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Item type

Journal Contribution

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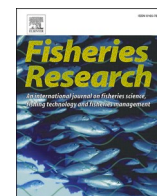
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Closing certain essential fish habitats to fishing could be a win-win for fish stocks and their fisheries – Insights from the western Baltic cod fishery

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ARTICLE INFO

Handled by Jie Cao

Keywords:

Area-based management
Fishing closures
Hotspot persistency analysis
Agent-based models (ABM)
Species distribution models (SDM)

ABSTRACT

The management of the western Baltic cod relies on a combination of regulation tools, including a seasonal spawning fishing closure. The complex population dynamics of the stock have nevertheless been posing considerable challenges to design closures, and the actual benefits of the seasonal spawning closure are still unclear. Often, only biological indicators have been used to evaluate the effectiveness of the closure, without considering socio-economic effects on the fishery. In this study, we applied a Species Distribution Model (SDM) integrating commercial fishery and research survey data on a 15-year time series to design multiple alternative spatial closures, all based on identifying persistent essential fish habitats (i.e., nursery, spawning, and feeding grounds). We further used the spatial-explicit Management Strategy Evaluation (MSE) tool DISPLACE to contrast the outcomes of these fishing closures, and identify which provided the optimal balance between socio-economic and biological demands and sustainability. Our results indicated that all closures benefitted the fisheries and stock. Although fishermen redirected their fishing effort to some extent to other stocks, increased profits were largely driven by increased cod catches as a consequence of reconstructed stock structure and enhanced spawning biomass. We conclude that the benefits of the closures are more linked to their size, than their actual purpose (i.e., protecting nursery, spawning, or feeding grounds).

1. Introduction

Fishing closures have gained momentum over the last decades given their potential for promoting sustainable fisheries exploitation while also serving as conservation areas for marine habitats, other species and certain life stages of targeted species (e.g., Halpern, Warner, 2002; Bailey et al., 2010; Gaines et al., 2010; Watson et al., 2014; Cabral et al., 2020; Ovando et al., 2021). The closures can be broadly classified according to their duration (seasonal or permanent), size (large vs small) and the level of fishing restriction (no-take or partial-take). For example, at the most protective end of the spectrum are the permanent no-take closures where marine areas are permanently closed for all kinds of fishing activities, typically no-take nature reserves. On the other side of the spectrum are the seasonal partial-take closures, where marine areas are closed only during specific times of the year and for specific fishing

fleets.

The design and establishment of fishing closures should ideally rely on the identification of Essential Fish Habitats (EFHs), which are broadly defined as those areas vital to the biological and ecological requirements of critical life-history stages of exploited fish species (Kraufvelin et al., 2018; EU, 2023). This mainly covers areas where fish aggregate in certain periods to spawn (spawning grounds), develop and grow (nursery grounds), and feed (feeding grounds). Moreover, these areas typically differ from low density and migration areas, and do not necessarily overlap with main fishing grounds.

Within this context, spawning and nursery grounds are particularly vulnerable to fisheries, given that fishing practices deplete the larger and mature (spawning) adults, and/or juveniles and undersized fish, both cornerstones to maintain healthy stocks and hence stock production in the long term (Clarke et al., 2015; van Overzee and Rijnsdorp,

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<https://doi.org/10.1016/j.fishres.2023.106853>

Received 25 February 2022; Received in revised form 15 August 2023; Accepted 10 September 2023

Available online 18 September 2023

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2015; Grüss et al., 2019). On the other hand, the feeding grounds are directly related to an individual fish's ecological fitness. Thus, securing areas where both juveniles and adults feed and grow may also be crucial to enhance their reproductive success, and ultimately guarantee long-term high production and future yield for fisheries.

Despite the appealing concept of fishing closures among management and conservation practitioners, several studies have reported that their actual effectiveness remains difficult to quantify partially because of the challenge to conduct and replicate field experiments, and its time-consuming nature to evaluate long-term biological responses to the closure (e.g., Moland et al., 2013; Bigné et al., 2019; Eero et al., 2019). The lack of empirical evidence has consequently promoted the development of a wide array of mechanistic models, which aim to evaluate the potential benefits of management actions such as fishing closures (Grüss et al., 2014; Ovando et al., 2021). Many of these models focus on the benefits of biological and ecological components, while typically ignore the sociological and economic consequences (e.g., Nielsen et al., 2018).

A vast body of literature report, nevertheless, that fishing closures lead to the spatial displacement of fishing effort, with some vessels dispersing more widely to reach other profitable fishing grounds, and others congregating along the closure boundaries (e.g., Rijnsdorp et al., 2001; Dinmore et al., 2003; Bastardie et al., 2014, 2015, 2017a; b). This is a clear behavioral response from the fishermen as an attempt to compensate for the short-term economic loss caused by the closures, whereby the vessel physical range (i.e., engine power) is an important limiting factor. From a biological viewpoint, such effort displacement can undermine overall conservation efforts, as it may increase the fishing pressure towards other species and/or life stages of the harvested species (e.g., Bastardie et al., 2015, 2017b). There is, therefore, an urgent need to evaluate the benefits and side effects of fisheries closures within the broader perspective of the Ecosystem Approach to Fisheries Management (EAFM), which also call for including the human dimension in managing the socio-economic and ecological systems (Hilborn, 2007; Bastardie et al., 2021; Thébaud et al., 2023).

On this basis, a primary goal of the present work was to assess potential benefits and side effects of various types of fishing closures by using a state-of-the-art Management Strategy Evaluation (MSE) tool and Species Distribution Model (SDM). We focused particularly on the western Baltic cod fisheries (hereafter WB cod), given it represents a data-rich stock within the management advisory context, and for which many relevant aspects could be explored in more details. Most importantly, however, is the fact that there has been an ongoing debate on the complexity and efficiency of designing fishing closures for the WB cod (Eero et al., 2019). Reasons for this include the complex nature of the stock's spatio-temporal dynamics (Hüssy et al., 2011), the partial overlap with nursery areas from other cod stocks (i.e., eastern Baltic cod; Eero et al., 2019), and the presence of an independent, and not yet fully understood, stock inhabiting the Sound straight (Øresund) between Denmark and Sweden (ICES SubDivision SD23; ICES, 2023). These factors altogether have been hampering a detailed identification of EFHs, and hence the enforcement of appropriate closures.

We start the present work by identifying persistent spawning, nursery and feeding grounds through a SDM applied to a 15-years' time series. These grounds were then used within the MSE framework as means to contrast the benefits and side-effects across the different closures, whereby we simulated the WB cod and fishery dynamics for a 10-year time horizon. We hypothesized that fishing closures will trigger positive effects to both cod and its fishery, irrespective of the closure purpose (i.e., spawning, nursery, feeding). We also hypothesized that the perceived effects would be more strongly related to the size and timing of the closure, than to its actual purpose given the relatively narrow time frame for which the closure effect was evaluated. Finally, we present and discuss our results, outlining opportunities for future spatial fisheries management in the area.

2. Material and Methods

2.1. Case study: the western Baltic cod fishery and its management

The Western Baltic (WB) cod is a heavily exploited stock that has endured a long-lasting fishing pressure. The increased fishing pressure linked to unfavorable environmental conditions in the more recent decades ultimately triggered the decline of the stock, with its recovery remaining uncertain and under vast academic debate (e.g., Dinesen et al., 2019; Möllmann et al., 2021; Receveur et al., 2022; Voss et al., 2022).

In Demark, the WB cod is targeted mainly by trawlers and gillnetters and managed under a Total Allowable Catch (TAC) regime (ICES, 2023). Other technical management measures are enforced as an additional corrective solution, including Minimum Conservation Reference Size (MCRS) and fishing gear regulations (EU, 2016; ICES, 2023). A historical ban on demersal trawling and seining has been in place in the Sound since 1932 (ICES SD23), and in 2016 a seasonal closure covering the western Baltic Sea (ICES SD22–24) was implemented during the bulk of the stock's spawning season (February 15–March 31) as part of the Baltic cod multi-annual management plan (EU, 2016). The fishing closure was further extended during 2017–2018 (February 1–March 31), and lifted in 2019 as a response to the increased stock size that resulted from a strong year-class incurred in 2016 (ICES, 2018, 2019a). However, given the further severe deterioration of the stock, the closure was reintroduced in 2022 as a possible helpful remedial measure to face the alarming stock decline (EU, 2021; ICES, 2023).

2.2. Methodological approach

Our methodological approach consisted in five consecutive steps (Fig. 1): (i) compilation of fishery-dependent and -independent data, (ii) modelling the abundance distribution of juveniles and adults, (iii) identification of abundance hotspots for juveniles, adults and spawners, (iv) identification of persistent nursery, spawning, and feeding ground hotspots, and (v) evaluation of the effectiveness of the alternative spatial closures and the seasonal closure implemented from 2016 to 2018 and in 2022. The first four steps are related exclusively to identifying persistent EFHs, whereas the last step consists of the MSE approach. The following sections describe these steps in more detail, all of which were conducted within the R programming platform (R Development Core Team, 2019).

2.2.1. Compilation of fishery-dependent and -independent data

We compiled 15 years of data from the Danish fishery-dependent and fishery-independent bottom trawl monitoring programs that were conducted between 2005 and 2019 in the western Baltic Sea (ICES SD 22–24) (Fig. 1).

The fishery-dependent data comprised information from 525 fishing operations (hauls) from the on-board observer's program, and was provided by the Danish Institute of Aquatic Resources (DTU Aqua) connected to the EU Data Collection Framework (DCF; see e.g. Storr-Paulsen et al., 2012). The main aim of this program is to gather information on the catches and discards rates of all demersal fisheries on a haul-by-haul level, except those in which discarding is negligible (Storr-Paulsen et al., 2012). Besides, on-board observers also collect information on fishing effort data (e.g., fishing time, geographical positions, and specific vessel features like gear type, mesh size, vessel length and engine horsepower), and biological data from the catch, such as species, individual fish lengths, weights and otoliths for age determination. The sampling design in the observer program is, a priori, randomly stratified according to ICES area, quarter of year and vessel groups (Storr-Paulsen et al., 2012). However, given that observers need permission from the skippers to go on-board their fishing vessels, sampling becomes rather quasi-random as not all skippers are willing to accept observers on-board.

