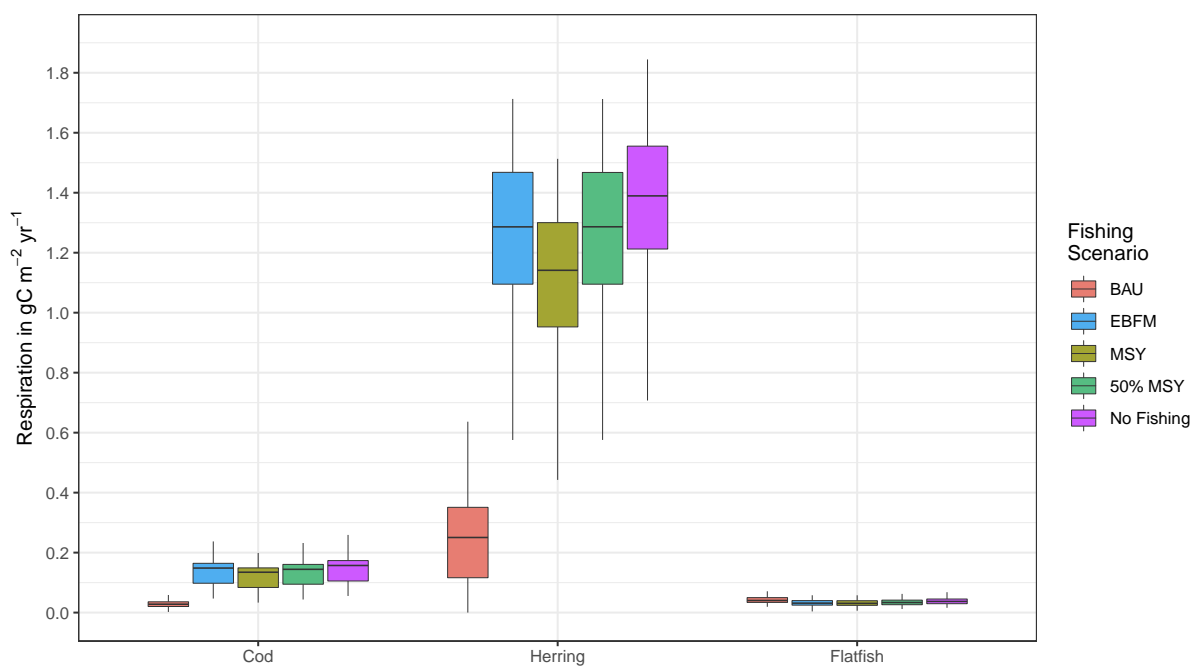


Fig. 16: Modelled respired organic carbon. The magnitude of respiration ($\text{gC m}^{-2} \text{ yr}^{-1}$) was obtained from 100 Monte Carlo simulations for cod, herring, and flatfish during the period 2050-2060, under four different management strategies and a reference "No Fishing" scenario.

4 Discussion

4.1 Model Accuracy Regarding Physiological Processes

4.1.1 Egestion

Reconstructing the amounts of organic carbon egested by cod, herring and flatfish stocks in the western Baltic Sea resulted in a good match between simulated values and ICES-derived calculations. Despite the manual calculation being much more refined, both approaches generated well-correlated outputs, indicating that the ratios used in the model were sufficient to realistically depict carbon egestion fluxes.

In the case of cod, both the degree of correlation ($\rho = 1.000$, $p < 0.001$) as well as the similarity between absolute values obtained from the model and manual calculations for all years between 1994 and 2019, evidently verify the model's accuracy with regards to the species' egestion. The same goes to say for herring where the correlation coefficient was high ($\rho = 0.987$) and significant ($p < 0.001$). Nevertheless, while the two approaches generated quantities in the same order of magnitude, the model slightly underestimates the amount of carbon egested by the western Baltic spring-spawning (WBSS) herring stock. This should be taken into consideration when interpreting the model's future forecasts, for which no real data yet exists to compare the results against. Based on the manual validation, it can however be concluded that the WBS model follows a rather conservative approach with regards to herring egestion, since the values of the model are lower than those calculated from ICES data.

Contrary to cod and herring, egestion flows estimated by the model and calculated from ICES data were not congruent for flatfish. While the model groups five different species, only the European plaice was used for the manual validation step due to insufficient ICES data on the other species. However, plaice can be assumed to be the most important flatfish species in the study region, both numerically and economically (Rau et al., 2019; ICES, 2022h,i), and the results can still give a hint on the consistency between the two time series. Considering the exclusion of four species from the manual calculations, it is not surprising that the latter resulted in smaller quantities. The fact that the two approaches still resulted in a pronounced correlation provides confidence in the model's capability to accurately model the process of carbon egestion in flatfish, despite the remaining data gap.

