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Combined effects of fishing and oil spills on marine fish: role of stock demographic structure for offspring overlap with oil

Running head: Demography and oil spill effects

Leif Chr. Stige[1,*], Geir Ottersen[1,2], Natalia A. Yaragina[3], Frode B. Vikebø[2], Nils Chr. Stenseth[1,4], Øystein Langangen[1]

[1]Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, P.O. Box 1066 Blindern, N-0316 Oslo, Norway.

[2]Institute of Marine Research, P.O. Box 1870, N-5817 Bergen, Norway

[3]Polar Research Institute of Marine Fisheries and Oceanography (PINRO), 6 Knipovich Street, Murmansk 183038, Russia.

[4]The Centre for Coastal Research, University of Agder, P.O. Box 422, N-4604 Kristiansand, Norway.

[*]*Corresponding author: tel: +47 22854608; fax: +47 22854001; e-mail: l.c.stige@ibv.uio.no*

Abstract

It has been proposed that the multiple pressures of fishing and petroleum activities impact fish stocks in synergy, as fishing-induced demographic changes in a stock may lead to increased sensitivity to detrimental effects of acute oil spills. High fishing pressure may erode the demographic structure of fish stocks, lead to less diverse spawning strategies, and more concentrated distributions of offspring in space and time. Hence an oil spill may potentially hit a larger fraction of a year-class of offspring. Such a link between demographic structure and egg distribution was recently demonstrated for the Northeast Arctic stock of Atlantic cod for years 1959−1993. We here estimate that this variation translates into a two-fold variation in the maximal proportion of cod eggs potentially exposed to a large oil spill. With this information it is possible to quantitatively account for demographic structure in prospective studies of population effects of possible oil spills.

Key words: oil spill; fishing; multiple stressors; fish eggs; Atlantic cod *Gadus morhua*; Barents Sea

Highlights

- We quantify maximal potential overlap between fish eggs and hypothetical oil spills
- Maximal overlap is highest when the spawning stock is dominated by small fish
- Fishing may thus influence sensitivity to oil spills through effect on demography
- Our results can be used in prospective studies to correct for this effect

Introduction

Multiple stressors such as over-exploitation and pollution often impact natural systems non-additively, implying a need to study such impacts in concert (Crain et al., 2008). High fishing pressure has led to demographic changes in many fish stocks, towards increased dominance of young and small spawners (Law, 2000; Longhurst, 2002; Berkeley et al., 2004; Ottersen, 2008). It is feared that heavy fishing thereby increases the stocks' sensitivity to environmental influences, including effects of acute oil spills (Hjermann et al., 2007). Specifically, erosion of demographic structure may reduce the diversity of spawning strategies and the spatiotemporal distribution of eggs and larvae (Kjesbu et al., 1992; Opdal, 2010; Opdal and Jørgensen, 2015), which are life-stages thought to be particularly sensitive to toxic oil compounds (e.g., Carls et al., 1999; Sørhus et al., 2015). Hence, the proportional overlap between these sensitive early life-stages and oil in the case of an oil spill may increase. However, quantitative knowledge on how erosion of spawning stock structure influences potential overlap of offspring with oil is scarce.

The Northeast Arctic (NEA) stock of Atlantic cod *Gadus morhua* is currently the world's largest and of high economic and ecological importance (Kjesbu et al., 2014). Spawning occurs along the west and north coasts of Norway from mid-February to early May (Ottersen et al., 2014) and the eggs and larvae drift pelagically north- and eastwards towards the Barents Sea nursery area (Olsen et al., 2010). The drift path of the eggs and larvae crosses areas with ongoing oil activities as well as areas that are closed for such activities due to concern for fisheries and the environment – a topic of political and scientific debate (Misund and Olsen, 2013; Blanchard et al., 2014).