Conversely, the fishery-independent data, included information from

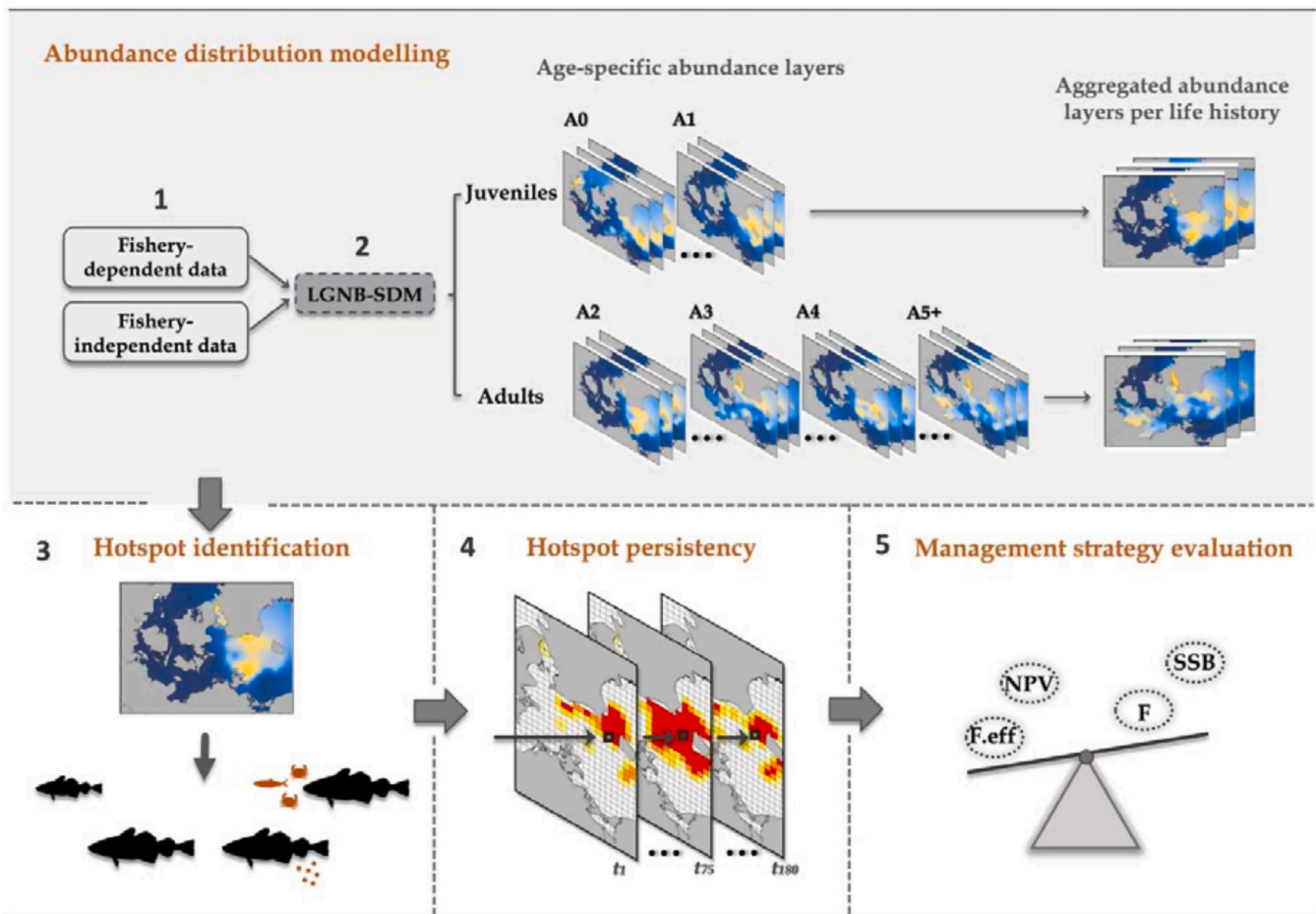


Fig. 1. Schematic overview of the methodological approach. Steps 1–4 are explicit to the identification of persistent nursery, spawning, and feeding grounds, each of which are subsequently assigned as alternative spatial fishing closures in step 5. Note that the last step is common to all the management scenarios tested in this study.

2291 hauls from the Baltic International Trawl Surveys (BITS), publicly available at the ICES Database of Trawl Surveys website (DATRAS; <http://www.datras.ices.dk/>). The BITS program aims at assisting stock assessment models by tuning the time-series of the commercially most important fish stocks from the Kattegat-Baltic Sea, covering catch rates in number and weight by length, age, gender, and maturity group by species. The sampling is conducted on a biannual basis (1st and 4th quarter), and relies on a random stratified design where the ICES subdivisions and the depth layers therein (10–39 and 40–59 m) are used as sampling strata (ICES, 2017; Nielsen et al., 2013; 2014). The allocation of the sampling stations is based on the cod's spatial distribution and its abundance. Whereas the bulk (60%) of the planned stations are randomly allocated along with the different ICES subdivisions and depth strata, the remaining stations (40%) are randomly placed in those areas where cod's catch was high in the last 5-year running mean (Nielsen et al., 2013, 2014).

2.2.2. Modelling the abundance distribution of juveniles and adults

To identify core nursery, spawning and feeding grounds, we used the comprehensive dataset described in the previous section to model the spatio-temporal abundance dynamics of juveniles (age groups A0–A1) and adults (A2–A5+), in addition to spawners which were here considered as adult individuals caught during the spawning season (Fig. 1). We also evaluated the abundance dynamics of old spawners (A5+), because heavily exploited fishery resources, such as the WB cod, often display age truncation that can have major consequences on the population yield (Shelton et al., 2015; Liu et al., 2018).

Species distribution Models (SDMs) are a well-suited class of models to identify EFHs, given they enable to predict where and to which extent fisheries resources aggregate along their life stages (e.g., Paradinas et al., 2015; Rufener et al., 2017, 2021; Grüss et al., 2019). SDMs usually relate the presence/absence (or abundance) of a species to a set of environmental predictors, and are thus well suited to identify EFHs. Here, we used the LGNB-SDM, which is a hierarchical model that can integrate fishery-dependent and -independent data sources simultaneously, while filtering out their relative bias contributions in the abundance estimator (Rufener et al., 2021). By borrowing complementary information from the two datasets, a more comprehensive, detailed, and statistically robust picture is obtained of the species' abundance and distribution dynamics (Rufener et al., 2021).

The abundance, herein catch-at-age (in numbers, N), was modelled via spatially and temporally correlated residuals, thereby allowing to capture the spatial and temporal dependency that are inherent to fisheries data. This required the specification of a spatial grid, where the abundances were predicted for each time-period that is defined by the user. For the present study, we constructed a 10×10 km grid (772 grid cells) covering the western Baltic Sea with a monthly temporal resolution (180 time-periods, from January 2005 to December 2019).

We followed the *predict first, assemble later* (PA) approach proposed by Ferrier and Guisan (2006) to model the spatio-temporal abundance dynamics of the three main life stages (i.e., juveniles, adults, and spawners). This implied in fitting a separate model for each age group, where in a second step, we assembled the age-specific abundance distribution maps within the given life stage to produce distribution maps

of the total juvenile, adult, and spawner abundance (Fig. 1). For further details on the LGNB-SDM model, its calibration and validation, we refer to Appendix A in the [Supplementary Material](#) and [Rufener et al. \(2021\)](#) for an in-depth model description.

2.2.3. Identifying essential fish habitats (EFHs)

Once all models were fitted, validated and the predicted abundance maps assembled, we identified areas that hosted the highest aggregations within each life stage, and from there derived the respective nursery, spawning and feeding grounds.

A main hurdle in defining hotspot areas is that they are often based on a subjective threshold value to differentiate between hot and coldspot areas ([Nelson and Boots, 2008](#); [Bartolino et al., 2011](#)). In this study, we relied on the spatial frequency method proposed by [Bartolino et al. \(2011\)](#), which sets the hotspot threshold upon the geometric properties of the cumulative relative frequency distribution (CRDF) curve.

The curve itself describes the frequency distribution of the abundance (y-axis) as a function of the relative abundance (x-axis), with both axes ranging from 0 to 1. The hotspot threshold is then based on the x-value where the slope of the tangent is 45° (see Fig. 2 for an example). The choice of this particular value relates to the fact that it identifies areas in which the abundance is proportional to the frequency, i.e., the relative increase along the y-axis is equal to the relative increase along the x-axis ([Bartolino et al., 2011](#)). Values above this threshold imply that the relative increase is higher for the abundance than in the frequency distribution, whereas smaller values imply the opposite reasoning ([Colloca et al., 2009](#); [Bartolino et al., 2011](#)).

For the three life stages, we derived monthly thresholds along

considered time-series. Since spawning and feeding aggregations occur on very specific months of the year, we selected only those months in which the main peak of spawning (January–March; [Hüssy, 2011](#); [ICES, 2019b](#)) and feeding (May–August; pers. comm. Stefan Neuenfeldt, DTU Aqua) is known to occur. Thus, along with the time series, we retrieved 45 spawner/old spawner thresholds (Jan.–Mar. from 2005 to 2019), 180 juvenile thresholds (Jan.–Dec. from 2015 to 2019), and 60 feeding thresholds for both juvenile and adults (May–Aug. from 2015 to 2019).

2.2.4. Identifying persistent EFHs

To examine the consistency of the hotspots over the time, hence identifying the most sensitive nursery, spawning and feeding grounds along the 15-year time series, we used a similar approach as [Colloca et al. \(2009\)](#). Particularly, for each cell i of the spatial grid we calculated an index of hotspot persistence (HP) as:

$$HP_i = \frac{\sum_{k=1}^n \delta_i}{n} \quad (1)$$

where n is the number of months (i.e., time-periods; 180 for juveniles, 45 for spawners and old spawners, and 60 for feeding juveniles and adults), $\delta_i = 1$ if the grid cell i in time-period k is a nursery/spawning/feeding area, and $\delta_i = 0$ otherwise.