4.1.2 Respiration

Despite the Pearson correlation coefficients being lower for the respiration of cod and herring than for egestion, they still indicate a strong correlation, especially for herring. Even though intermediate small-scale fluctuations vary between the two approaches, the overarching trend of a decreasing stock respiration can be seen in both curves and the highly significant Pearson correlation coefficients provide robust evidence, that the respiration computed by the WBS model

coincides with the respective physiology of both species.

Contrary to cod and herring, a deviation between modelled and manually-generated outputs was found in the case of flatfish. As mentioned in section 4.1.1, the number of species differed between the two approaches. Nevertheless, the example of egestion provided evidence that the comparison still is robust, since plaice, in numerical terms, serves as an adequate representative for the flatfish. The non-existent correlation between the model and the manual output ($\rho = 0.086$, $p = 0.733$) is instead striking. The manual calculations result in a steady and relatively smooth increase in the amount of respired carbon, which is in alignment with the observed stock development of plaice (ICES, 2022h,i), but also that of other numerically abundant flatfish species such as flounder (ICES, 2022d,e) in the ICES subdivisions 22 and 24. The model output, on the other hand, depicts pronounced interannual fluctuations and no detectable long-term increase or decrease. Since in theory, the amount of respired carbon in a fish stock should be directly driven by the underlying biomass as a physiological determinant, it was tested whether the respiration flux computed by the model correlates with the stock biomass. To obtain a broader picture, this correlation analysis was extended to a cross-comparison conducted for all trophic groups, further including the SSB and the amount of respired carbon from manual calculations (Table 3).

Table 3: Pearson correlation coefficients (ρ) between the amount of respired carbon (R) and the stock biomass. Fully factorial comparison was carried out using both data obtained from the WBS model and manual estimates. This latter term refers to the manual calculation of respiration based on independent physiological coefficients and ICES stock data. The comparison is shown for all three trophic groups.

	Cod		Herring		Flatfish	
	SSB _{ICES}	SSB _{Model}	SSB _{ICES}	TSB _{Model}	SSB _{ICES}	TSB _{Model}
R_{ICES}	0.995 p < 0.001***	0.965 p < 0.001***	1.000 p < 0.001***	0.954 p < 0.001***	1.000 p < 0.001***	0.815 p < 0.001***
R_{Model}	0.839 p < 0.001	0.794 p < 0.001***	0.893 p < 0.001***	0.869 p < 0.001***	0.087 p = 0.731	0.477 p = 0.046*

Manually-calculated amounts of respired carbon (R_{ICES}) show a better correlation with the stock biomass derived from both the model and the ICES stock data for all three trophic groups. Correlations with the manually calculated stock biomasses always outperform those with model-derived biomasses (SSB_{Model}/TSB_{Model}). Nevertheless, the correlation with the latter is still strong for all groups. However, when looking at the respiration derived from the model (R_{Model}) and how it correlates with the biomass from both approaches, substantial differences become clear. While in the cases of cod and herring, respiration still displays a good correlation with the modelled and manually-derived biomasses, even though less pronounced than for R_{ICES} , it is weak to non-existent for flatfish. Here, the stock biomass from both approaches does not ex-

plain the strong fluctuations found for the modelled respiration (Figure 7). Even using the total stock biomass and the respiration estimated by the model only a Pearson coefficient of 0.477 ($p = 0.046$) was obtained.

The explanation for this weak correlation could potentially be rooted in the way Ecopath with Ecosim computes respiration. EwE assumes in fact mass balance (Christensen & Walters, 2004), meaning that all of the carbon entering a compartment is reallocated in accordance with the consumption equation (Eqn. 2) and no carbon is lost. Respiration, contrary to egestion, is not calculated by applying a defined ratio to the underlying biomass. Instead, the software program determines the amount of respired carbon by using all residual model currency that could otherwise not be assigned to any of the other groups or flows in the system, and which is needed to obtain mass balance. Respiration is thereby not coupled to any physiological parameter but calculated after a long chain of preceding computations, each with the risk of slight inaccuracies. The unexplained fluctuations in the case of flatfish and the consequently poor correlation with the underlying stock biomass are hence most probably a product of the strict standards adopted by EwE regarding the mass balance constraint.

As a consequence, there is no certainty that respiration fluxes in the WBS model coincide with the physiology of the respective species. While it still turned out into physiologically reasonable values for cod and herring, the remaining risk related to the computation mechanisms adopted to quantify respiration is the reason why trends displayed by this variable are not the main focus of this thesis. From a modelling perspective, egestion is anyway the more impactful and thereby important flow since in the WBS model, the respired carbon is not reused. The ecological role of respired CO₂ in fuelling primary production is hence not considered by the model but should nevertheless be kept in mind in the further discussion.

