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Sediment suspended by bottom trawling can reduce reproductive success in a broadcast spawning fish

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A B S T R A C T

Suspended sediment adheres to pelagic fish eggs, affecting their buoyancy. In the stratified southern Baltic Sea, eggs of the Eastern cod depend on neutral buoyancy in the "reproductive volume" (RV) (approx. >11 salinity and >2 ml O_2/L) for successful hatching. With increased suspended sediment concentrations (SSC), eggs risk sinking out of the RV into deeper, unfavourable conditions. Bottom trawling, which increases SSC, has been intense around the Eastern cod spawning ground. We modelled the transport of sediment suspended from trawling at this spawning ground to estimate the degree to which eggs could be affected by increased SSC. SSC >1 mg/L above background levels was found 3 km away, one trawl track subjecting a water volume equivalent to 0.01% of the RV to this excess SSC for >12 h. At this excess SSC, it would take c. 6 d for an egg to sink out into unfavourable conditions; insufficient time for it to become a larva. Extrapolating to real bottom trawling intensities in the area of the RV where suspension is highest showed that a water volume equivalent to half the RV experiences excess turbidity of >1 mg/L for c. 24 h during a year. However, fishing effort is heterogeneous; spatio-temporal overlap between trawling and the RV will enhance the duration and/or frequency of turbidity in the spawning area, affecting a higher fraction of the eggs than the model predicts. We conclude that bottom trawling at this spawning ground could decrease cod's reproductive success through increased SSC. Such effects are likely in populations of other fish with pelagic eggs that spawn at trawling grounds.

1. Introduction

Bottom trawling is a fishing method used to catch fish or invertebrates living on or close to the seabed. It is performed worldwide using a range of different fishing gears, most commonly beam trawls, otter trawls and various types of dredges, which are dragged along the sea floor. Bottom sediment is suspended by direct contact of the gear with the seabed as well as by turbulence created around the gear (O'Neill and Ivanović, 2016). Sediment suspension can be quite substantial, particularly on fine-grained seabeds, with local turbidity in the bottom water reaching many hundred mg per L and increasing natural turbidity by orders of magnitude (Durrieu de Madron et al., 2005; Dellapenna et al., 2006: Mengual et al., 2016). The sediment plume can be transported kilometres away from the trawl track (Bradshaw et al., 2012, 2021) and, depending on the frequency of trawling, may create areas with semi-permanent increased turbidity (Bradshaw et al., 2012; Linders et al., 2017) and be the main source of suspended sediment in areas with low natural disturbance or at times of year when natural disturbance is low (Mengual et al., 2016). These studies provide important data from field measurements associated with commercial or experimental trawling; however, fewer studies have attempted to model the implications of such suspension for sediment transport at a local or regional level (Mengual et al., 2016; Payo-Payo et al., 2017; Porz et al., 2023).

Turbid water has detrimental effects on the physiology, behaviour and reproduction of many marine organisms (Wenger et al., 2017; Magris and Ban, 2019). Eggs and larvae appear to be the most sensitive life stages for fish (Lloyd, 1987; Bash et al., 2001; Wenger et al., 2017) and both concentration of suspended matter and duration of exposure are important (Wilber and Clarke, 2001). Most studies on fish eggs have been on salmonids, whose eggs are usually benthic and thus susceptible to smothering and abrasion (e.g. Morgan et al., 1983; Bash et al., 2001), however ichthyoplankton may also be affected by suspended sediment; experiments have shown delayed or less successful hatching (Morgan et al., 1983; Phan et al., 2020), reduced length and viability and increased abnormalities in larvae (Phan et al., 2020). One mechanism for these effects is the adhesion of sediment to the chorion (Morgan et al., 1983; Griffin et al., 2009; Wenger et al., 2017; Phan et al., 2020), even after a short exposure (2–3 h; Griffin et al., 2009; Phan et al., 2020), which can reduce oxygen uptake to the eggs (Griffin et al., 2009; Phan et al., 2020) and lead to loss of buoyancy (Isono et al., 1998), resulting in egg mortality due to physical bottom contact (Hüssy et al., 2016).

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The Bornholm Basin in the southern Baltic Sea has a strong thermohaline stratification (surface salinity 4–8 (PSU), bottom waters 13–17) (Snoeijs-Leijonmalm and Andrén, 2017) and the bottom waters are semi-permanently anoxic (Carstensen et al., 2014). It is also the last main recruitment area for the threatened Eastern Baltic cod (*Gadus morhua*) (Hinrichsen et al., 2016; Köster et al., 2017). The eggs of this cod population have very specific requirements for survival; they have neutral buoyancy at a relatively narrow range of salinities (Nissling and Vallin, 1996), with a lower limit at 11 (MacKenzie et al., 2000; Hinrichsen et al., 2007, 2016). Together with oxygen requirements this has led to the concept of a "spawning layer" or "reproductive volume" (RV), defined at its upper boundary by the salinity 11 isobath and at its lower boundary by the 2 ml O_2/L isobath (e.g. Mackenzie et al., 2000; Hinrichsen et al., 2007). Decreased buoyancy from suspended sediment adhesion to Baltic cod eggs (Westerberg et al., 1996) could therefore lead to eggs sinking out into deep water with unfavourable oxygen conditions (Nissling et al., 1994; Hinrichsen et al., 2016).

In the southern Baltic Sea, bottom trawling with otter trawls has been used for decades to catch mainly cod (ICES, 2021). Fishing intensities here were very high from the 1970s to the early 2000s (ICES, 2021), with some areas trawled up to 10x per year (Eigaard et al., 2017; Amoroso et al., 2018), often on or near the spawning grounds. The fishery for Eastern Baltic cod is currently closed due to the depleted status of this stock (ICES, 2022), but there is a pre-existing spawning area closure in the Bornholm Basin. However, this closure only partially covers the spawning area and the period of peak spawning (ICES, 2018; Eero et al., 2019). In their second holistic assessment of the Baltic Sea, HELCOM (2018) identified bottom trawling as one of the activities that had the greatest potential for physical disturbance in this area, although they noted that the effects of this disturbance were unknown. Recent oceanographic modelling has suggested that bottom trawling in the southern Baltic may increase horizontal sediment transport by up to 30% (Porz et al., 2023).

The aim this study is to evaluate if bottom trawling during the cod spawning period could increase suspended sediment concentrations (SSC) to levels that could decrease the time that eggs are buoyant and maintained in the right conditions for survival. To investigate this question, we modelled the transport of sediment suspended from two single trawl tracks near the Eastern cod spawning ground in the Bornholm Basin, for a model year, 2016. We calculated the percentage of the RV that could be affected at different excess SSCs, and for how long, and extrapolated this to fishing intensities in the area. The aim was not to perform detailed mechanistic modelling but to understand on a broad scale whether there could be consequences of trawl-suspended sediment for the reproductive success of these pelagic fish eggs.