Statistical analyses of egg survey data for NEA cod for 1959−1993 revealed positive associations of distributional extent of cod eggs with mean weight (and alternatively, age) in the spawning stock, spawning stock biomass and a liver condition index (Stige et al., 2017). We here build on results of Stige et al. (2017) and use the same egg survey data to quantify in more detail how changes in mean weight and biomass of spawners are likely to influence the egg distribution and thereby the potential overlap between eggs and oil. We first consider a case study where overlap between oil and cod eggs is simulated for a large oil spill near the main spawning grounds of NEA cod for one year, and assess how hypothetical changes in egg distribution associated with demographic variables influences overlap calculations. Subsequently, we construct an index of "worst-case" overlap rate by identifying the areas with highest cod egg concentrations and calculating how large a fraction of a year-class is maximally contained within an area of a given size. We then assess how this fraction depends on spawning stock biomass and mean weight of spawners. We thus quantify the roles of stock size and demographic structure in influencing potential year-class susceptibility to geographically bounded events such as oil spills. We hypothesize that both low mean weight and low total biomass of spawners lead to increased susceptibility to oil spills.

Methods

Data

Eggs of NEA cod were sampled during dedicated ichthyoplankton surveys by the Polar Research Institute of Marine Fisheries and Oceanography (PINRO), Murmansk (Mukhina et al., 2003). The survey covered main drift areas of eggs and larvae of NEA cod between 67°30'N and 74°30'N from about 7 km (4 nautical miles) to 500 km from the coast. From around 10 % to 25 % of the landings from the fisheries on spawning fish in years 1959−1969 were from south of the survey area (Opdal, 2010), with the long-term trends in the proportion apparently covarying with the mean age of the spawners [(Opdal and Jørgensen, 2015) but see (Sundby, 2015)]. The survey was conducted in April−May, i.e. 0−2 months after the peak spawning of the cod (Ellertsen et al., 1989), each year from 1959 to 1993, except 1967, when there was no survey. On average 156 stations were sampled each year, but with considerable variability among years in the extent and timing of the survey (Mukhina et al., 2003; Stige et al., 2015). Cod eggs were classified into four developmental stages based on morphology. Stage-1 eggs could not be reliably differentiated from the eggs of haddock. Stage-1 eggs were therefore classified to species according to the fraction of cod compared to haddock eggs of stages 2−4 in the sample. For further details on the ichthyoplankton data we refer the reader to Mukhina et al. (2003) and Stige et al. (2015).

Spawning stock biomass (*SSB*, tonnes) data were obtained from ICES (2009). *SSB* is computed using values for stock number at age from extended survivors analysis (XSA) based mainly on fisheries data, weight-at-age in the stock and maturity-at-age, calculated as weighted averages from Russian and Norwegian surveys during the autumn and winter seasons (Marshall et al., 2006; ICES, 2009). We used log-transformed biomass, *logSSB* = $\log_e$(*SSB*), hence assuming a log-linear relationship with egg abundance in the statistical analysis.

Mean biomass-weighted weight in the spawning stock ($\overline{W}$, kg) was calculated from abundance-at-age estimated by XSA, weight-at-age and maturity-at-age, all from ICES (2009):

$$(1) \qquad \overline{W}_j = \frac{\sum_{a=3}^{a=13+} W_{aj}(N_{aj}W_{aj}M_{aj})}{\sum_{a=3}^{a=13+}(N_{aj}W_{aj}M_{aj})}$$

Here, N_{aj}, W_{aj} and M_{aj} are, respectively, number, mean weight (kg) and proportion mature at age *a* in year *j*. The product $(N_{aj}W_{aj}M_{aj})$ is thus mature biomass-at-age and the denominator sums up to SSB_j. By weighting by biomass and not abundance of each age class, $\overline{W}$ represents the sizes that dominate the spawning stock in terms of potential egg production. $\overline{W}$ is highly correlated with mean age in the spawning stock (product-moment correlation, *r* = 0.92).

The liver condition index (*COND*, %) is liver wet weight, measured as percentage of total wet weight for cod of lengths 41−70 cm for January−December the year before spawning (Yaragina and Marshall, 2000).