4.2 Stock Biomass Under Different Management Scenarios

Modelling a continuation of the way western Baltic fish stocks are currently managed clearly resulted in a stagnation or an even further decrease of cod, herring and flatfish stocks. Nowadays, cod and herring are already far below the sustainable biomass threshold (ICES, 2022b,g), so maintaining the too high fishing pressure equals an ongoing unsustainable management of both stocks. This is supported by the ratio between stock biomass under BAU against the biomass attained in the absence of fisheries; such ratios clearly fall below the threshold of 0.5 for both cod and herring in all three modelled time periods (Figure 9). Both in an ecological but also economical interest, maintaining the status quo can therefore not be the option in favour. A temporary closure of fisheries like in the case of herring (ICES, 2022c) is evidence of a rethinking in fisheries management, however, far-sighted management strategies are needed to ensure the viability of the stocks in the decades to come.

From an ecological viewpoint, the aim has to be the implementation of a more considerate strategy. One example could be the EBFM, which not only incorporates fisheries biology knowledge but also ecological criteria and thereby constitutes a multi-faceted approach to fisheries management. The latter aspect separates EBFM from the MSY strategy, which aims at avoiding the overexploitation of the stocks but treats each species as a separate entity with less consideration for any interdependencies throughout the food web. The biomass achieved under EBFM is therefore generally higher than under MSY for all three trophic groups (Figure 8). Nevertheless, compared to BAU, all modelled scenarios can be considered an improvement since the stock biomasses of both cod and herring experience a substantial increase as a consequence of a more sustainable management (Figure 9). Looking at flatfish, one could come to a different conclusion since the stock biomass here is highest under BAU. However, there are a number of points to take into consideration. Firstly, the flatfish stocks inhabiting the western Baltic Sea are currently in an ecologically reasonable state (ICES, 2022d,e,h,i), hence there is not the same need of recovery as for cod and herring. Secondly, a continuation of the present fishing pressure does not result in any considerable increase in flatfish biomass, which instead solely attains a stable level (Figure 13). Thirdly, implementing an EBFM or (50%) MSY strategy most likely still equals a sustainable management of flatfish (Figure 9) and finally, all strategies except BAU show an overall increase of fish biomass across all three trophic groups (Figure 13).

The importance of fisheries management in driving the stock biomass of the three investigated trophic groups exhibit some variability. For cod and herring, the switch from BAU to any of the other management strategies has a tremendous impact. The implementation of EBFM as opposed to BAU in 2050-2060 leads to an increase in average stock biomass of ~470 and ~540% for cod and herring, respectively (Figure 10). In the case of flatfish, this relative change between BAU and EBFM (-44%) is in a different order of magnitude than for cod and herring, and the percentage decline is even much lower when considering the other management strategies. It can therefore be hypothesised that the current state of the stocks is strongly regulated by the fisheries management strategy implemented for cod and herring, and to a much lesser degree for flatfish. For the latter, it can only be speculated what stock biomass is mainly driven or limited by. One theory could be a top-down control or the competition for food and habitat. However, flatfish is both partly preyed upon by and competes with cod for benthic habitat and prey (Figure 4), hence a decrease in cod should be in favour of flatfish. This would be coherent with the observed stabilization of the flatfish stock, even though a substantial increase remains absent.

4.3 How Fisheries Management Impacts Ecosystem Carbon Fluxes

Considering that the amount of egested carbon and sinking fish carcasses is closely tied to the size of the stock, it does not come as a surprise that the trends observed for the flow of carbon to the detritus mimic those of the stock biomass. The same goes to say for respiration, even though

the model validation indicated a potentially arbitrary computation of the respiration fluxes by the EwE software tool. However, calculating the egestion/biomass and the respiration/biomass ratio for all 100 Monte Carlo simulations revealed very stable and physiologically reasonable values for cod and herring, and to a lesser degree also for flatfish (Table 4) so that the model output can be seen as reliable.

Due to different underlying stock biomasses, the absolute changes varied widely across the three trophic groups. Nevertheless, it is obvious that a switch from BAU to one of the three other management strategies goes hand in hand with tremendous changes in the amount of fish-related carbon being contributed to the detritus, which shows trends coherent with those of the stock biomass. Interestingly, the percental change for all three trophic groups combined is much more pronounced than for biomass, despite the WBS model ap-

Table 4: Standard deviations of the egestion/biomass and respiration/biomass ratios for cod, herring and flatfish.

	E/B	R/B
Cod	0.011	0.055
Herring	0.016	0.031
Flatfish	0.046	0.081

plying a more or less fixed ratio to derive egestion from biomass. This deviation occurs because the flow to detritus further includes sinking fish carcasses. EBFM, (50%) MSY and a fisheries closure imply a decrease in fishing mortality as a consequence of a lower fishing pressure. Under high fishing pressure, dying of age is less likely, since the probability to be caught by fishing gears increases with body size. Hence, more fish can fully mature when F is lower, increasing the number of fish that die of age and subsequently sink to the bottom.