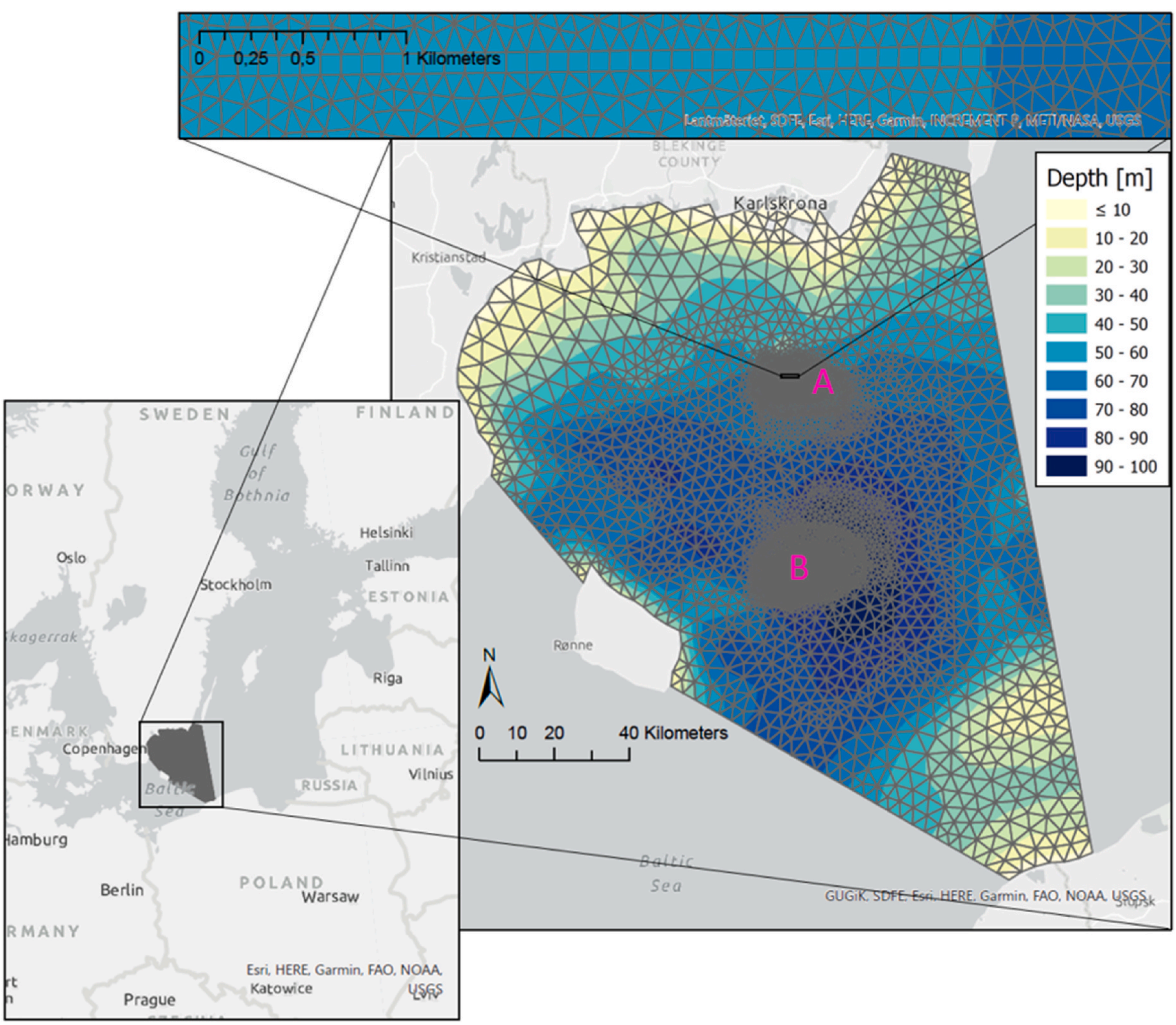

Fig. 1. Domain and bathymetry of the model area, with increasing horizontal resolution in the model mesh closer to the modelled trawl tracks A and B. The top panel shows a detail of the area immediately around the 4 km-long trawl Track A (the row of quadratic cells (in total, 4 km × 100 m) in the centre of the panel). Track B had a similar appearance and lies in a roughly E-W direction under the letter 'B'.

2. Methods

2.1. Study area

The Bornholm Basin lies east of the island of Bornholm in the southern Baltic Sea (Fig. 1). Its bathymetry, infrequent exchange of water with the North Sea and inputs of freshwater from the Baltic drainage basin mean there is a strong thermohaline stratification; surface salinity is c. 4–8 and bottom waters are c. 13–17 (Snoeijs-Leijonmalm and Andrén, 2017). This restricted water movement, in combination with large organic inputs from eutrophication, leads to semi-permanent anoxia in the bottom waters (Carstensen et al., 2014). Areal extent and frequency of hypoxia/anoxia have increased during the last 50 years (Carstensen et al., 2014). The seafloor sediments in the area are mainly silt and clay, with some fine sand (Christoffersen et al., 2007; own unpublished data).

Eastern Baltic cod eggs have neutral buoyancy at a relatively narrow range of salinities (Nissling and Vallin, 1996), with a lower limit at 11 (MacKenzie et al., 2000; Hinrichsen et al., 2007, 2016), where the halocline is strong and their abundance is often highest (Wieland et al., 1994; Hinrichsen et al., 2007). In addition, successful development is limited to waters with oxygen concentrations >2 ml O_2/L (Nissling and Westin, 1991; Bagge et al., 1994). The cod 'reproductive volume' (RV) in this area is therefore commonly defined as the water volume in which salinity is > 11 and oxygen concentration is > 2 ml O_2/L (e.g. Mackenzie et al., 2000; Hinrichsen et al., 2007). In terms of water depth, this is usually found at between approximately 50 and 70 m (Wieland et al., 1994), although there is a large interannual variation in the thickness and total volume of the RV (Mackenzie et al., 2000; Hinrichsen et al., 2007).

2.2. Modelling

2.2.1. Hydrodynamical model

A detailed description of the flow field is needed in order to model the dispersal of eroded sediment from a trawl passage. For this purpose, a high-resolution hydrodynamic 3D-model of the Bornholm Basin was built in the oceanographic model software MIKE 3 FM (DHI, 2022). The model is a dynamic downscaling of an operational model covering the Baltic Sea and Kattegat (DHI & MFVM 2019). It is forced by hourly meteorological and hydrological data and by salinity, temperature, sea surface height and current velocities at the open sea boundaries. The domain modelled in this study covers the area from the south-east coast of Sweden (from Simrishamn to the southern tip of Öland) to a central part of the Polish coast (from Koszalin to Gdynia) (Fig. 1). MIKE 3 FM uses a triangular flexible mesh and when building the computational mesh for the model, two locations for trawl tracks were chosen in advance to ensure high horizontal resolution in these areas. The horizontal resolution was 100 m at the trawl tracks (resolved with quadratic grid cells to ensure the same track width throughout), gradually increasing away from the tracks (Fig. 1). The vertical resolution was 1 m all the way to the seafloor. The model solves the primitive Navier Stokes equations and calculates the water velocities, temperature and salinity in every grid cell, and the flow data is saved hourly to be used as input for the off-line sediment dispersal calculations. The model was set up from April to October (the cod spawning season) for the year 2016. The year 2016 was chosen since there was good fishing intensity data available and hydrological conditions (e.g., temperature, salinity and oxygen concentrations) were within the normal range of variability according to national monitoring data (see S2.1.2). The model details are further described in Supplementary Material S2).