The index ranges between 0 (grid cell i was never considered as a hotspot) and 1 (grid cell i was consistently identified as a hotspot throughout the time-periods) (Fig. 1). Here, arbitrary thresholds could be imposed to identify the persistent hotspots, and which ultimately would impact the size, shape and number of identified hotspots. Yet, as

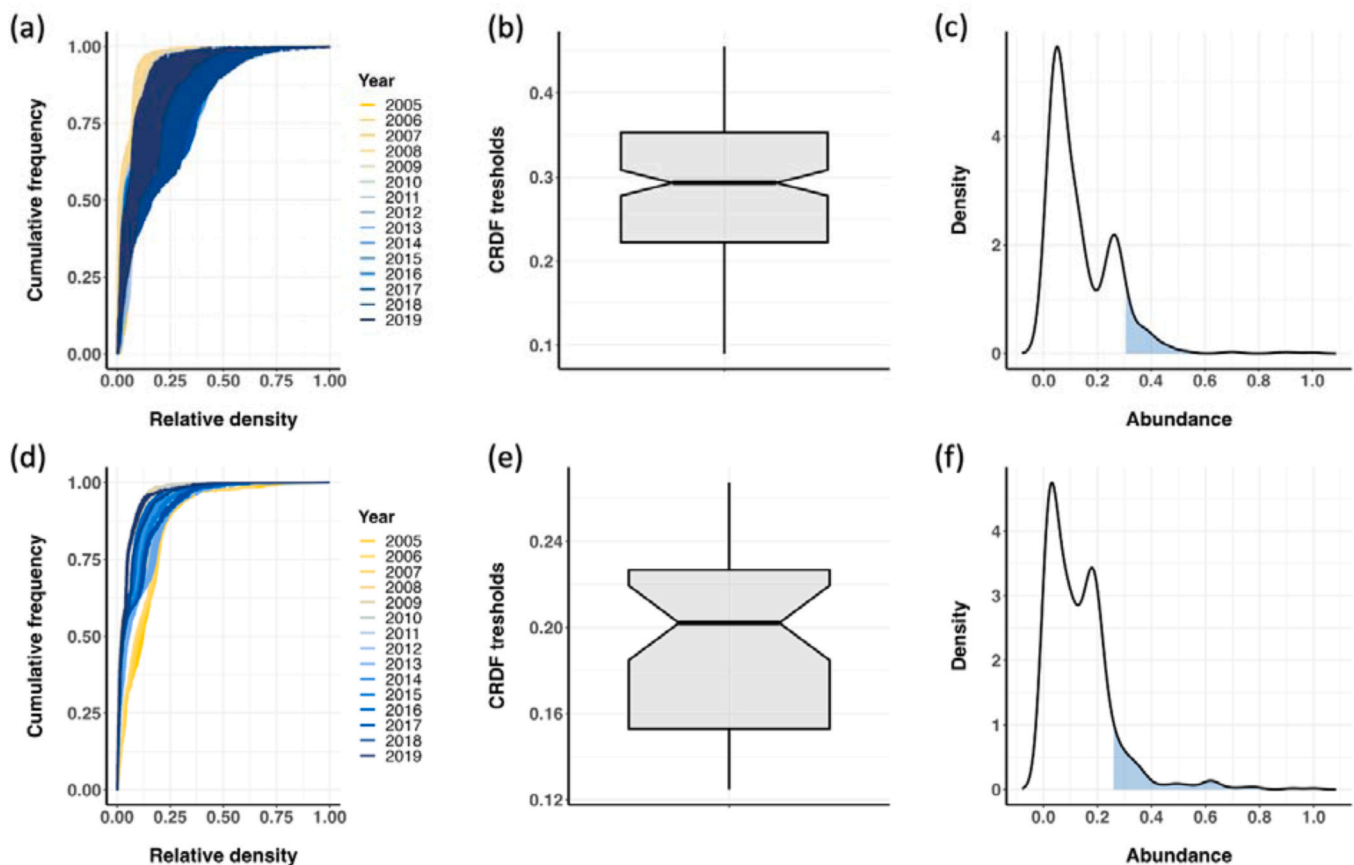


Fig. 2. Illustrative summary of the abundance hotspot analysis conducted for cod juveniles (upper panels) and spawners (lower panels). Panels (a) and (d) denote the CRDF curve, and (b) and (e) the corresponding thresholds derived from the 45° slope tangent (see also Fig. 1 panels 3–4). Panels (c) and (f) are an example of the frequency distribution of the estimated juvenile/spawner density in $t = 5$, highlighting the area (blue shading) that corresponds to the proportion of density above the calculated threshold (juveniles=0.31, spawners=0.26). Results for the remaining hotspots, i.e., old spawners and feeding grounds, can be referred in Fig. C3 in Appendix C.

the EU STECF (2019) recommends selecting values > 0.75 , we used a global threshold of 0.8 to delineate persistent and very conservative EFHs. These areas were then converted into GIS shapefiles such that they could be imported as alternative fishing closures in the MSE simulations (see next section).

2.2.5. Assessing the effectiveness of fishing closures

2.2.5.1. DISPLACE calibration.

We relied on the spatial explicit bio-economic model DISPLACE (Bastardie et al., 2014) to assess the potential benefits of the various types of fishing closures. Briefly, DISPLACE evaluates the interlinked effects that alternative harvest control rules and area-based management have on the biological (e.g., fishing mortality), behavioral (e.g., fishing effort displacement), and economic (e.g., revenue from fishing) components, where the underlying model is an agent-based model that simulates individual fishing vessels (i.e., the ‘agents’) as a function of spatial resource availability and fishing agent incentives. The latter aspect relates to all behavioral aspects that lead the fishers deciding on when, where and what to fish (e.g., reacting to fishing restrictions or economic constraints imposed by the management), such that the economic impact on individual vessels is minimized (i.e., maximized profitability) with respect to the evaluated management scenario.

DISPLACE is essentially based on four sub-modules that can be specified according to data availability, i.e. biological (stock), fleet, economic, and benthic sub-modules (Bastardie et al., 2014, 2020). This means that upon data availability, the model can mimic real-case fisheries and individual footprints by using fisheries-related data (e.g., Vessel Monitoring System (VMS) data coupled to logbook data to deduce historical fishing grounds, catches and landings; see Bastardie et al., 2014 and 2017a for some examples). Whereas the biological and the benthic sub-models include information that is specific to the biology of the targeted/non-targeted fishery resources (stocks) and benthic animals (e.g. growth rate, length at maturity, etc.), respectively, the fleet and economic models retrieve information on the fishing fleets (e.g., vessel size, gear type, fuel tank, etc.) and the fishery economics (e.g., fuel price, ex-vessel price, crew costs, etc.), respectively.

For the purpose of this study, we used the Baltic Sea application implemented by Bastardie et al. (2020) and tailored it further to the western Baltic Sea region, such that the results would strictly reflect the fish and fishery dynamics in our study area. By default, all sub-modules are activated, but we focused only on the biological, economic and fleet modules as we did not aim to evaluate the benthic impact from the fisheries. Within the Baltic Sea application, some fishery stocks are modelled explicitly while others implicitly. The difference between the two approaches relates to whether the stocks’ respond dynamically to the fishing agents or not, and ultimately reflects the data availability that are used to inform the parameters of the biological module. In explicitly modelled stocks, the abundance is gradually depleted from the simulated fishing agents and natural mortality, and increase through individual growth and when new annual recruits join the stock. In contrast, stocks whose dynamics are implicitly modelled do not get iteratively depleted from fishing, mainly due to insufficient or lacking data. However, these stocks do still get accounted for in the final catches as high-level information can be obtained from dedicated advisory reports.

Overall, our application integrated all 17 stocks that are assessed annually by the ICES Baltic Fisheries Assessment Working Group (WGBFAS; ICES, 2023), in addition to 18 stocks located at the edge of the Baltic Sea and reaching the North Sea (Table B1). The latter stocks were included, as they are within the range of the stocks exploited by the Danish fishing fleets (Bastardie et al., 2020). Of these stocks, eight were modelled explicitly (including WB cod), while the remaining stocks were considered only implicitly (Table B1). Following DISPLACE’s default set-up, all stocks were categorized into 14 size groups (5-cm size bins),

each of which was then modelled individually and made available to the fisheries. We note that DISPLACE is a length-based approach, and therefore initial population numbers-at-age were sliced into size groups using recomputed Age-Length Keys (ALKs).

The stock growth from a given size group was simulated via stock-specific growth transition matrix (GTM), and updated at the beginning of each quarter of the simulation year. Both GTM and ALKs were deduced from the Von Bertalanffy growth parameters, namely: asymptotic size (L_{∞}), growth rate (K), and theoretical age at size 0 (t_0). Moreover, recruits were added annually at the start of the simulation year, whereby stock-specific age-based Ricker functions were applied to dispatch the individuals over the size groups according to ALKs computed internally by DISPLACE (Bastardie et al., 2014). This internal computation typically results in limited recruits that end up in the smallest 0–5 cm size group, i.e., the parameterized growth is too quick to capture what happens in the 0–5 cm bin, whereby the growth parameterization redistributes the annual recruits to the larger size groups. In addition, predator-prey interactions between fish species were also accounted for to some extent, where key inter-specific dynamics were regulated through Blanchard’s et al. (2014) size-spectra model. This means that cod can eat smaller fish of herring and sprat whenever a spatial overlap occurs, while sprat can feed on cod eggs. For detailed description on the biological parameters, we refer to table B2 in Appendix B.