The substantial increase in detrital carbon flux highlights the incentive of a management strategy revision beyond an overall growth of the stock biomasses. Simulations for the years 2050-2060 revealed that the implementation of an EBFM or 50% MSY strategy would result in a carbon surplus of ca. $42,000 \pm 850$ tonnes of organic carbon being contributed to the detritus annually in SD 22 and 24 by the three trophic groups combined; the ± 850 tonnes constitute the 95% confidence interval.

A continuation of the current fisheries scenario would withhold a tremendous amount of carbon from being available to processes related to its sequestration, which is highly dependent on both depth and location (DeVries et al., 2012). Altogether, only a very small fraction of the carbon exported below the thermocline ends up being sequestered (Saba et al., 2021). Quantifying exact sequestration rates in the western Baltic Sea is therefore far beyond the scope of this thesis and could be subject to future studies. Nevertheless, it is safe to say that fisheries disrupt carbon ecosystem fluxes in the first place and, by reducing carbon fluxes of cod and herring to detritus, most likely also cause a decline in sequestered carbon. One could argue that a decline in fish-related carbon fluxes to the detritus could conversely increase the contribution of prey species to the latter as a result of reduced predation pressure. However, fish faecal pellets have been estimated to have much faster sinking rates than that of other groups such as zooplankton,

making fish potentially more efficient exporters of organic carbon (Saba & Steinberg, 2012). In the case of a pelagic species as herring, a reallocation of detrital carbon flux to the zooplankton would therefore most likely not yield an equally high carbon export.

Changes in stock biomass directly alter the biological carbon pump but the CO₂ emitted with respiration also acts as fuel for phytoplankton and bacteria (Saba et al., 2021), two important components involved in the pumping mechanism. A decline in stock biomass and subsequently the amount of respired CO₂ thereby weakens the link between fish and phytoplankton (Figure 1). Apart from an increase in biomass and carbon export, rebuilding stocks through the implementation of alternative management strategies thereby comes with a third incentive. An increase in respiration amplifies phytoplankton productivity that, in turn, positively impacts fish stocks through the bottom-up effect exerted on zooplankton biomass (Figure 4).

4.4 Implications of Environmental Changes

Knowing the impact of fisheries management on the status of the stocks is of great importance. However, changes in the environmental conditions further complicate the picture beyond the reach of fisheries management authorities. An increase in water temperature and fluctuations in bioproductivity both had an effect on stock biomass and subsequently the detrital flux of organic carbon, at least for cod and herring. Those effects were mostly detrimental, causing a decline in both parameters. Only an increase in bioproductivity generated a slight increase in the case of BAU. More importantly, the introduction of environmental changes into the model increased data uncertainty for both cod and herring with the latter showing the most pronounced data scatter, obscuring the forecast capability of the WBS model. The inclusion of multi-stressors further heavily impacted the relative difference between BAU and EBFM. In general, the fact that the performance of different fisheries strategies is susceptible to changes in the environmental conditions has crucial implications for management authorities beyond the field of fisheries. It implies that other players might have to be involved to tackle issues like eutrophication or ocean warming and thereby mitigate the uncertainty increase in planning future fisheries management strategies.

These findings demonstrate that, despite fisheries playing an essential role in driving stock biomass, there are further factors in play outside the influential sphere of fisheries management authorities. It is important to delineate between absolute variations and changes in the relative difference between BAU and EBFM, which can act partly independently of each other. The relative difference does not serve as an ecological indicator to assess whether or not a certain scenario is beneficial or detrimental for the study system and should not be confused as such. One example for that is the impact of a 25% phytoplankton increase on cod and herring. While it has a neutral or even slightly beneficial effect on the stock biomass and the detrital flux of the two species under BAU and EBFM, the relative difference between the two scenarios decreases.

Even though the relative difference between the two scenarios does not bear any ecological relevance, it still is of high interest since it quantifies the climate change mitigation potential of EBFM over BAU. While for cod and herring, EBFM consistently outperforms BAU in all environmental scenarios, ocean warming and fluctuations in bioproductivity, in most cases, weaken the benefits conferred by EBFM, which is the case when the normalised ratio is lower than for the base scenario (Figures 11 and 15). This condition has direct implications for the regulatory power of fisheries management. A decline in the relative difference consequently means less management power over the viability of the stocks and could, depending on the future extent of the environmental changes, even lead to a loss of control. The fact that the relative difference in average stock biomass of cod in a +3 °C scenario is more than 100% lower than in the base scenario (Figure 11a) should be alarming, especially considering that EBFM out of all simulated management scenarios (fisheries closure excluded) generates among the highest stock biomass for both cod and herring by concurrently maintaining high catch levels, well beyond those attained under BAU. This decrease is even more pronounced for herring, although the extraordinarily high data scatter potentially distorts the image, making confident conclusions very difficult. It is further important to keep in mind that the starting conditions for these simulations, namely extremely low biomasses for both cod and herring, facilitate the convergence of the values generated under BAU and EBFM.