2.2.2. Sediment dispersal model experiments

Two trawling locations were chosen in areas with high fishing intensity according to yearly surface swept area ratios (SAR) from 2012 to 2016 (ICES, 2017). Both locations are located on the slope to the Bornholm Deep, Track A in the north-west part at depths between 60 and 63 m and Track B in the deeper area to the south at 84–87 m depth. Although Track B is below the RV and at a depth at which periodic hypoxia occurs, it is evidently still a hotspot of fishing intensity and we therefore chose it as a contrast to Track A.

Each of the two trawl tracks, A and B, was modelled as a box covering 4 km × 100 m. The 100 m width of the track was chosen given the door spread for otter trawls catching demersal fish according to Eigaard et al. (2016). Trawling was set to occur every 5 days from May to October, covering the main spawning season, adding up to a total of 36 consecutive trawling events per track.

Sediment was assumed to be suspended instantaneously to a height of 1 m above bottom across the whole 4 km × 100 m track and to attain an initial SSC of 1000 mgDW/L. This start value derives from the value of 500 FTU (Formazin Turbidity Units) measured from turbidity loggers attached to a trawl net (c. 2 m above the seafloor) during field experiments (Fig. 2 and Supplementary Material S1). Peak SSC regularly exceeded 500 FTU over the course of 3.5 h of measurements (Fig. S1). FTU was converted to SSC (mgDW/L) using the approximation SSC = 2 x FTU. This is in broad agreement with the relationships derived from sediment suspended in the bottom water up to 24 h after trawling in two experimental trawling experiments on muddy seabeds (Linders et al., 2017; Bradshaw et al., 2021). All modelled SSCs are excess concentrations, ie. do not include natural background SSC.

The dispersal of SSC was modelled with the MIKE MT module, a transport model for fine sediments that calculates settling and resuspension of a range of sediment fractions simultaneously (DHI, 2022), using a 30 s timestep and the off-line hourly flow data from the hydrodynamical model as input. From an initial field of 1000 mg SSC/l above the trawl track the sediment particles drift with the currents and move vertically, sinking or rising depending on the combination of their individual settling velocity and the vertical velocity of the surrounding water. Once the particles settle, they can resuspend if the bottom shear stress is large enough. Based on grain size distributions in the area from Christoffersen et al. (2007), the model was run with four sediment fractions (Table 1) and the settling velocity used was based on Stokes' Law and did not include flocculation or aggregation of particles.

The dispersal of SSC away from Track A or B into the model domain was modelled for five days after the trawl passage (at which time the bulk of the particles was estimated to have settled) and the model output (concentration of SSC) was stored every 5 min in every grid cell. All 36 trawling events per track were modelled in separate model runs, so no overlap of suspended sediment plumes occurred. The results were then analysed for the water depths between 50 and 70 m, as this is the average depth delimited by a salinity of 11 and 2 mlO_2/L, i.e., the reproductive volume (RV) corresponding to essential conditions for cod egg survival (see Section 2.1). This means that depending on the currents at the time of the trawl passage at Track A or B, the sediment plume could travel freely in and out of the part of the model domain that was analysed, and the SSC in the analysed volume (50–70 m) could differ between the trawling events. A more detailed description and evaluation of the assumptions and limitations of the model can be found in Supplementary Material S2.

2.3. Data analysis

2.3.1. Analysing and scaling up the model output from Track A and Track B

The output from the 3D sediment dispersal model gives the excess SSC from the trawl passage at Track A or B in all grid cells in the whole model domain every 5 min during the 5 days after each trawling event. At each track (A, B), the modelled dispersal of excess SSC after each of the 36 consecutive modelled trawl passages was averaged for all 36 events to give an average effect of a single trawl passage but capturing the range of hydrodynamic variability over the season. The output from the dispersal model is SSC in 4 dimensions, spreading in 3D from the 4

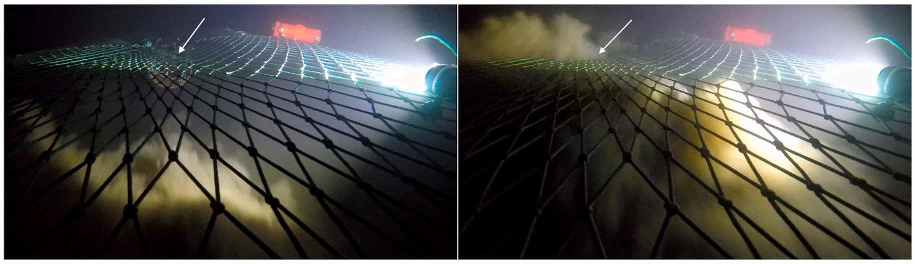

Fig. 2. Stills from a video taken during experimental trawling. The turbidity logger is mounted inside the PVC tube indicated by the white arrow. During trawling, pulses of resuspended sediment intermittently hit the logger that is attached to ceiling of the trawl positioned c. 2 m above the bottom.

Table 1
Summary of main parameters used in the sediment dispersal modelling.

Parameter	Parameter description			
Trawl track area	4 km × 100 m			
Trawl track depth range	Area A: 60–63 m, Area B: 84–87 m			
Length of each model experiment	5 days duration, starting every 5 days, non-overlapping			
Time period	May–October			
Initial concentration of SSC	1000 mg/l at 1 m above the seabed			
Type and fraction of sediment	Fine silt/clay 46%	Medium silt 23%	Coarse silt 21%	Fine sand 10%
Modelled settling velocity [mm/s]	0.02	0.1	1	6.3
Critical shear stress for erosion	Resuspension start at 0.1 N/m^2 (newly deposited sediment)			
Output parameter	Concentration of excess SSC [mg/l], stored every 5 min in all model grid cells			
Water depth analysed	50–70 m, based on salinity and oxygen requirements for cod eggs			

km long trawl track, during 5 days and, due to the dynamics of the surrounding waters, the sediment disperses in different ways at different times during the season. This multidimensionality makes it difficult to summarise or visually represent the net effect. We therefore chose to summarise the multidimensional output in several different ways, and using a stepwise approach, to highlight different spatial aspects of the data.