With respect to the fishing vessel, publicly available data from the EU fishing Fleet Register (https://ec.europa.eu/fisheries/cfp/control/codes_en) were used to derive information on individual vessels and their gear characteristics. The application simulated vessels larger than 8 m in length, with their homeport based in the western Baltic Sea and parts of the Eastern Baltic (i.e., the Polish ports with quotas attached to WB cod). While the larger vessels (> 12 m) were simulated individually, smaller vessels (8–12 m) were grouped into gear category (e.g., bottom set gillnets and bottom trawlers) to reduce the overall computation costs. In total, fishing activities from 196 individual large vessels and 188 small “super-individual” vessels ($n = 1407$ initially) were simulated, spanning 12 different fishing gears (i.e., métiers) from 4 countries (Denmark, Sweden, Germany, and Poland). However, we note that here we focused only on gillnetters and trawlers as they are the main gears targeting WB cod. Also, because some vessels can deploy multiple gears in the same fishing trip, we assumed that the main and secondary gears were deployed 75% and 25% of the time in each trip, respectively.

Parameters regarding the economics of these fleets were retained from the STECF Annual Economic Report (AER; STECF, 2018), which provided the cost structure of the fleets (variable and fixed costs), and income from the landings that were assumed similar for vessels belonging to the same fleet. For more in-depth description on the fleet dynamic simulation and economic sub-module, we refer to SM2 in Bastardie et al. (2020).

2.2.5.2. Evaluating the effect of fishing closures.

As in Bastardie et al. (2020), we set the calibration year to 2016 as it reflected the management actions set by the Baltic cod multi-annual management plan (EU, 2016). This included the seasonal spawning closures for the western Baltic (February 1 to March 31) and for the eastern Baltic (July 1 to August 31) cod, besides the biological reference and target points that are set by the EU CFP-related TACs and F_{MSY} .

To evaluate the effectiveness of the seasonal spawning closure that was enforced in the past (hereafter *seasonal spawning* scenario) and the alternative spatial closures described further below, we created a hypothetical *baseline* scenario in which no fishing closure was imposed in the study area, yet with all management actions set as in the Baltic multi-annual management plan. Moreover, to minimize the redirection of fishing effort to other stocks outside the western Baltic, we set a zero TAC policy to all stocks outside the study region for all the simulated vessels. Vessels targeting WB stocks (e.g., cod, sprat, herring, and flatfish

such as plaice and dab), on the other hand, were all constrained by stock-specific TACs. As such, fishing can still continue on stocks defined across several areas including the WB until their TACs are reached. In the absence of logbook data to inform Individual Transferable Quotas (ITQs) from countries other than Denmark (e.g., Germany, Sweden, and Poland), we deemed that constraining the fisheries by TACs would mimic appropriately any extreme behaviour from the fishing vessels.

On top of these two scenarios, we also analyzed the potential benefits that could have been achieved if setting spatial fishing closures, in this case the ones based on the core nursery, spawning, and feeding grounds identified by the LGNB-SDM approach (see Sections 2.2.3–2.2.4). This included 4 alternative scenarios, namely: (i) *spawning area closure* (A2–A5 +), (ii) *old spawner area closure* (A5 +), (iii) *nursery area closure* (A0–A1), and (iv) *feeding area closure* (Table 1). For the feeding area closure, prior sensitivity analysis indicated overlapping grounds between juveniles and adults. Thus, to ensure more robust and conservative results, we assigned only the overlapping grounds for the feeding area closure scenario.

For each scenario, we conducted 20 stochastic simulations mimicking a 10-year horizon at an hourly time resolution. From the simulations, we retrieved 14 socio-economic and biological indicators that could be used to assess the benefits of the tested closures relative to the baseline: spawning stock biomass (SSB, tons), fishing mortality rate (F, per year), catches (total and cod-specific, tons), and landings (total and cod-specific, tons landed), fishing effort (hours at sea), steaming effort (hours at sea), number of fishing trips, trip duration (hours), income from landings (EUR), net present value (NPV, EUR), value-per-fuel-unit (VPUF, EUR per litre fuel consumed), and income inequality (Hoover Index). For more detailed description of the evaluated indicators, we refer to Table B3 in Appendix B, and in general to Bastardie et al., (2014, 2020).

3. Results

3.1. Essential fish habitats of the western Baltic cod

The predicted spatio-temporal abundance maps from the LGNB-SDM showed high levels of inter- and intra-annual variability for both juveniles and adults, in addition to strong spatial segregation between the two life stages (Fig. C1 and C2 in Appendix C). Whereas juveniles were mainly found in the surroundings of Bornholm Island and the Arkona Basin (Fig. C1), adults were more widespread, occurring mostly in the Sound straight, Arkona Basin west of Bornholm, and in the Mecklenburg and Kiel bays (Fig. C2).

This seasonal and yearly variability was consequently reflected on the CRDF hotspot thresholds (Figs. 2a and 2d), with threshold values being slightly more variable for the juveniles (min=0.09, max=0.45; Fig. 2b) than for the spawners (min=0.12, max=0.26; Fig. 2e). An example of the frequency distribution of the estimated juvenile/spawner is illustrated in panels c and f of Fig. 2, whereby the blue shaded area highlights the proportion of juvenile/spawner density that is above the calculated threshold (juveniles=0.31, spawners=0.26). With respect to the hotspot threshold values for old spawners, and adults and juveniles during the feeding peak, our results revealed that all values were within the juvenile/spawner threshold range (old spawners: min = 0.13, max = 0.27; feeding juveniles: min = 0.09, max = 0.45; feeding spawners: min = 0.09, max = 0.27) (Fig. C3 in Appendix C).

The fact that all calculated thresholds had a relatively small range implies that nursery, spawning, and feeding grounds of the WB cod are spatially rather narrow (i.e., spatially more concentrated). This becomes even more evident when investigating the persistency of these hotspots along the 15-year time series, which were subsequently assigned as spatial closures in the DISPLACE MSE simulations. Following Fig. 3, all the evaluated essential habitats had a modest size given the extent of the study area, and occurred in similar regions within the Arkona Basin and Sound straight. Among these cases, persistent spawning grounds of old

Table 1

Description of the management scenarios that were benchmarked by the DISPLACE Baltic Sea application. NA = not applicable.

Scenario	Description	Type of closure	Length of enforcement
Baseline (no-closure)	All management actions are set as the Baltic multi-annual management plan (EC, 2016), except that the 2-month (February 1st to March 31st) seasonal closure for the cod fisheries throughout the western Baltic Sea (ICES SD 22–24) is not enforced. In addition, a 0 TAC policy is enforced to all stocks outside the western Baltic Sea, as a means to minimize the fishing pressure on those stocks when fishing spatial/seasonal closures are set.	NA	NA
Seasonal spawning closure	As the baseline scenario, but this time accounting for the 2-month seasonal spawning closure that was enforced from 2016 to 2018, and again in 2022.	Seasonal	Two months a year (February 1st to March 31st)
Spawning area closure (A2 +A5 +)	The seasonal spawning closure is replaced by the persistent spawning grounds that were identified by the LGNB-SDM (Fig. 3). All other management actions are set as in the baseline scenario.	Spatial	Three months a year (January 1st to March 31st)
Spawning area closure for old cod (A5 +)	The seasonal spawning closure is replaced by the persistent spawning grounds that were identified for the oldest cod (A5 +) by the LGNB-SDM (Fig. 3). All other management actions are set as in the baseline scenario.	Spatial	Three months a year (January 1st to March 31st)
Nursery area closure (A0–A1)	The seasonal spawning closures replaced by the persistent nursery grounds that were identified by the LGNB-SDM (Fig. 3). All other management actions are set as in the baseline scenario.	Spatial	Year round
Feeding area closure	The seasonal spawning closure is replaced by the persistent feeding grounds that were identified by the LGNB-SDM (Fig. 3). Note that only overlapping feeding grounds between adult and juvenile cod were considered. All other management actions are set as in the baseline scenario.	Spatial	Four months a year (May 1st to August 31st)

spawners were more numerous and widespread, revealing two additional hotspots when comparing to the more general spawning grounds in which all adult cod were considered (see upper panels in Fig. 3).

Feeding grounds between juvenile and adult cod were also located in similar areas, with two overlapping grounds placed west and south of Bornholm Island (lower right panel in Fig. 3). The Sound straight was consistently pointed out as an important spawning and feeding area of