Statistical analysis of how spawning stock variables influence egg distribution

To quantify the change in spatial distribution of cod eggs under contrasting biomass and size structure in the spawning stock, we fit a spatiotemporal statistical model to the cod egg data. Following results of time-series analyses by Stige et al. (2017) identifying significant predictors of cod egg distributional extent, we included sampling day-of-year (*Day*), sampling location (*Lon*, °N, and *Lat*, °E), *COND*, $\overline{W}$ and *logSSB* as predictor variables. Following the same results, no abiotic environmental variables were included. The spatiotemporal statistical model was used to estimate the spatial distribution of cod eggs as function of $\overline{W}$ and *logSSB* and mean values of the other predictor variables. Specifically, the expected stage-specific and total egg abundances at different locations in the survey area at a date representing a peak in observed egg abundance halfway through their development (10^{th} April) were calculated by multiplying estimated probabilities from a binomial submodel with estimated conditional abundances from a lognormal submodel. The spatiotemporal statistical model is described in detail in the Appendix.

Simulation of overlap between oil and fish offspring

To illustrate how spawning stock size and demographic structure can be accounted for in oil spill simulations we used results from Vikebø et al. (2014), who modelled overlap between oil compounds and eggs and larvae of NEA cod for four hypothetical oil spill scenarios, all simulated for the same year (i.e., 1997). The modelling is described in details by Vikebø et al. (2014) and only summarised here. Specifically, 94 500 particles each representing a large number of cod eggs were released at the known spawning grounds and in the spawning period (1 March − 30 April) of NEA cod and transported horizontally based on their vertical positioning in the water column and ocean currents. Ocean currents were simulated using a regional ocean model system for the Nordic Seas with resolution 4×4 km (Lien et al., 2014). The transport and fate of oil compounds were simulated based on the same ocean model. We here investigated two oil spill scenarios representing a large oil spill at the peak of the spawning season (i.e., 4500 tonnes of oil per day for 30 days, 1−30 April) but differing in oil spill location (scenario 1: N 68.67, E 13.92, scenario 2: N 68.83, E 13.45). Two other scenarios with oil spill locations farther south investigated by Vikebø et al. (2014) were not analysed here because the majority of the impacted eggs were outside of the survey area (N 67.5−74.5, E 8−31.5). For each particle we found the maximal concentration of total polycyclic aromatic hydrocarbon (TPAH) along its drift trajectory through the egg and larval stages, here using the highest concentration in the water column (Vikebø et al., 2014, also considered ambient concentrations at the depths of the particles). Overlap was calculated as percentage of individuals having maximal TPAH concentration above thresholds of 0.1 parts per billion (ppb) or 1.0 ppb, representing, respectively, order of magnitude thresholds for sublethal and lethal effects. Note that work is still ongoing to refine these values for different stages and species.

The simulation results of Vikebø et al. (2014) represent a historical average situation in terms of spawning stock size and –structure. To assess the effect of altering $\overline{W}$ or *logSSB* we weighted the particles, i.e. the number of individuals each particle represented, based on the results of the statistical analysis of how spawning stock variables influence egg distribution. The weighting was based on the location of the particles half-way through the egg development, i.e., around the transition from the second to the third egg stage. To simulate the egg distribution expected under high $\overline{W}$ each particle was weighted by the predicted egg abundance for that location for the 90th percentile of $\overline{W}$ divided on the prediction for the same location for mean $\overline{W}$. The predictions were for total numbers of stage-2 and stage-3 eggs at April 10, which was between the peaks of abundance for these two stages. Note that effects of $\overline{W}$ and *logSSB* on egg distribution in the statistical model were assumed to be independent of day-of-year and egg stage (at the linear scales of the predictors in the binomial and lognormal submodels); hence the application of these weights based on locations at a single developmental stage independent of when that stage is reached is consistent with the statistical model. Particles outside of the survey area (representing 20 % of the individuals) were excluded from the analysis in order to avoid extrapolation. Subsequently we calculated the fraction of the year-class exposed to sublethal or lethal concentrations of oil for each oil spill scenario. Corresponding calculations were made for the 10th percentile of $\overline{W}$ and for the 10th and 90th percentile of *logSSB*.

How does "worst-case" potential overlap rate depend on spawning stock variables?