The modelled excess SSC from the trawl passages was analysed both regarding the volumes of water affected by increased SSC (i) and regarding the distance from the trawl track over which the SSC was increased (ii). First, the impact of the single trawl passage was calculated (i and ii), then the results were scaled up to five trawl passages (iii) and then to realistic bottom trawling intensities during a year (iv). The analyses of the model data were all done within the waters defined as the reproductive volume (RV), between 50 and 70 m depth, and the results were expressed as an equivalent % of the RV. Note that a given % of the RV is a total and may comprise several events affecting the same volume of water.

i. Percentage of RV affected by excess SSC from one trawl track.

To assess the volume of the RV that was affected by excess SSC spreading from the trawl track, and the total time that SSC was above background in the RV, we counted every occasion where SSCs were above three thresholds (0.5, 1 and 5 mg/L) in every model grid cell at all depths within the RV during the whole 5-day period. This data was then made into a histogram, where the volumes of the grid cells were binned by total time of exceedance, and then summarised cumulatively. Each “time bin” then represents the total volume where a given SSC was exceeded for at least that length of time. This was repeated for each of the three chosen threshold SSCs. The analysis was done for a single trawl passage every 5 days over the season (36 in total), and the resulting histograms averaged to estimate a mean effect over the modelled spawning season on the excess SSC for a single trawl passage.

This analysis was performed for dispersal from Tracks A and B. However, since Track B is located deeper than the RV (84–87 m), the impact of suspension there was calculated to be small and the following analyses were done for Track A only.

ii. SSC at different distances from trawl Track A

The SSC was logged during the 5 modelled days at a large number of points at fixed (horizontal) distances away from Track A, at all realized depths within the RV for each point. The maximum of all SSCs from each distance from the track (regardless of depth) was then saved. This data was then averaged over all 36 trawl passages during the season, providing information on the maximum SSC that occurred in the RV with distance from the track (regardless of direction), averaged over the season.

iii. Scaling up to five trawlers fishing simultaneously

The results from analyses (i) and (ii) are based on a single trawl passage. However, it is more likely that several trawlers operate at the same time, within a few km of each other. We used two scenarios to frame the extremes of spatial and temporal variability of five trawlers trawling at the same time:

(a) the effect of five trawlers with overlapping trawl tracks; in this case, the full post-processing and analysis in (i) was redone, but the data was scaled to represent the outcome of an initial SSC five times higher (ie. 5000 mg/l) prior to the calculations. In reality, trawl tracks will not exactly overlay each other, but at the trawling intensities documented in this area (Fig. 3) it is not unreasonable to expect substantial overlap over a relatively short space of time.

(b) the effect of five boats trawling simultaneously, but at distances from each other where there would be limited overlap of suspended sediment; this as calculated by simply multiplying the results from (i) by 5.

iv. Scaling up to realistic fishing intensities

We extrapolated the modelled average water volume affected by sediment suspension from a single trawl track (0.4 km^2 area of seabed; 4 km × 100 m) to the actual seabed area disturbed by bottom trawling in 2016 in the Bornholm Basin, as provided from official fisheries statistics compiled by ICES (2017). We used the surface swept area ratios (SAR) from 2016, estimated per c-square grids (0.05 × 0.05°, or c. 17 km^2),

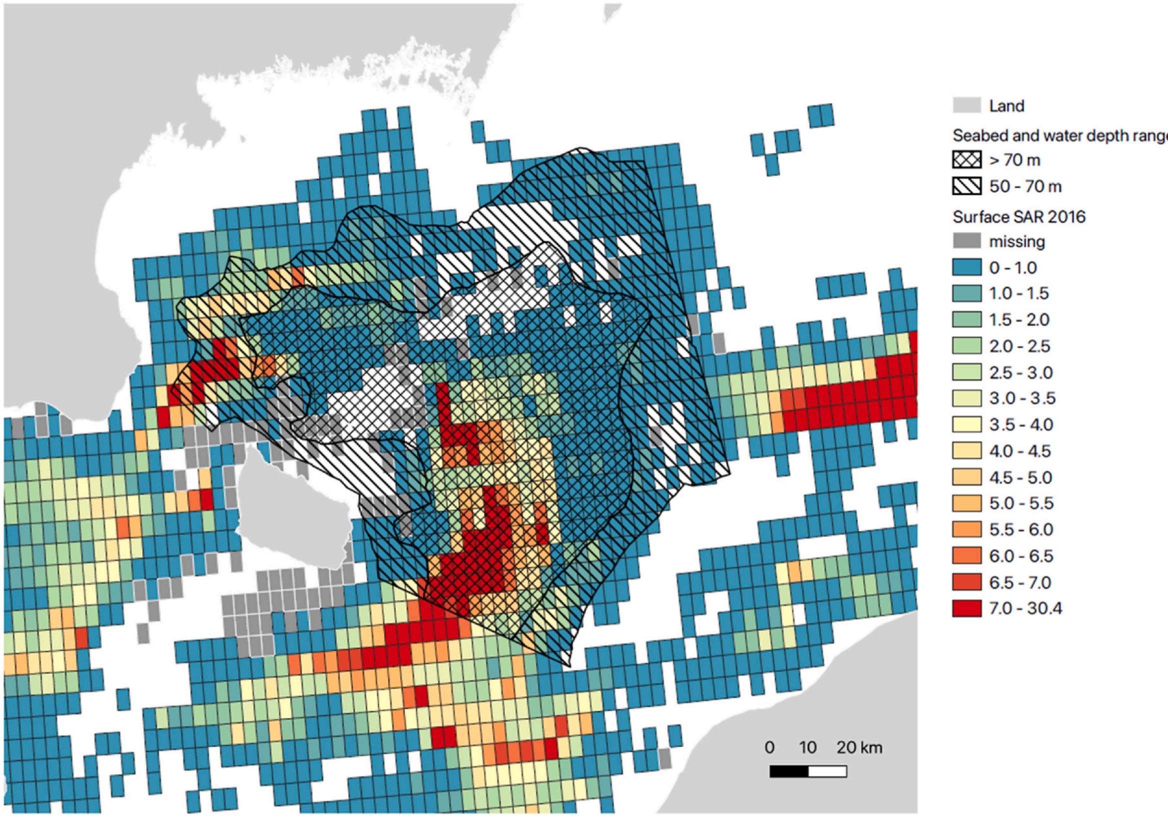

Fig. 3. Surface swept area ratios (SAR) by bottom trawlers in the southern Baltic Sea in 2016 (background colours). A SAR of 1 means that an accumulated surface proportional to the entire grid cell (c-square, c. 17 km^2) was disturbed once during a year. Data are from ICES (2017). Between the 50 m and 70 m depth contours (diagonal shading), the RV extends to the seafloor. In the area within the 70 m contour (cross-hatched area), the RV (50–70 m) lies above deeper (>70 m) water. The 50 m and 70 m contours (solid black lines) are only shown to the edge of the modelled domain. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

covering all vessels ≥12 m equipped with Vessel Monitoring System (VMS) (Fig. 3). A SAR of 1 means that an accumulated surface proportional to the entire c-square is disturbed once during a year.