The results indicate that the fate of western Baltic fish stocks is decided on multiple levels and time scales. Firstly, fisheries have a pronounced impact on the viability of the stocks. They are capable of flexibly adjusting their management strategies to fit the stocks' needs and to facilitate stock recovery, the ramifications of which come into effect on a relatively short time scale. Since the setting of catch quotas is an exclusive EU competence (Reusch et al., 2018) and is reassessed annually, fisheries are able to quickly adapt to changing stock conditions, thereby enabling a direct and immediate effect. Secondly, bioproductivity shows at least some effect on the stocks, which is the logical consequence of the architecture of trophic interactions in the food web (Figure 4). Since phytoplankton biomass is directly coupled to the amount of available nutrients, it is partly open to anthropogenic influence. Due to its semi-enclosed location, large and densely inhabited drainage area and long water residence time, the Baltic Sea region is susceptible to eutrophication (Snoeijs-Leijonmalm et al., 2017). Transnational efforts exist to reduce the amount of nutrient inputs (Reusch et al., 2018), however, these are taking place on a longer time scale than the setting of quotas and, given the weaker effect, most likely do not have the power to crucially determine the progression of stock size and viability on their own. Nevertheless, it is important to consider that only two distinct scenarios ($\pm 25\%$) were investigated. Temporary and regionally restricted fluctuations could be more pronounced and might have much stronger effects on the stock biomass, and could be subject to further research. The results also propose that a multi-approach fisheries management might be reasonable instead of relying on quotas alone, meaning that eutrophication effects should not be disregarded by future management frameworks. Lastly, ocean warming has an impact on stock biomass and

consequently the detrital carbon flux, causing a decline for cod and increasing data scatter and hence the forecast significance in the case of herring. Since climate change takes place on a global scale, mitigating its extent is restricted to an international level. Reducing the warming of the Baltic Sea can therefore only partly be addressed at a national or European scale by committing to the objectives of international treaties such as the Paris Agreement. The success of these joint efforts, however, is highly dependent on the willingness of all international partners combined, and only brings about an effect in the long term.

The impact of environmental changes on the flatfish group has not been discussed so far. That is because the direct effects of temperature on this species group are not included in the WBS model. The slight changes that can be seen for flatfish instead derive from indirect effects, meaning a reallocation of carbon flows throughout the food web due to changes in phytoplankton biomass or the decline of cod and herring. Therefore, the flatfish rather serve the purpose of a reference group. If little to no change in flatfish and more pronounced changes in cod and herring biomass can be observed, that increases the certainty that the latter originate from the inclusion of ocean warming, since its effects are considered for cod and herring but not for flatfish.

4.5 Does Climate-Friendly Management Mean Less Catches?

Stock recovery implies the reduction of fishing pressure and consequently catch quotas. Although in the short term, this decision may lead to a decline in catches and an economic loss for fisheries targeting the stocks in question, medium- to long-term benefits are evident and will result in higher yields at lower fishing efforts, thus increasing the scope for an economic gain. On a long-term scale (2050-2060), the more sustainable management scenarios (EBFM, (50%) MSY) yield in fact higher catches than a continuation of the current fishing pressure, while at the same time substantially increasing the amount of fish-related carbon contributed to the detritus (Figure 17). Under EBFM and (50%) MSY, data scatter is much lower than in the case of the BAU scenario, indicating that more sustainable management strategies also have the potential to stabilise fisheries catches and thereby the forecast certainty. Moreover, yielding higher landings with less effort most likely corresponds to a reduction in fisheries-related CO₂ emissions due to the linear correlation (Tyedmers, 2001; Ziegler & Hansson, 2003), thereby mitigating the direct impact on the world's climate.

Transforming western Baltic fisheries into a more sustainable industry sector is hence both economically and ecologically advantageous. More sustainable fisheries strategies increase catches and reduce emissions by also promoting stock viability and thereby indirectly the carbon uptake potential of the entire ecosystem. To achieve such a win-win scenario, far-sighted decision-making is needed. Most important is the willingness to accept temporary financial losses, which have to be compensated to be able to politically implement the necessary changes. One example of such compensations being tested in practice is the Baltic Sea Ranger living lab, a work

package of the SpaCeParti project (www.spaceparti.de/en/living-lab/). Otherwise, many of the jobs involved in western Baltic fisheries might be at stake, with long-lasting consequences for the entire economic sector even after a partial recovery of the stocks.