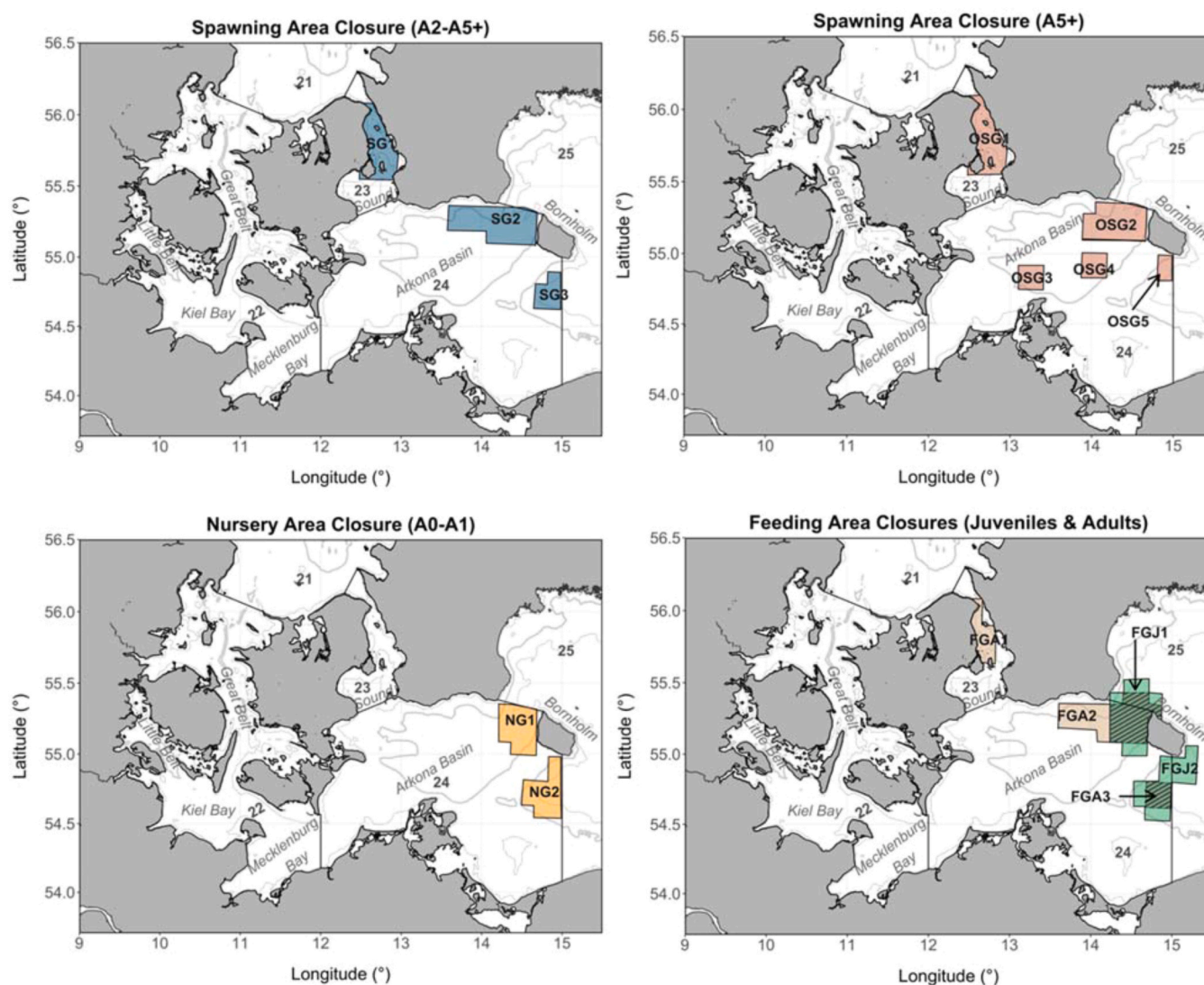


Fig. 3. Map of the alternative fishing closure areas for the western Baltic cod based on the outcomes of the LGNB-SDM and hotspot persistency analysis. Upper panels highlight the core spawning grounds for all adult (left) and old (right) cod individuals, while the lower panels display the core nursery (left) and feeding grounds for both juveniles and adults (right). Acronyms in each map stand for: SG – spawning ground, OSG – old cod spawning ground, NG – nursery ground, FGA – feeding ground of adults, and FGJ – feeding ground of juveniles. We note that the SG1, OSG1, and FGA1 boxes lie already within an area (the Sound straight) in which towed-gear fisheries have been permanently banned since 1932, and were thus not considered within the MSE framework.

adult cod, but since these grounds are placed inside a permanent closure, they were not addressed as spatial closures in the DISPLACE simulations. In terms of their sizes, all were similar with the largest ones associated to the spawning grounds of old cod (235 km²), followed by the spawning areas of all adult individuals (226 km²), nursery grounds (208 km²), and overlapping feeding grounds (159 km²) (Table 2).

3.2. Effectiveness of seasonal and spatial fishing closures

The simulations indicated that the implementation of either the seasonal or alternative spatial closures affected only marginally the spatial distribution of fishing effort (left panels in Fig. 4; also see Fig. C4 for interpretation in relative terms). Irrespective of closure type, fishing effort remained high in the more coastal areas from the little Belts down towards Mecklenburg Bay (ICES SD22) and along the German coast in the Arkona basin (ICES SD24). Higher fishing pressure was also observed in the surrounding west off Bornholm Island (ICES SD24) and, to some extent, in the eastern Baltic (ICES SD25).

The effect of the distinct closures was nevertheless much more pronounced when evaluating the spatial distribution of the WB cod catches

Table 2

Size of the essential fish habitats assigned as spatial closures in the DISPLACE MSE simulations. The total area within each closure type was calculated without considering the boxes located inside Kattegat's permanent closure (ICES SD 21). Box numbers are as in Fig. 3.

Closure	Box	Area (km2)	Total area (km2)
Spawning area closure	SG1	133.8	226.3
	SG2	174.1	
	SG3	52.2	
Old spawner area closure	OSG1	143.1	235.7
	OSG2	136.0	
	OSG3	38.1	
	OSG4	38.9	
	OSG5	22.7	
Nursery area closure	NG1	105.9	208.7
	NG2	102.8	
Feeding area closure	FG1	118.8	159.6
	FG2	40.8	

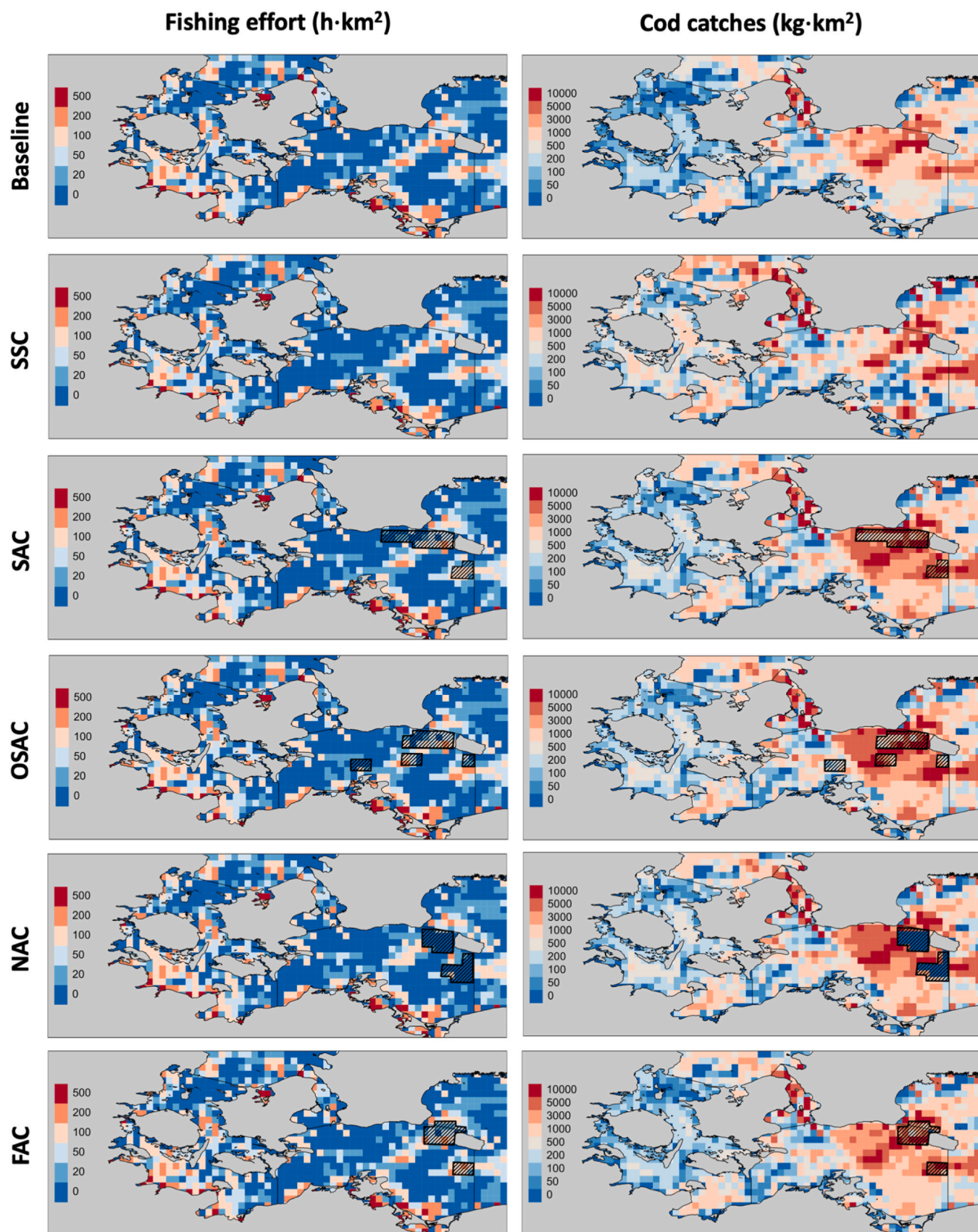


Fig. 4. Spatial distribution of the 10-year cumulative fishing effort (left panels), and western Baltic cod catches (right panels) averaged over the 20 replicates and the two supporting fisheries (trawlers and gillnetters). Acronyms stand for: SSC – spawning seasonal closure, SAC – spawning area closure, OSAC – old spawner area closure, NAC – nursery area closure, and FAC – feeding area closure. Polygons in panels SAC-FAC denote the alternative (spatial) fishing closures retrieved from the LGNB-SDM approach (see Fig. 3 and Tables 1–2 for additional support).