By overlaying the mapped trawl statistics with the bathymetry from the model we selected all grid cells in the fisheries statistics where the seabed depth was between 50 and 70 m, ie. where the RV extends to the seabed. We did not include trawled grid cells deeper than 70 m since suspension upwards into the RV was shown to be minimal (see Results for Track B). The area of each fisheries grid cell trawled per year was calculated by multiplying the proportion of the cell area trawled (i.e., surface SAR) with the area of the grid cell (17 km^2). The trawled areas in all the grid cells were summed, giving a total trawled area in waters between 50 and 70 m of 7690 km^2. By upscaling the modelled results of volumes of water affected by excess SSC from Track A (0.4 km^2) to the total trawled area from the fisheries statistics (7690 km^2), we obtained a crude estimate of the volume of water (and % of the RV) affected by excess concentrations of 0.5, 1 and 5 mg/l sediment suspended from actual trawling in the region in 2016.

The fisheries data was only available for the whole of 2016, while our modelled data was an average result from modelled sediment dispersal during May to October 2016. For the extrapolation, we therefore had to assume that the average affected water volume from one trawling event does not differ depending on the time of year. However, from Fig. 3 it is clear that fishing is spatially patchy, and we used the fisheries data to estimate the proportion of the RV where most trawling occurred and thus where most suspension was likely to occur.

2.4. Assessing the potential impact on cod egg buoyancy and survival

To assess whether excess SSC from trawling activity could affect cod egg buoyancy in the RV, we used Westerberg et al. (1996)'s experimentally derived 'sinking factor' of 0.02 PSU/h, mg/l – i.e., for every mg/l SSC, an egg loses buoyancy equivalent to 0.02 PSU per hour. For those authors' three experimental SSCs (5, 16 and 40 mg/l), we calculated the number of hours that it would take for a cod egg at the top of the RV (salinity 11) to lose buoyancy equivalent to 4 salinity units and thus sink to the bottom of the RV (salinity 15) and thus into unfavourable conditions below. We used these sinking times, together with an assumed sinking time of 15 days (to ensure sufficient time for hatching) at a background SSC of 1 mg/l, to derive a new equation that extrapolated below the range of Westerberg et al. (1996)'s data (see S3.1). Finally, we used this equation to calculate the egg sinking times for the three excess SSCs used in the earlier modelling (total SSCs of 6, 2 and 1.5 mg/l; excess SSC plus a background SSC of 1 mg/l). The background value of 1 mg/l was an average of field measurements in the area May 2019; see S3.1.

3. Results

3.1. Model results

i) Percentage of RV affected by excess SSC from one trawl track

Suspension from the single 0.4 km^2 Track A results in a water volume equivalent to 0.01% of the entire RV being exposed to an excess SSC of at least 1 mg/l for at least 12 h or 0.5 mg/l for c. 21 h (Fig. 4a). At Track A, the trawling occurs between 60 and 63 m, i.e., within the same depth range as the modelled RV (50–70 m). At Track B, trawling occurs at 84–87 m, which even though it is deeper than the RV still results in some suspended sediment being transported upwards into the RV (Fig. 4b),

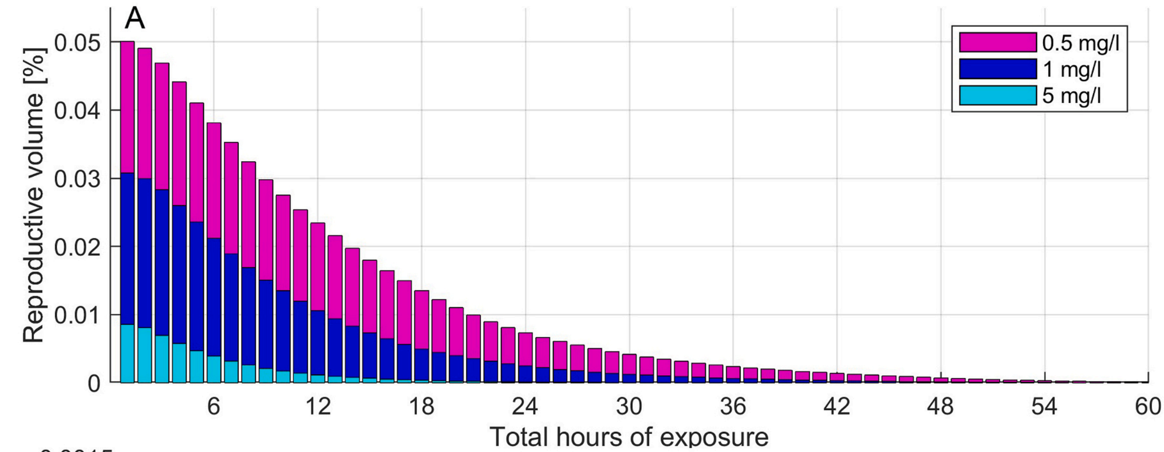

Fig. 4. Cumulative percentage of the total reproductive volume affected by excess SSC from an average single trawl passage, a) Track A and b) Track B, for up to 60 or 18 h after trawling, respectively. At Track B, excess SSC of 5 mg/l was not observed. Note the difference in scales in both the x and y axes. Actual affected volumes (m^3) are presented in Fig. S3.

albeit 50 times less than from Track A.

Since we only analysed the RV part of the model domain (waters between 50 and 70 m) but the sediment particles move freely in all of the model domain, particles can move in and out of the RV depending on the currents. Hence, the time in the histograms is not necessarily consecutive, but shows the sum of time during the modelled five days after the trawl passage when SSC was elevated.

ii) Excess SSC at different distances from trawl Track A

Maximum excess SSC decreased with distance from the modelled trawl track but was still elevated by 10 mg/l at a distance of 1 km from