While the oil spill simulation illustrates the role of stock size and demographic structure for two oil spill scenarios, other scenarios with the same spatial extent but different locations of oil could conceivably give higher overlap with cod eggs and larvae (e.g., Carroll et al., 2018). We thus constructed an index of maximum number of cod eggs contained within an area representative of a large oil spill and investigated how this index varied with spawning stock variables. To construct this index we used the spatiotemporal statistical model of how spawning stock variables influence egg distribution and calculated stage-specific as well as total egg abundance for a grid at fixed 1° longitude and 1/3 ° latitude intervals over the study area. The area represented by each grid cell is given by $Area_i = 20 \cdot 1.852 \cdot 60 \cdot 1.852 \cdot \cos(\pi \cdot Lat_i/180)$ km^2 and varied from 1111 km^2 in the north to 1564 km^2 in the south. For given values of $\overline{W}$ and *logSSB* we ranked the grid cells according to expected egg concentration and calculated the cumulative number of expected eggs as function of cumulative area. Note that these grid cells were not necessarily contiguous. We then compared the maximal proportions of the eggs contained within 10 000 km^2 or 40 000 km^2 dependent on $\overline{W}$ and *logSSB*. These area sizes represent the approximate range in surface coverage of oil components at lethal concentrations in a large oil spill scenario for the region (Vikebø et al., 2014; Langangen et al., 2017).

In the presence of strong compensatory density dependence locally (e.g., Ciannelli et al., 2007), distribution area may hypothetically be a better proxy for year-class strength than abundance. We therefore also calculated maximal proportion of the total cod egg distribution area (km^2) contained within 10 000 km^2 or 40 000 km^2. For this calculation, egg occupancy area was calculated for each grid cell by multiplying grid cell area with expected probability of cod egg occurrence dependent on $\overline{W}$ and *logSSB*.

The uncertainty of the estimates was quantified by non-parametric bootstrap, whereby we generated 1000 bootstrap data sets by resampling years (with replacement) and analysed the bootstrap data sets with the same procedure as the original data.

The analyses were performed using the programming environment R version 3.2.4 (R Core Team, 2016). The mgcv package version 1.8-12 (Wood, 2006) in R was used for generalized additive modelling.

Results

The size and demographic structure of the spawning stock of NEA cod varied considerably during the studied period 1959−1993 (**Fig. S1**), with *SSB* varying by a factor of 9 between 0.10 million tonnes (*logSSB* = 11.5, in 1965) and 0.89 million tonnes (*logSSB* = 13.7, in 1992), and $\overline{W}$ varying between 2.8 kg (in 1990) and 7.9 kg (in 1974). The variation in *logSSB* and $\overline{W}$ was uncorrelated (product-moment correlation $r = -0.04$), allowing us to study each factor independently.

The generalized additive model results showed a wider spatial distribution of cod eggs at high compared to low $\overline{W}$ and at high compared to low *logSSB* (**Fig. 1**). We find that at high *logSSB*, cod egg concentrations were particularly high off the main spawning grounds at 68−70 °N, while there was no such peak at low *logSSB* (**Fig. 1**).

Results of the oil spill simulation showed that adjusting the egg distribution to that expected at low or high $\overline{W}$ or low or high *logSSB* changed the calculated oil spill effects by approximately ±5 % for the scenarios considered (see **Table 1** for exact numbers and **Fig. S2** for spatial distributions of eggs with drift paths overlapping or not with above-threshold concentrations of oil).

The maximal proportion of cod eggs contained within areas of 10 000 km^2 or 40 000 km^2 was about two times higher at the low end of the $\overline{W}$ range compared to at the high end of the $\overline{W}$ range (**Fig. 2A**). Specifically, the maximal proportion of cod eggs contained within an area of 40 000 km^2 was 0.32 (95 % confidence intervals, c.i.: 0.24, 0.40) at $\overline{W}$ = 7.9 kg and 0.57 (c.i.: 0.42, 0.71) at $\overline{W}$ = 2.8 kg. The corresponding proportions for 10 000 km^2 were 0.13 (c.i.: 0.07, 0.21) at high $\overline{W}$ and 0.29 (c.i.: 0.16, 0.43) at low $\overline{W}$. Similarly, the maximal proportion of the total distribution area contained within areas of 10 000 km^2 or 40 000 km^2 were higher at low compared to high $\overline{W}$ (**Fig. S3**).