(right panels in Fig. 4; also see Fig. C4 for interpretation in relative terms). The implementation of different fishing closures clearly affected the amount of catches, especially the spatial extent from where these catches were taken. Whereas the seasonal closure resulted in more intensified catches on a narrower area west of Bornholm, spatial closures

triggered fishers to expand their catches on a much broader area across the Arkona basin (ICES SD24). Moreover, higher catch rates around Fyn (the Little and Great Belts in ICES SD22) was observed in the seasonal closure scenario, and to some degree also in the southern region of Kattegat (ICES SD21). Unlike the other areas, however, catches in the

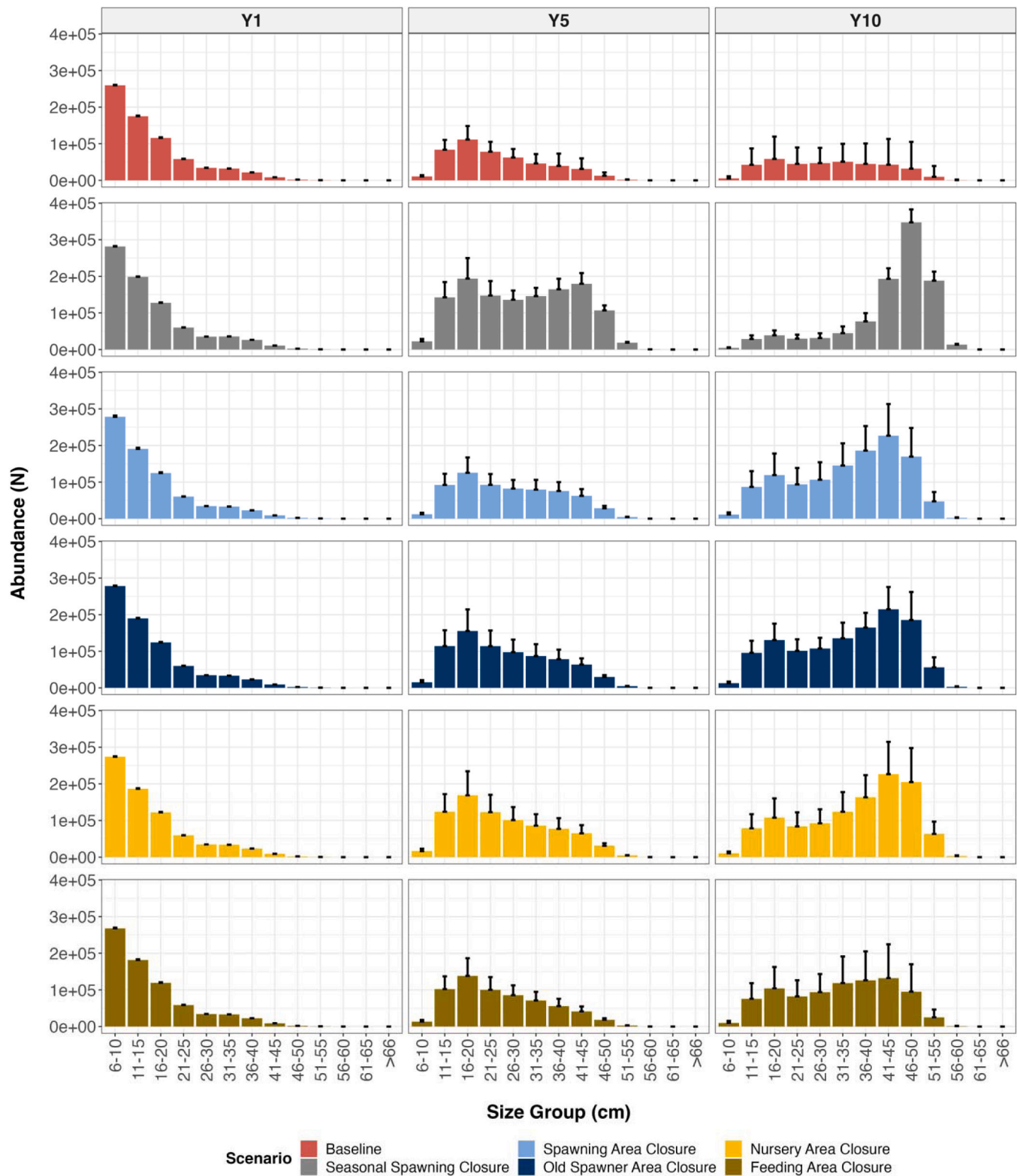


Fig. 5. Average total abundance of the western Baltic cod calculated yearly across the 20 stochastic replicates for different size groups and scenarios, with error bars indicating the standard deviation. Left, middle and right panels display the abundance at the end of the first (Y1), middle (Y5), and last (Y10) year of the of the 10-year simulation horizon, respectively.

Sound straight (ICES SD23) remained indifferent to the enforcement of fishing closures.

Besides the observed effects on the spatial distribution of catches, the simulation outcomes also depicted a clear impact of the closures on the stock's abundance distribution along different size groups (Fig. 5). Compared to the baseline scenario in which no closure was enacted, both seasonal and spatial closures resulted in a gradual increase in the abundance of the mid- to large-sized cod along the 10-year horizon. This clearly shows that fishing closures exert an important role in changing the exploitation pattern, unlike an only TAC-based policy that is not specific to protect certain vulnerable size groups (e.g., juveniles and old spawners). In contrast, the abundance of the smaller-sized individuals (i.e., recruits) dropped towards the latter years of the simulation. We remind, nevertheless, that this is mainly an artifact created by DISPLACE's internal growth parametrization (i.e., ALK), as well as the increased predation pressure on the smaller cod size group as specified by the trophodynamics in the model (see Methods section).

Among the different closures, the seasonal closure resulted in the largest abundance increase of the larger cod when evaluating the trends at the end of the simulation period (size classes 41–55 cm in Fig. 5). However, spatial closures seemed to outperform the seasonal closures when it comes to increased abundance of small to mid-sized length

groups (size classes 11–40 cm in Fig. 5). Interestingly, the abundance of the largest cod (size classes 56–66 + cm) remained at very low levels throughout all simulation scenarios, suggesting that they continue to be quickly overfished.

The different catch rates allied to both fishing effort and size-specific abundance distribution naturally affected the socio-economic and biological indicators across the simulated scenarios. For the sake of clarity, we explore the results separately for each fishing closure.

3.2.1. Spawning closures

The implementation of any type of spawning closure revealed beneficial to both trawl and gillnet fisheries when compared to the baseline scenario, given the increase in their economic fishing efficiency (VPUF) and, thereby, their income (revenue) from landings (total and WB cod) and profits (NPV) (Fig. 6). Overall, benefits were greater when the seasonal spawning closure was implemented, followed by the area closures of old spawners and spawners.

Catches and landings from cod increased at a much higher rate than the total catches and landings (Fig. 6). Allied to the lowered fishing mortality (F) and increased Spawning Stock Biomass (SSB) observed at the end of the simulation period (Fig. 7), such a result could indicate that the stock might be moving towards recovery. Accordingly, fishers could

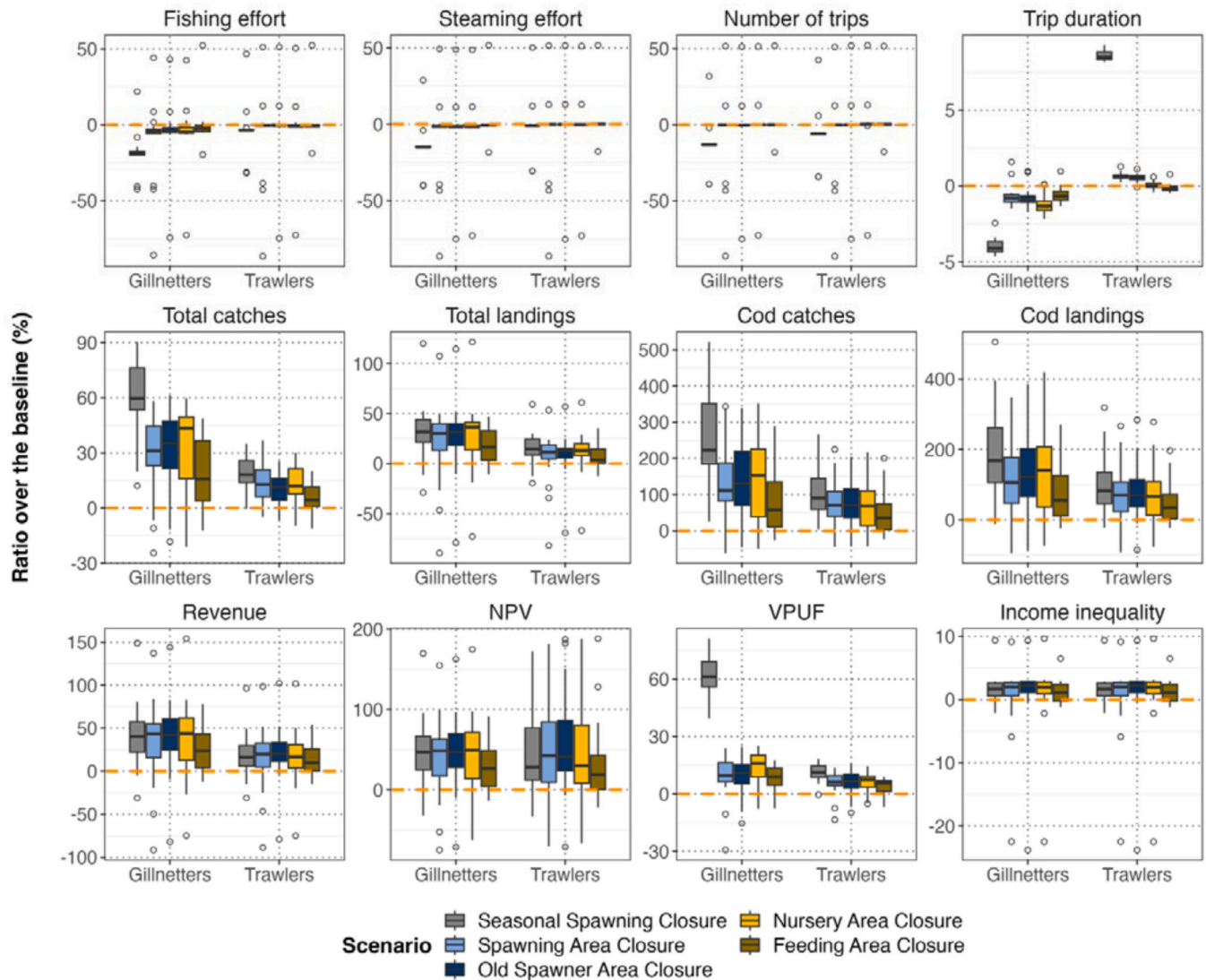


Fig. 6. Boxplots of the socio-economic and biological indicators from the simulated fishing closure scenarios. The percentages are relative to the baseline scenario (Table 1).