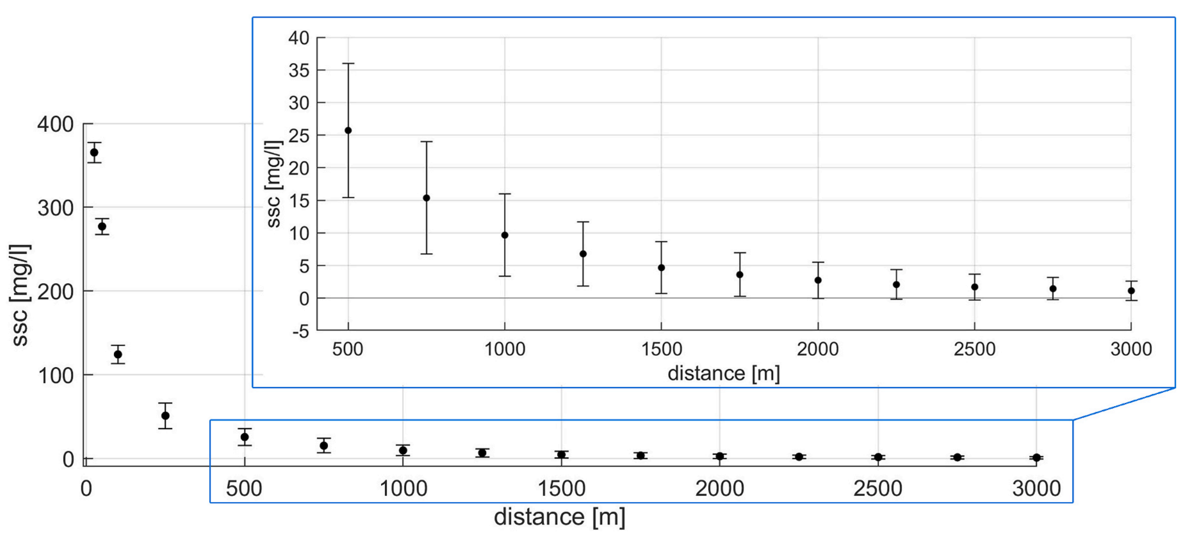

Fig. 5. The maximum modelled excess SSC that occurred in the water between 50 and 70 m depth, at different horizontal distances from the modelled trawl Track A, averaged over all trawl passages during the season. The inset magnifies the part of the main graph showing a distance of 500–3000 m from the track.

the track, 5 mg/l at 1.5 km and was above background SSC up to c. 3 km away (Fig. 5). The figure can be interpreted as a 2D-representation of the plume of maximal values of SSC from the trawl track, where the track has been reduced to a point (0,0) and the concentration of SSC is given regardless of direction or depth.

iii) Scaling up to five trawlers fishing simultaneously

When five boats trawled close together, the initial excess SSC was five times higher but there was only a small increase (<57%) in the total water volume affected by increased SSC (Fig. 6, dashed-dotted lines), presumably since the same water volume was affected by all five trawlers. However, when five boats trawled at least 3 km apart (Fig. 6, dashed lines) the opposite was the case; maximum excess SSC was the same, but the total water volume with increased SSC was five times

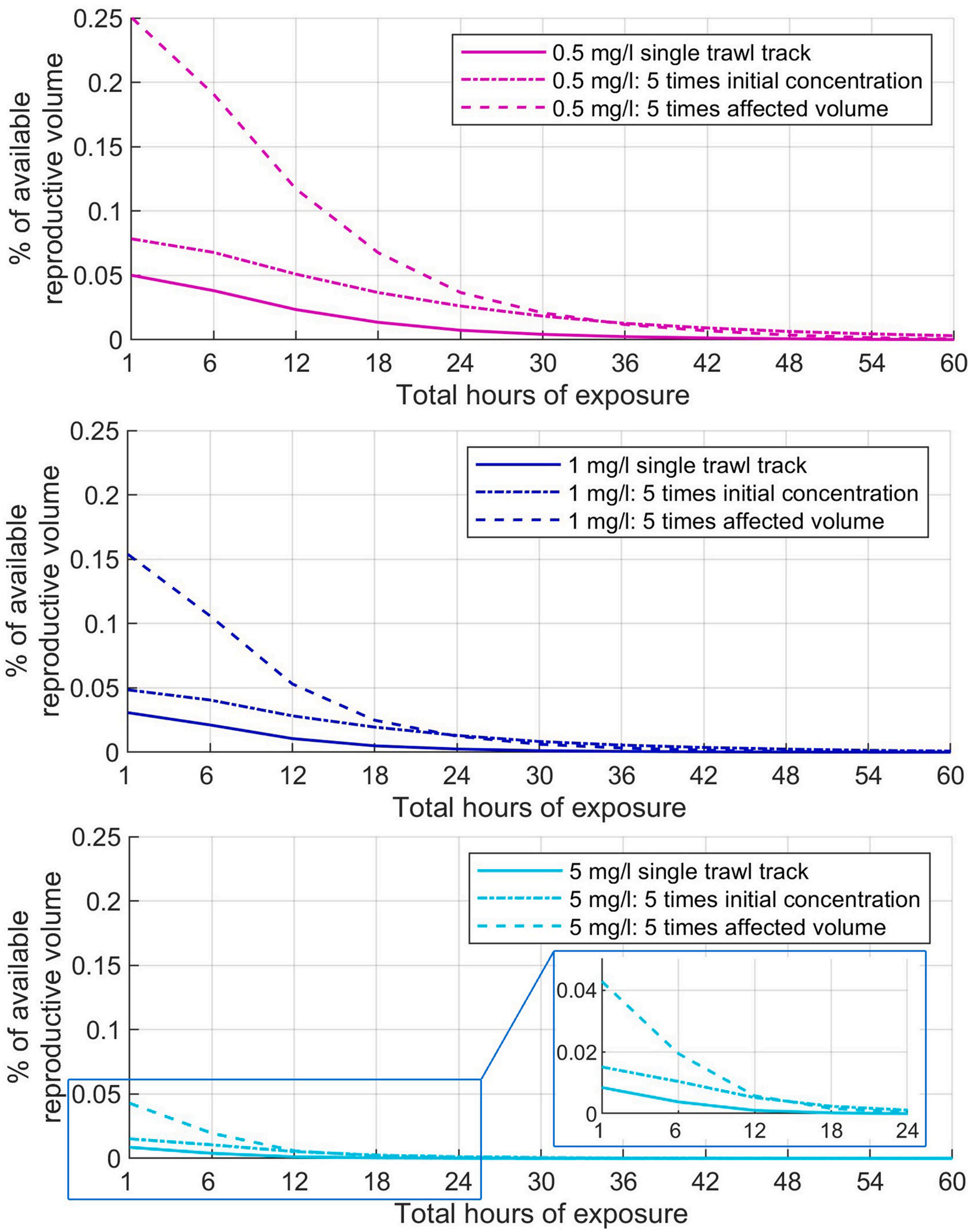

Fig. 6. Cumulative % of the RV experiencing excess SSC of a) 0.5 mg/l, b) 1 mg/l and c) 5 mg/l for three different model scenarios. Solid line: one single trawl track (scenario (i); same data as in Fig. 3). Dashed-dotted line: five boats trawling close together (scenario iii-a). Dashed line: five boats trawling at a distance where the resulting suspension does not overlap (scenario iii-b).