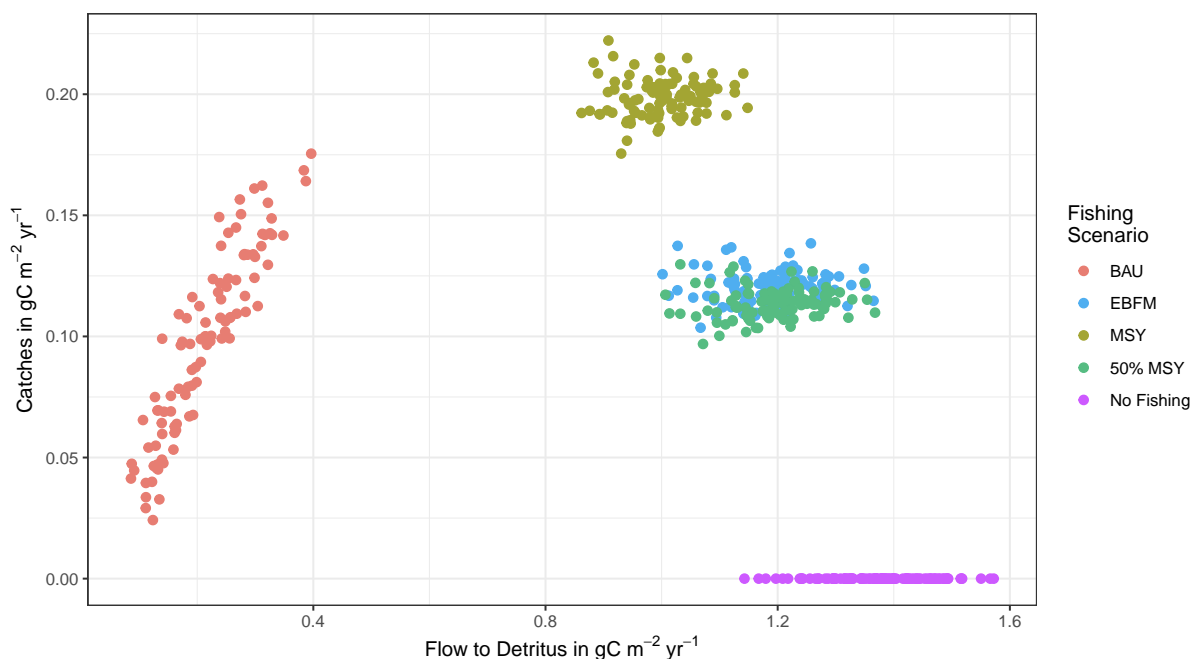


Fig. 17: Catches compared to the detrital carbon flux. The comparison between catch and detrital carbon flows, expressed as $\text{gC m}^{-2} \text{yr}^{-1}$, is visualized for cod, herring, and flatfish combined. Data were obtained from 100 Monte Carlo simulations and refer to the values attained in 2050-2060 under four different management strategies and a reference “No Fishing” scenario.

4.6 Limitations

An ecosystem model is an approximation to the real world and while it is capable to reproduce and forecast the state of an ecosystem, it is limited by the capabilities of the software program. This condition does not imply that model results are inaccurate, however, it remains an artificial construct and conclusions drawn from it should be treated as such. Nevertheless, models are the only established tool to make predictions about the future state of the oceans and provide great service in detecting and preventing problems before they arise.

Some caveats of the WBS model, however, should be considered when assessing the results and are discussed in the following, starting with the spatial and temporal resolution. The model uses yearly averages for an area of more than 42,000 km^2 to compute the biomass of functional groups and the carbon fluxes between them. It thereby neglects seasonal variations as well as potential patchiness and the high mobility of some of the trophic groups, especially those at higher trophic levels (Scotti et al., 2022). Moreover, while the investigated scenarios differ in their fishing pressures, the latter are constant and are not able to adjust and respond to changes in e.g. stock sizes. Thus, any feedback to management is lacking (Chagaris et al., 2015; Scotti et al., 2022), inhibiting the flexibility of fisheries that could otherwise be expected.

One crucial limitation to this study was the computation of some of the carbon fluxes by the EwE software tool. In the case of adult cod (>35 cm), the calculation method of respiration regularly generated negative values, which would have obscured the results. Such an issue might derive from the use of the multi-stanza routine to model juvenile and adult individuals of cod. The application of the average respiration/biomass ratio from the manually calculated model-validation data between 1994 and 2019 corrected these inconsistencies in the respiration flows. However, this solution constitutes a post hoc modification of the model output, which potentially distorts the mass-balance constraint.