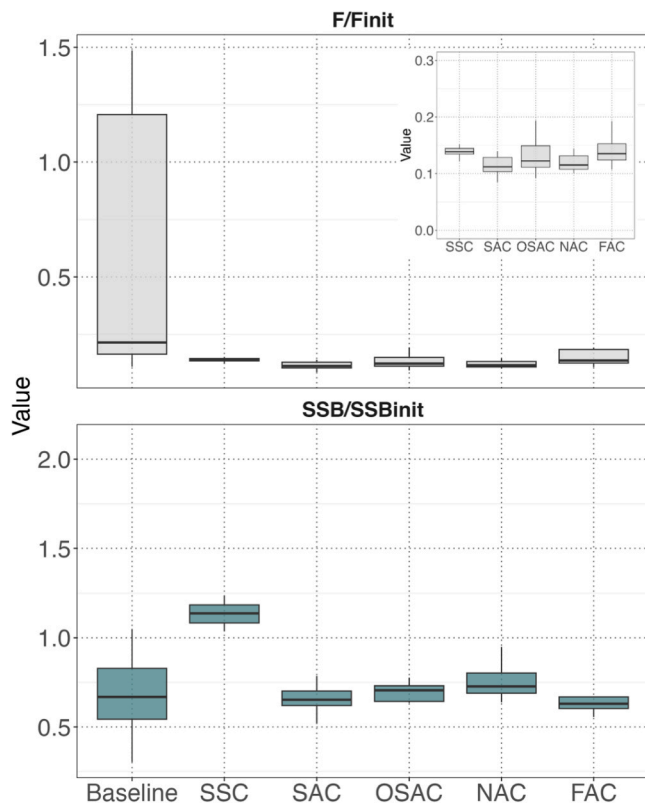


Fig. 7. Boxplots of the scenario-specific biological indicators (F = fishing mortality, SSB = spawning stock biomass), with 20 stochastic replicates per fishing closure scenario (SSC = spawning seasonal closure, SAC = spawning area closure, OSAC = old spawner area closure, NAC = nursery area closure, and FAC = feeding area closure; Table 1). Values are expressed as the ratio between the last and first year of the given indicator, whereby both indicators were averaged over the two fisheries (i.e., gillnetters and trawlers).

be profiting more from higher cod catch/landing rates than from other species, as relative values were comparatively smaller in both fisheries for species such as plaice (gillnetters) and herring and sprat (trawlers) (Fig. C5-C6). However, we note that results from Fig. 7 should be interpreted with care, as values below 1 for the SSB/SSB_{init} ratio indicate that the final state (SSB) is lower than its initial state (SSB_{init}). Thus, despite the lowered fishing pressure (Fig. 7) and the recovered stock structure (Fig. 5), all except for the seasonal spawning closure seemed far less effective in promoting the recovery in terms of SSB .

Between the two fisheries, median revenues for the gillnetters were two times greater than those of the trawlers across all spawning scenarios (gillnetters = +42.1%, trawlers = +19.8%), suggesting that the latter were more affected by the spawning closure implementation (Fig. 6). This is to be expected, as all evaluated spawning closures were located within the Arkona Basin, the most important fishing area for the trawl fishery. A direct reflection of the closure impact can be traced by the slight increase in the trip duration of the trawlers particularly for the seasonal closure scenario where the Arkona basin remained fully closed for two months a year (median increase of +8.1%; Fig. 6 and Table 1). Conversely, results for gillnetters have shown that they spent less time at sea (up to -4.2% less in the case of the seasonal spawning closure), where the decreased steaming effort and number of trips likely imply that they started to fish closer to their departure harbour; hence the highest efficiency (VPUF) (Fig. 6).

The fact that trawlers landed on average less cod than gillnetters across all spawning closure scenarios could further indicate that both fisheries are in direct competition (trawlers = +69.8%, gillnetters = +121%), explaining therefore the minor increase of their landings of herring as a remedial solution (Fig. C6). Despite of this, income

inequality remained virtually the same and showed only a marginal increase (median of +2% across all spawning scenarios and the two fisheries; Fig. 6). We remind that positive numbers for the latter indicator essentially mean that the social gap among the fishermen increased as a reflection of the income being retained in the hands of only a few fishers. Thus, besides the competition between the two fisheries, fishers of the same fishery also seem to compete to a minor degree.

3.2.2. Nursery closures

The implementation of a spatial closure aiming at protecting core nursery grounds yielded similar outcomes as those of the spawning closures. Unlike the latter closures, however, fishing pressure was completely released from inside the protective area as it is enforced year-round (Fig. 4; Table 1). All socio-economic and biological indicators depicted similar trends as those highlighted for the spawning closures. Yet, a few differences could be observed especially those regarding the biological and economic indicators when compared with the two spawning area closures (i.e., spawners and old spawners).

Total catches and landings slightly increased when nursery grounds were protected, with similar patterns also observed for cod catches and landings (Fig. 6). This nevertheless did not significantly impact the fishers' income, since average revenues (gillnetters = +43.9%, trawlers = +16.6%) and fishing efficiency (gillnetters = +43.9%, trawlers = +16.6%) remained nearly the same (Fig. 6). When comparing the fishing mortality between the initial and final states of the simulation, no substantial difference could be detected; although we note that fishing mortality was marginally lower compared to the old spawner area closure, and slightly larger than in the scenario where all spawners are protected (Fig. 7). In contrast, the effect of nursery closures on the SSB has shown that protecting juveniles in the mid-term does not enhance cod's reproductive output, since the SSB ratio is below the value 1 and thus indicating a continued declining trend of the SSB (Fig. 7).

3.2.3. Feeding closures

The simulation outcomes regarding the protection of both juveniles and adult cod during their feeding peak followed the same trends as those detected in the spawning area closures and the nursery closure scenarios (Fig. 6). However, the perceived effects on all indicators were comparatively smaller (Figs. 6–7, and Figs. C5-C6). The fact that the feeding closure resulted in the smallest, yet still positive, benefits is likely a result of the smaller area being protected (Table 2). This naturally reflects the higher fishing mortality when compared to all scenarios but the seasonal spawning closures, and the lowered reproductive output (Fig. 7).

4. Discussion

This study adds to a growing body of work on the effects and consequences of fishing closures, where we specifically anticipated the intended and unintended consequences of various types of closed areas on the WB cod stock and its fisheries. Three general findings could be retrieved from the present study. First, as anticipated, our results have shown that both juveniles and adults are highly dynamic in space and time within the western Baltic Sea. Despite of their complex migration behavior, persistent nursery, spawning and feeding grounds could still be identified along the 15-year time series, whereby all grounds overlapped to some extent. Secondly, closing off areas to fishing resulted not only in a stock enhancement, but also in a better fisheries economy, whether the closure was specific to the life stage, or its size and timing. Lastly, our simulations suggested that the seasonal spawning closure, where the cod fisheries is prohibited for two months a year across the western Baltic Sea, seemed far more efficient for helping the cod stock towards potential recovery and improving the fisheries economic return, compared to the alternative narrower spatial closures (i.e., nursery, spawning, and feeding closures). For the sake of clarity, we will discuss

these findings in more detail in the following sections.

4.1. Essential fish habitats for the western Baltic cod

Our findings from the species distribution model indicated that the abundance dynamics of juvenile and adult WB cod were highly variable within and between years, with clear spatial segregation between the two life stages. This spatial segregation was expected given that fishes often exhibit different habitat requirements along their life cycle (e.g., Støttrup et al., 2019). Notwithstanding, we also detected a large area where both life stages overlapped (west of Bornholm including the Arkona Basin), being consequently an indicative of a highly vulnerable area to fishing.

Although the present study focused only on the westerly area of the Baltic Sea, our results indicated that juveniles mainly aggregate around Bornholm Island and in the Arkona Basin. These findings are consistent with those described by Nielsen et al. (2013), who additionally reported that the extent of the nursery grounds seemed very much dependent on the strength of the year class, the hydrographical conditions, and the vertical water layer stratification. Other studies also revealed that juveniles exhibit, to some extent, migration patterns that are dependent on the size class and habitat quality (Nielsen et al., 2014; Hinrichsen et al., 2017). Altogether, these set of factors are likely to result in protraction or expansion of the aggregation areas between different years, and could therefore justify the different abundance hotspot thresholds we found from the CRDF analysis.

Unlike juvenile cod, however, adult individuals have shown to exhibit a far more complex and widespread migration pattern that is not yet fully understood, where they progressively move from the Kattegat and Sound straight towards the most southerly (the Belts, Kiel Bay and Mecklenburg Bay) and easterly (Arkona Basin and Bornholm Island) areas of the western Baltic (Hüssy, 2011). We identified similar aggregation patterns, and noted that the abundance densities in the Belts were nearly extinguished after 2007 (Fig. C2 in Appendix C). Because of the gradual migration, The spawning season of the western Baltic cod tends to follow the same progression along the year, with the season lasting up to seven months and a spawning peak restricted to 1–3 months within the season (Hüssy, 2011).

Overall, two major spawning peaks have been reported for the current stock: one in the spring that occur in the Mecklenburg and Kiel Bay, and another in the summer which is associated with the Arkona and Bornholm area (Bleil et al., 2009). Albeit the seasonal difference, general management practices assume that the main spawning peak for this stock occurs between early February and late March throughout the full spatial extent of the cod distribution (STECF, 2016; Eero et al., 2019; ICES, 2018, 2019a). This was also the case in the present study, where we actually considered one extra month (January) into our hotspot evaluation approach as an attempt to include the spawning peak of the most northerly fraction of the stock. Our evaluated period certainly does not correspond to the full complexity of the stock's spawning timing, and therefore caution is warranted when interpreting the findings from the MSE simulations. Future research on this aspect is very much encouraged, as defining separate closures for each spawning peak could possibly alter the DISPLACE simulation outcomes, and thus the conclusion that can be taken from the spawning closures.

Aside from the nursery and spawning areas, the present study also identified potential feeding grounds for both juvenile and adult WB cod. Although the feeding ecology of Baltic cod is well known in terms of stomach content analysis (Funk et al., 2021), knowledge on where such process occurs spatially remains blurry. In this sense, we proposed an innovative approach to identify feeding areas by aligning the known feeding period to a state-of-the-art species distribution model and a hotspot persistency analysis. Our results indicated two major feeding grounds for both juveniles and adults, which overlapped largely west and south of Bornholm. This therefore represents a first step towards localizing potential feeding grounds, and future research should

cross-validate these grounds with further stomach content analysis and the spatial distribution of cod preys. The fact that the feeding grounds were located in similar areas as the spawning and nursery areas, reinforces that the region around Bornholm represents a highly vulnerable area to fishing. Hence, it represents clear evidence for proposing spatial and/or temporal protective measures in this area.