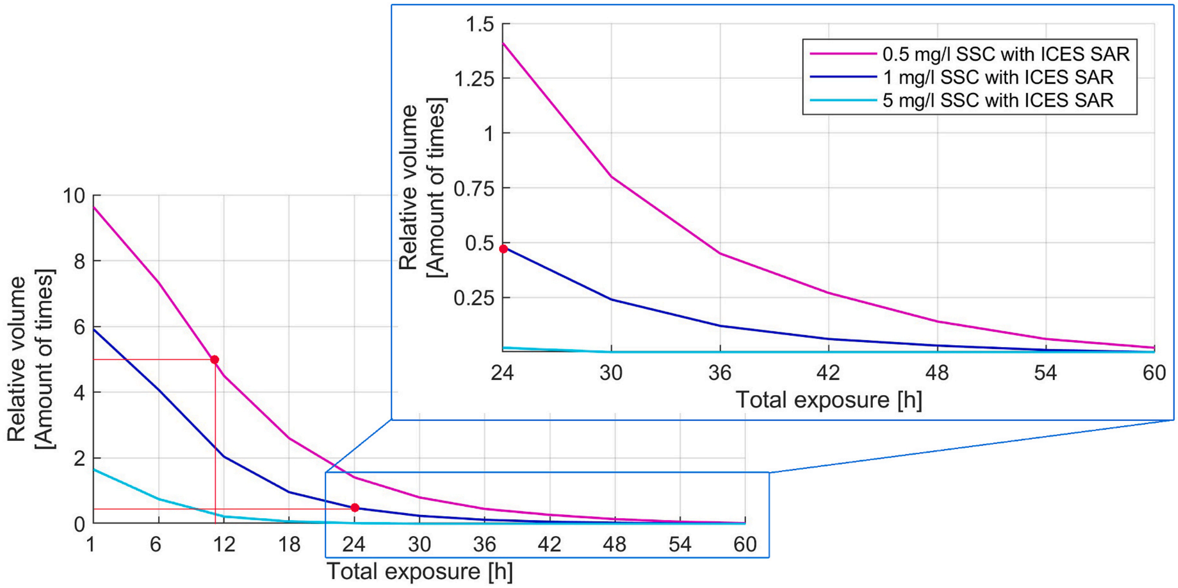

Fig. 7. Total volume, expressed in "number of times the total RV" affected by 0.5, 1 and 5 mg/l excess SSC up to 60 h after exposure to realistic bottom trawling intensities (from ICES, 2017), upscaled from modelling of a single trawl track (A). The inset magnifies the time period 24–60 h after trawling. The red dots show the specific data examples discussed in the text. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

larger than that caused by a single trawl track (solid line).

iv) Scaling up to realistic fishing intensities

We used the calculated SSC and average volume of water affected by the 0.4 km^2 modelled Track A (Fig. 4a) to estimate the potential extent of sediment suspension in the part of the RV where seabed depth is 50–70 m, expressed as the % of the whole RV. A volume of water equal to the entire RV experiences excess SSC of at least 0.5 mg/l for c. 10 h five times during one year (Fig. 7), and a volume equal to half of the RV experiences excess SSC of at least 1 mg/l for a total of 24 h during the year (Fig. 7, inset). However, this is a 'best case' estimate since these values are averages across the entire RV; in reality the majority of the suspended sediment remains within approximately 3 km of the track (Fig. 5). It is therefore reasonable to assume that the actual excess SSC will mostly occur within the 33% of the RV where the seabed is also between 50 and 70 m (sub-area diagonally shaded area in Fig. 3); In addition, trawling is not evenly distributed within this 33%, but is focussed in the NW and SW (SAR is >1 in 25% of this 33%) (Fig. 3); excess SSC will therefore occur mostly in this 1/12 of the total RV; or put another way, excess SSC will be 12x more frequent or long-lasting in this sub-area. Lastly, the extrapolation estimates the water volume affected in total over a year, but there is temporal variation in fishing intensity.

3.2. *Effect of increased SSC on cod egg buoyancy*

For the three excess SSCs of 5, 1 and 0.5 mg/L, we calculated that it would take 1.7, 5.9 or 8.3 days, respectively, for an egg at the top of the RV (50 m water depth, salinity 11) to sink out of the RV (70 m water depth, salinity 15) into unfavourable conditions below (see Supplementary Material S3.2). The modelled increase in SSC from trawling thus speeds up the time taken for an egg to sink through the RV; the sinking times are 11, 40 and 55%, respectively, of the assumed time taken at background SSC.

4. Discussion

We showed that even a single track from a bottom trawl can cause substantial volumes of water to experience SSC >0.5 mg/l above background for many days. Scaling up from a single modelled trawl track to five boats fishing simultaneously showed that their positions relative to each other determined the maximum SSC and the total volume affected. In a realistic scenario based on actual bottom trawling intensities for the year 2016, we showed that a water volume equivalent to the entire reproductive volume for Eastern Baltic cod can experience elevated SSC several times a year. Excess SSC may be higher, more frequent or last longer depending on the exact spatiotemporal distribution of fishing effort in or near the RV; mortality of cod eggs and larvae will ultimately depend on the spatial and temporal overlap between spawning and trawling events during the reproductive period for a broadcast spawner like cod.

4.1. *Trawling-induced sediment suspension could affect cod egg survival*

A number of studies have examined the conditions required for Eastern Baltic cod egg survival, providing models or relationships based on parameters such as oxygen, salinity and temperature (e.g., Nissling et al., 1994; Wieland et al., 1994; Köster et al., 2005; Hinrichsen et al., 2007, 2016; Hüssy, 2011). However, only a few experimental studies have specifically considered sinking rates, relative to variable salinity (Nissling et al., 1994) or turbidity (Westerberg et al., 1996). Those authors highlighted that increased sinking rates would mean that eggs risk more quickly entering deep water with unfavourable oxygen conditions. It is known that sediment particles adhere to the chorion of fish eggs (Griffin et al., 2009; Phan et al., 2020), causing a loss of buoyancy (Isono et al., 1998), but there is only one available study linking turbidity with loss of buoyancy of Baltic cod eggs (Westerberg et al., 1996). Using a modified version of their 'sinking factor', we estimated that at excess SSCs of 5–0.5 mg/l it would take 1.7–8.3 days for a cod egg to sink from the top of the RV into unfavourable conditions below. Considering that cod eggs take approximately 14 days to hatch into larvae (at 7°C; Wieland et al., 1994; Hüssy, 2011), this means that there is a significant risk that the eggs will not have sufficient time in the RV to hatch. For eggs that are found deeper in the RV when exposed to suspended sediment, eggs will reach unfavourable conditions even more quickly. Our estimates should be taken as gross approximations, since they are based on extrapolations from a single SSC-egg buoyancy study, and we used number of assumptions in the calculations (see S3.1 and S3.3). However, as approximations we consider them robust; varying the assumptions of background SSC and sinking times at background SSC did not substantially alter the sinking times at excess SSCs, which remained <14 days and between 8 and 10%, 28–35% and 43–52% of the sinking time at background SSC (for 5, 1 and 0.5 mg/l, respectively) (S3.3).

Since cod eggs take c. 2 weeks to hatch under normal conditions, the eggs in the water column at any one point in time are the result of 2 weeks of accumulated production. Thus, exposure to even a single excess SSC event that causes the eggs to sink out of the RV may in effect eradicate 2 weeks of egg production in the exposed water volume. It will take days to weeks to replenish the eggs through new spawning and influx from adjacent areas. In the 1/12 of the RV most affected by trawling and where the RV reaches the seabed, this may occur frequently enough to prevent successful hatching during the spawning season. We did not take temporal variation into consideration in this study, since the timing of peak egg abundance varies widely from year to year and due to a lack of temporally resolved fishing data. However, there is spatio-temporal overlap of the RV and the demersal trawl fishery that is concentrated in the areas where the eggs originate within the Bornholm Basin (Fig. 3; Eero et al., 2019). Fishers also often target aggregations of cod to maximise their catches, and it is most likely that the patchiness of the fishery matches the aggregation of spawners and thus the origin of the eggs. In summary, with an increasing fraction of the RV affected as the number of trawlers increases and concentrates in the spawning sites within the RV, a proportionally higher fraction of the total number of eggs will have reduced buoyancy and elevated mortality.