In the case of cod, the amount of fish falls, meaning the contribution of dead fish biomass to the detritus, generated extremely high values when both a 25% decrease in phytoplankton and ocean warming were considered (Figure 18). While such ratios can be achieved by species with very high production rates like phytoplankton (Jarre-Teichmann, 1995; Harvey et al., 2003), they are unrealistic for western Baltic cod that only spawn once a year in early spring (Hüssy, 2011). The reason for such high deviations in the model output could again be the mass balance condition, which might be further complicated by introducing the effects of two environmental changes as additional forcing variables. Although extreme flow values were observed in three out of 27 scenarios only, these should be treated with caution. The fact that some of the Monte Carlo simulations for the years 2090-2100 resulted in even higher estimates was one of the main reasons to focus on 2050-2060 as an intermediate forecast period.

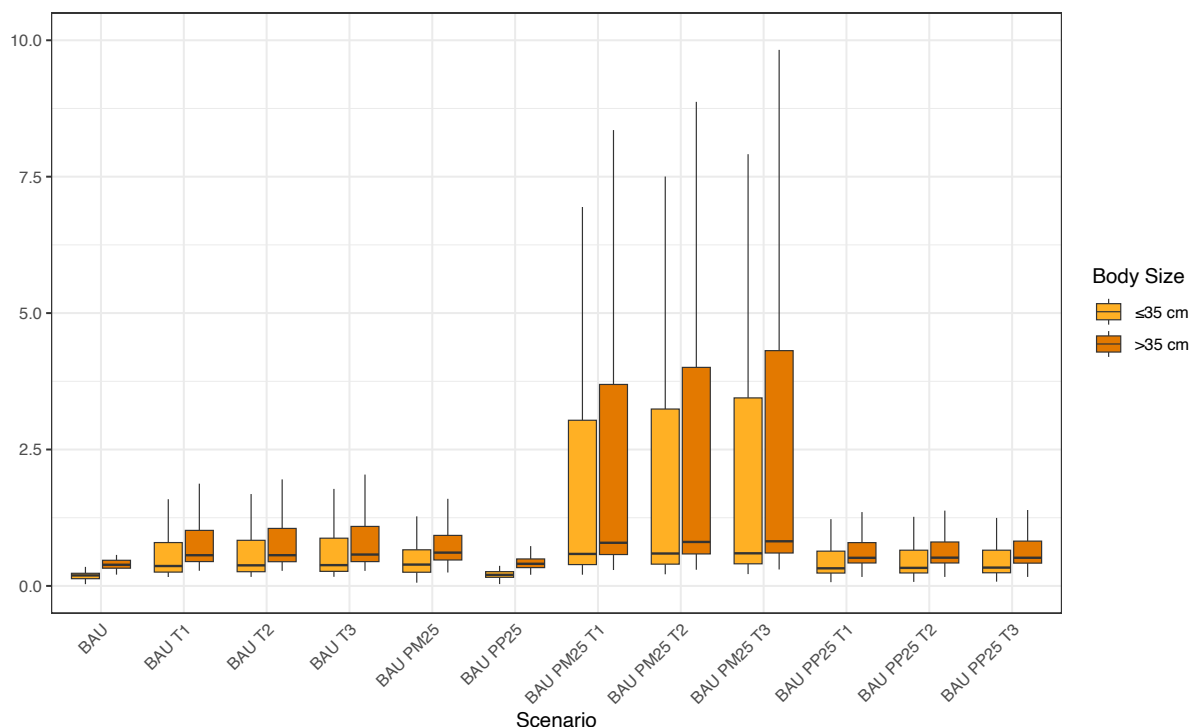


Fig. 18: Distortions in the modelled sinking/total biomass ratio occurring under BAU. Values were obtained from 100 Monte Carlo simulations for the two size classes of cod, ≤35 cm (juvenile) and >35 cm (adult), in 2050-2060 under BAU. Barplots illustrate the ratios for twelve different scenarios incorporating changes in both ocean temperature, T1-3 being a mean SST increase by 1, 2, and 3 °C, and phytoplankton biomass, with PM25/PP25 being a decrease/increase by 25% compared to the reference scenario.

Even though the model already incorporates environmental changes in water temperature and phytoplankton biomass and their effects on the ecosystem, these represent only some of the potential consequences that global change will exert on the WBS ecosystem. For now, ocean warming is in fact only included for its impact on cod, herring and sprat recruitment, expressed as changes in total mortality or stock biomass (Scotti et al., 2022). Also, the consequences of resulting environmental parameters like acidification, toxic algal blooms or the expansion of oxygen minimum zones are not considered. Including more functional groups and additional stressors could alter the state of the ecosystem, meaning that the presently modelled scenarios accounting for these environmental changes should be treated as preliminary. Also, the metabolic parameters used by the model are set at the beginning of the simulations, meaning that it does not account for any evolutionary response to environmental changes (Scotti et al., 2022).