4.2. The effect of fishing closures on WB cod and its fishery

We evaluated the effectiveness of fishing closures by considering both biological and socio-economic aspects. Overall, our simulations indicated that irrespective of their size and primary goal (i.e., protecting nursery, spawning, or feeding grounds), fishing closures triggered positive effects not only on cod (reestablishment of the stock structure and increased SSB), but also on the fishery (increased income). From an economic perspective, our results further suggested that in the medium-term fishers could increase their profits by > 40% in the best-case scenario.

This can be partially explained by the fact that the implementation of either a seasonal or spatial closure did not impact considerably their fishing behaviour in terms of spatial allocation of fishing effort and other indicators such as steaming effort and number of days spent at sea. As such, fishers could remain within their usual fishing grounds, where they occasionally redirected their fishing to other stocks (e.g., herring, sprat, and plaice) possibly to compensate for the short-term economic losses that arise during the closure timing. Comparatively, however, our results have shown that catches and landings from WB cod were much larger, indicating thereby that the increased income was driven by the enhanced cod production rather than from changed catches from other stocks.

It is widely recognized that cod stocks in the Baltic Sea have been at their lowest historical levels, mainly due to a combination of poor recruitment, unfavorable environmental conditions, and high fishing pressure (e.g., Köster et al., 2005; Hinrichsen et al., 2017; ICES, 2023). Some studies suggest that the WB cod stock reached a tipping point that is beyond recovery (e.g., Möllmann et al., 2021). Whether this is certain and irreversible remains an open question, as regime shifts are still poorly understood, can unfold slowly over many generations that can pass our perception, and have shown to depend on the resilience of the affected ecosystem in the light of human-induced pressures like fishing and climate change (e.g., Hughes et al., 2013; Bossier et al., 2020; Tomczak et al., 2022). Despite the very low productivity levels, Voss et al. (2022) advocate that rebuilding efforts of the central Baltic cod stock can still provide a win-win situation for the fishery and the stock. They nevertheless argue that such outcomes are only tangible if fisheries management would move from biological to economic target points (i.e., Maximum Sustainable Yield (MSY) to Maximum Economic Yield (MEY), which consist of deploying less fishing effort and save on costs that are less extensive than the ones reaching MSY. In parallel, accounting for the multispecies context of the cod fishery would also move Baltic fisheries toward better economic performance (i.e., Multispecies Maximum Economic Yield, MMEY).

From the perspective of the present findings, we argue that the current Baltic cod management approach should consider area-based practices on top of the right-based regulations such as TACs and ITQs. By simulating the implementation of fishing closures as additional management measures, we have shown that closed areas could boost to some extent the WB stock towards potential recovery. Yet, it is important to stress that within our simulation window (10 years), it is unlikely that the extra recruits supply from the few generations would be enough to fully rebuild the stock, given that the average time for the stock to reach maturity is around 2 years, and the currently extreme poor state of the stock (ICES, 2023). In fact, it may take several years for the fisheries to perceive the spillover effect of a targeted stock (Brown et al., 2014). A 10-year horizon as tested here, nevertheless, can still provide a solid basis to perceive initial signs of stock recovery, especially with respect to

the reestablishment of a healthy stock structure. That said, we foresee that the cod enhancement will possibly benefit the fisheries on a longer time horizon than the one we tested here. Furthermore, the eastern Baltic cod stock is also likely to benefit from the suggested closure areas, since they lay within a zone (SD 24) where both western and eastern Baltic cod mix (Hüssy et al., 2016), and which eventually led ICES to redefine geographical area of the east cod stock to include this area.

We should also note that the stock's SSB enhancement was not exclusive to all tested closure scenarios, and recovery is therefore not warranted. Indeed, only the seasonal spawning closure (SSC) indicated a potential SSB recovery, given the higher SSB at the end of the simulation period compared to its initial state. Our simulation experiment therefore suggests that the size of closed areas seemed a far more important criterion in driving the stock towards recovery, than their actual purpose and timing of enforcement. For example, the seasonal spawning closure is much bigger than the alternative, narrower, spatial fishing closures (spawning, nursery, and feeding closures). If we consider that closures must cover at least 20–30% of the management area such that their benefits can be perceived (Roberts and Hawkins, 2000), it is of no surprise that the WB stock benefitted more when the seasonal spawning closure was enacted (at least, from recovered SSB). When the question boils down to whether nursery, spawning, or feeding grounds should be protected, no significant difference could be detected from the present study in terms of resulting stock production. Although all tested cases lead to similar stock recovery outcomes, each was driven by a distinct underlying mechanism, as indicated by the size-specific stock abundance.

For example, nursery closures are often enacted to reduce the unwanted mortality of juvenile (i.e., Recruits, R) and unmarketable fish (Støttrup et al., 2019). As a consequence, the spawning output and exploitable biomass should improve (i.e., SSB), as the closure would allow them to grow, mature and be more numerous when recruited by the fisheries (Liu et al., 2018; Grüss et al., 2019). On the other hand, protecting the spawners can reduce the fishing mortality rate of older and larger fish, which secures and improves the reproductive output that consequently boost the recruits in the following years (Grüss et al., 2014; van Overzee and Rijnsdorp, 2015; Liu et al., 2018); thus, an SSB-R driven mechanism. Ultimately, by improving the recruits in the SSB-R relationship, spawning closures can potentially reduce the evolutionary effects of fishing and re-establish a healthy stock structure (Law, 2007; Eero et al., 2019).

Such aspects could be captured to some extent in the present study. For the nursery closure, we found that the abundance of medium to large-sized individuals increased in a larger proportion than the alternative spatial closures, which was likely due to the improved R-SSB relationship. Moreover, our results also indicated that protecting the spawners generally resulted in slightly larger abundance of the small-sized individuals when compared to the nursery closures, and hence supporting the SSB-R mechanism. An exception to this pattern was the case of the seasonal spawning closure, where the abundance of small to medium-sized individuals dropped massively at the end of the simulation period. Given the significant increase in the medium-sized individuals, especially those between 46 and 50 cm, this suggests a strong intra-specific density-dependent mechanism regulating this portion of the population (Svedäng and Hornborg, 2014; Liu et al., 2018). The fact that this mechanism was not as pronounced in the alternative spawning closures (i.e., spatial closures for spawners and old spawners) can be possibly justified by their sizes; thus, the smaller stock production compared to the seasonal closure.

4.3. Management implications of fishing closures

In the context of continued mistrust by the fishermen towards the effectiveness of fishing closures, and more generally Marine Protected Areas (MPAs; Beare et al., 2013; Moon and Conway, 2016), a positive result like the one presented here could help to restore some confidence

and increase compliance. Fishermen and stakeholders in the EU have been particularly skeptical about the implementation of the ecosystem-approach to fisheries management (EAFM), as in their perspective most of the proposed measures are unrealistic, do not provide the intended benefits and impact severely the fishing sector (Suuronen et al., 2010; Soma et al., 2018).

A major source of the lack of compliance has been attributed to the deficient communication and connection between the fishermen and enforcers (Moon and Conway, 2016). Although the EAFM advocates for a bottom-up guidance in the decision-making process (Soma et al., 2018), the fishermen's and stakeholder's outlook are often neglected (Garcia and Cochrane, 2005; Suuronen et al., 2010), impairing as such adherence to protective measures. The fisheries management in New Zealand, British Columbia and Iceland, for example, illustrate successful cases in which the continued dialogue between the industry, scientists and enforcers played a vital role in decreasing the mistrust among the fishing community (see Liu et al., 2018 and references therein). Extensive spatial management in these regions led to significant improvement of their stocks, which eventually contributed to positive fishery outcomes and thereby greater support from the industry. Thus, encouraging the participation of the fishing sector and maintaining a consistent dialogue throughout the decision-making process is paramount to lessen resistance towards protective measures (Röckmann et al., 2012).

The fact that the fishermen displayed a realistic behavioral response to the fishing closure within our simulation framework, shows the importance of accounting for the social aspect within the management decisions (Hilborn, 2007; Nielsen et al., 2018). Given the current outlook of climate change and increased human pressure, ecosystems are and will respond accordingly (Bossier et al., 2021), and fisheries will inevitably perceive the consequences. The results presented in the current therefore reinforce the urgent need for (Baltic) fisheries management to move towards a more robust and adaptive outlook (Walters, 2007; Voss et al., 2022). The interplay between stakeholders and the marine ecosystem needs to be acknowledged (e.g., Travis et al., 2014; Trochta et al., 2018; Bastardie et al., 2021), so that spatial and temporal area-based management are also seriously considered by the sector as part of the solution.

CRedit authorship contribution statement

Marie-Christine Rufener: Conceptualization, Methodology, Software, Formal analysis (lead), Investigation, Data curation, Writing – original draft, Writing – review & editing (lead), Visualization. **J. Rasmus Nielsen:** Conceptualization, Investigation, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Kasper Kristensen:** Methodology, Writing – review & editing. **Francois Bastardie:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Resources, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data and code are stored in the first author's GitHub page (<https://github.com/mcruf/FishClosures>).

Acknowledgments

This work was part of MSPTOOLS (Grant Agreement No. 33113-B-16-064), and COFASP ECOAST (Grant Agreement No. 321553) projects, funded by the European Maritime and Fisheries Fund (EMFF) and the

Danish Fisheries Agency during the period of 2017–2021. We thank Josefine Egekvist, Kirsten Håkansson and Line Pinna from DTU Aqua for providing all fisheries-related commercial fisheries data. A special thanks to Paul Marchal and Pierre Petitgas for their helpful comments on the first draft of this manuscript. We also wish to thank the anonymous reviewers for their insightful comments.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fishres.2023.106853](https://doi.org/10.1016/j.fishres.2023.106853).

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