Modelling studies that have incorporated cod egg buoyancy have generally assumed constant buoyancy throughout the model runs, with vertical movement occurring due to transport into areas with different salinities (Pacariz et al., 2014; Hinrichsen et al., 2016). In fact, cod eggs increase in density towards the end of their development (Petereit et al., 2014), so these mortality rates are likely to be underestimates. Here we additionally show that decreased buoyancy due to suspended matter attached to the eggs should be considered in such estimates. If eggs sink out to the seafloor, egg mortality may also increase through abrasive bottom contact, smothering by bottom sediment or increased predation (Henley et al., 2000; Pacariz et al., 2014; Hinrichsen et al., 2016).

This study focussed on the implications of increased SSC on cod eggs, but other life stages and species are also negatively impacted by suspended matter. Cod larvae that hatch at or near the bottom of the RV will face sub-optimal oxygen levels, reducing their viability (Nissling et al., 1994; Wieland et al., 1994). Suspended sediment in itself also leads to poorer condition and increased mortality in newly hatched cod yolk-sac larvae at 10 mg/l (Nissling et al., 1994; Wieland et al., 1994; lower concentrations were not examined in those studies) and fish larvae in general are sensitive to suspended sediment (Kjelland et al., 2015; Wenger et al., 2017), effects being determined by a combination of SSC and exposure time (Wilber and Clarke, 2001). Adult cod actively avoid water where SSC is > 3 mg/l (Westerberg et al., 1996) and adults of other fish species also show avoidance behaviour, but when this is not possible, physiological performance often decreases, largely due to gill clogging and damage and resulting oxygen stress (Kjelland et al., 2015). Even small decreases in egg hatching success or physiological condition and mortality of eggs and larvae can have large effects on the overall recruitment success and population size (Rijnsdorp et al., 2009). Additionally, changes in the timing of spawning or hatching can be ecologically important since they may cause a mismatch in timing with species that rely on eggs and larvae for food (Morgan et al., 1983).

Suspension of organic-rich sediments, such as those in the Bornholm Basin, leads to enhanced organic matter remineralisation rates by chemical and microbial processes (Riemann and Hoffman, 1991; Ståhlberg et al. 2006; van de Velde et al., 2018). This can result in a 5–10% decrease in oxygen concentration in the water in the 1–2 h after initial suspension (Riemann and Hoffman, 1991; Sloth et al., 1996), or as much as 59% over c. 12 h (Almroth et al., 2009). The Bornholm Basin is already seasonally or permanently hypoxic/anoxic and the areal extent and duration of hypoxia are increasing (Bendtsen and Hansen, 2013; Carstensen et al., 2014), so suspended sediment may exacerbate (or already be a partial cause of) this problem. Van Denderen et al. (2020) highlighted that bottom trawling and hypoxia act together to impact benthic communities in the southern Baltic. These two stressors overlap and occur in adjacent seabed areas; they are not disconnected, due to temporal and spatial variability. Our study additionally shows connectivity due to sediment transport. It should also be noted that most trawling in the Bornholm Basin occurs at depths that are rarely disturbed by natural processes such as waves and storms (Jönsson, 2006). Lastly, suspended sediments can contain naturally-occurring metals or anthropogenic contaminants, hydrogen sulphide and bacteria that might also contribute to decreased fitness or mortality (Isono et al., 1998; Roberts, 2012). Much of the research on the effects of suspended sediment on fish has been done in the context of seabed dredging. These operations require risk assessments of SSC, and measures are often taken to minimize effects on local fauna and flora, for example by carefully choosing the timing of operations (Suedel et al., 2008). However, these aspects are not considered in the case of bottom trawling, despite it affecting much larger seabed areas (Tjensvoll, 2014).

4.2. Implications for fish recruitment and fisheries management

The Eastern Baltic cod stock has been depleted due to historical overfishing and in poor condition for many years, potentially due to low oxygen, food limitation, parasitism and predation (Mackenzie et al., 1996; Köster et al., 2005; ICES, 2022). Numbers have decreased, population structure has been altered, recruitment is poor and adults have poor body condition (Eero et al., 2012). Previously, recruitment occurred in the Gdansk and Gotland Deeps, but this has been very limited since the 1980s, leaving the Bornholm Basin as the only Eastern cod recruitment ground (Köster et al., 2017; Karaseva, 2018). The stability and sustainability of the stock is highly uncertain (Eero et al., 2015) and since July 2019 there has been a closure for the cod fishery, though limited bottom trawling has continued for flatfish (ICES, 2022). Since 1995, there has been a seasonal closure in the spawning area of the Bornholm Basin to protect the spawning stock from disturbance. The size, shape and time of closure has varied (Eero et al., 2019) but it only partially covers the spawning area and the time of the closure is too short to cover the whole spawning period (ICES, 2018). In addition, there is evidence for displacement of fishing effort to the edges of this area during the closed season (Suuronen et al., 2010; Bastardie et al., 2015; Eero et al., 2019), which therefore could have maintained excess SSC entering the spawning ground just as eggs are being produced.

Moving the perimeter of the seasonal spawning closure outwards would dramatically decrease the SSC entering the spawning area. Our study has shown that SSC 3 km away from a trawl track is still above background (by c. 1 mg/l, Fig. 3), in line with other studies (Linders et al., 2017; Bradshaw et al., 2021). Restricting fishing to at least 3 km away from the RV would be a straightforward measure to minimize potential impacts from sediment suspended by bottom trawling. However, the RV is not a static feature, but varies both in horizontal and vertical extent within the season (Köster et al., 2005) and from year to year (Plikshs et al., 1993; Mackenzie et al., 1996; Hinrichsen et al., 2007). Additionally, peak spawning time has changed over time (Eero et al., 2019) and seasonal hypoxia is more frequent and prolonged (Carstensen et al., 2014). Previous changes in closure management have apparently not been based on clear biologically-based reasoning (Hinrichsen et al., 2007; Suuronen et al., 2010; Eero et al., 2019). From the perspective of trawl-suspended sediment, a scientific rationale could be to prohibit trawling between 50 and 70 m and not closer than e.g. 3 km to the maximum historical extent of the RV.

CRediT authorship contribution statement

Hanna Corell: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Clare Bradshaw:** Writing – review & editing, Writing – original draft, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Mattias Sköld:** Writing – review & editing, Writing – original draft, Visualization, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

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 will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2023.108232.

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