4.7 Take Home Messages

- The WBS model accurately calculates fish-related carbon fluxes in accordance with the species' physiology, despite applying only stock-averaged bioenergetic ratios.
- Fisheries in the western Baltic Sea have a considerable impact on stock biomasses and, consequently, the fish-related carbon ecosystem fluxes of cod and herring; the top-down regulation of fisheries on flatfish is less pronounced. Different fisheries management scenarios projected for the years 2050-2060 result in substantially distinct ecosystem states, with a continuation of the current management strategy having an overall detrimental effect on cod, herring, and flatfish combined and impeding stock recovery of cod and herring. The implementation of an EBFM or a (50%) MSY strategy, however, corresponds to a sustainable exploitation of all three stocks as opposed to BAU. EBFM shows the potential to drastically enhance both stock sizes and the export of fish-related organic carbon to the detritus by generating a surplus of exported carbon of 41,000-43,000 tonnes annually compared to BAU, thereby increasing the system's carbon uptake capacity.
- Changing environmental conditions add new layers of complexity by often negatively impacting stock viability and constraining the leverage of fisheries management. This means that future management frameworks might be advised to operate on multiple levels instead of only relying on fishing pressure as a management tool.
- In the long term, sustainable fisheries result in higher and more stable catch scenarios despite the lower fishing pressure, incentivising a much-needed revision of the current management strategy. However, the more sustainable fisheries management strategies go hand in hand with short-term financial losses in the first years of stock recovery, which would have to be compensated to prevent job losses in the fishing sector.

4.8 Outlook & Conclusion

This work is an attempt to shed light upon the impact of fisheries on ocean carbon biogeochemistry. It provides quantifiable results on the role of fish stocks and consequently fisheries in steering carbon fluxes relevant to the ecosystem but also the world's climate using the example of the well-studied western Baltic Sea region. These results should be further developed to complete the formulation of carbon footprints directly applicable in fisheries management.

While this thesis modelled changes in the detrital carbon flux of three commercially important groups, not all carbon is sequestered and stored and thereby retained from the atmosphere in the long term. The results are however of high relevance as a starting point for future studies to quantify carbon sequestration rates by incorporating bacterial activity, faecal pellet sinking rates, and physical parameters like water depth, stratification and currents affecting the system's sequestration efficiency (Saba et al., 2021; DeVries et al., 2012).

Furthermore, direct carbon emissions of fishing fleets constitute a substantial fraction of fisheries' total climate impact (Mariani et al., 2020). During the course of this thesis, the attempt was already made to include them in the analysis. While there exists a substantial amount of data on fishing effort of several national fleets, among others in the STECF reports or the fisheries databases of Denmark (Statistics Denmark) and Sweden (SHARKweb), it was however not feasible to resolve these to a stock/fisheries-specific level restricted to the ICES subdivisions 22 and 24 within the scope of this thesis. Further effort would have to be spent on that matter to generate reliable, high-resolution emission data, something that could be subject to future research.

A third objective to consider is the effects of bottom trawling on sediment-bound carbon. Sala et al. (2021) state that seafloor disturbance by trawling gears is responsible for the release of up to 0.4 PgC per year globally. Although the extent of their estimate has been questioned (Hiddink et al., 2023), there is good evidence that bottom trawling causes a release of sediment-bound carbon. Quantifying these effects for the western Baltic Sea would add valuable knowledge to the carbon budget of fisheries in SD 22 and 24.

The outcome of this thesis allows for one clear conclusion: Fisheries are an essential player in steering the carbon chemistry of targeted stocks and presumably that of the entire ecosystem. This condition intensifies the responsibility of political decision-makers and fisheries authorities to diversify their management approach beyond stock conservation by acknowledging the climate impact of fisheries. Such an impact occurs both directly, through carbon emissions and seafloor disturbance, as well as indirectly, through the alteration of in-system carbon fluxes and consequently the ocean's carbon uptake potential. Despite fish playing a subordinate role in the total ocean's carbon budget with regards to magnitude, they are one important lever that we have direct and immediate control over, an opportunity that should not be underestimated. In compliance with the Paris Agreement and the signatories' commitment to implementing nature-based

solutions, fisheries, therefore, have the potential to do their part in mitigating climate change by facilitating stock recovery. What is needed is far-sighted, cross-border management and while that is easier said than done, the prospect of a long-term win-win situation and the detrimental consequences of inaction should be incentive enough to transform the sector towards ecological, social and economical sustainability.

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Declaration

I hereby declare that I have prepared this thesis independently and without outside assistance. I have not used any sources or aids other than those indicated. The submitted written version of the thesis corresponds to the one on the electronic storage medium.

Furthermore, I certify that this work has not been submitted as a thesis elsewhere.

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