Contrary to hypothesized, the maximal proportion of cod eggs contained within areas of 10 000 km^2 or 40 000 km^2 were higher at high compared to low *logSSB* (**Fig. 2B**). This result is linked to the high concentrations of cod eggs found near the main spawning grounds at high *logSSB* (**Fig. 1**). According to our estimates, nearly 80 % of the cod eggs can be contained within an area of 40 000 km^2 in years with high *logSSB*, compared with maximally around 40 % in years with low *logSSB*. On the other hand, the maximal proportion of the total distribution area contained within areas of 10 000 km^2 or 40 000 km^2 were higher at low compared to high *logSSB* (**Fig. S3**), which is a direct result of the total distribution area being smallest at low *logSSB*. Results for single egg stages (**Fig. S4**) resembled those for total egg abundance (**Fig. 2**).

Discussion

Our results show that fishing, by influencing size and demographic structure of the spawning stock (Law, 2000; Longhurst, 2002; Berkeley et al., 2004), may affect the potential overlap between offspring and oil in the case of an oil spill. Such an influence of the multiple pressures of fishing and oil has been suggested before (Hjermann et al., 2007; Rooker et al., 2013), but the quantitative value and hence the potential importance has until now been generally unknown.

The oil spill simulation illustrates how potential changes in egg distribution caused by changes in stock size and demographic structure can be accounted for in prospective studies. In these particular scenarios the effects of changes in spawning stock variables on overlap between oil and fish offspring were found to be small. The similarity in results for the scenarios considered is probably related to the alternative oil spill locations being relatively close to one another and that only one year was considered. It should be noted that there appeared to be fewer simulated egg particles in offshore regions than expected from the observation data (**Fig. S2** cf. **Fig. 1**) and lack of particles in these marginal areas could lead to underestimation of the effect of $\overline{W}$ on variability in egg distribution and hence overlap rate. Moreover, we found that that worst-case overlap rate is more strongly dependent on stock size and demographic structure than what overlap rate is for these scenarios.

Demographic structure has the clearest effect, and we find that potential overlap rate, measured as maximal proportion of eggs contained within an area of size as a large oil spill, varies by a factor of two in response to the near three-fold variation in $\overline{W}$ observed for NEA cod in the 1959−1993 period. Potential overlap rate is highest when $\overline{W}$ is low, as the eggs are then concentrated in a smaller area than when $\overline{W}$ is high. Low $\overline{W}$ signifies a low proportion of old and large fish in the spawning stock, a commonly described consequence of high and often size-selective fishing pressure (Law, 2000; Longhurst, 2002; Ottersen, 2008). A high proportion of old and large spawners may lead to wide offspring distribution, by allowing for a high diversity in spawning strategies (e.g., location and duration of spawning) and offspring traits (e.g., viability and egg buoyancy) that influence offspring distribution (as discussed by Hixon et al., 2014; Stige et al., 2017). Note that our analysis mainly quantified effects of $\overline{W}$ on spatial distribution; a possible seasonal contraction of spawning at low $\overline{W}$ (Wright and

Trippel, 2009) would tend to accentuate the negative effect of $\overline{W}$ on potential overlap rate.

Spawning stock biomass has a less clear effect: An oil spill may potentially hit a larger fraction of the eggs but a smaller fraction of the egg distribution area when *logSSB* is high. This is because at high *logSSB*, there is a peak in egg abundance off the main spawning grounds, at the same time as the margins of the egg distribution area expand. The mechanisms behind this peak in egg abundance at high *logSSB* are not clear. The magnitude of *logSSB* effects on potential overlap rate is similar to that of $\overline{W}$.

The population consequences of an oil spill hitting eggs in parts of the distribution depend on the spatial pattern in natural mortality (Langangen et al., 2017). Natural mortality in central parts of the distribution appears to be higher than in marginal areas (Ciannelli et al., 2007; Langangen et al., 2014a); hence, a high fraction of eggs killed if an oil spill hits these areas does not necessarily translate into high cohort loss in the long-term. This is because eggs in the high-density area have very low survival anyway. For $\overline{W}$ we get similar results if potential overlap rate is calculated from total egg abundance or from distribution area, suggesting that results also hold if local-scale compensatory density dependence in survival is strong. For *logSSB* on the other hand, the direction of its effect on maximal long-term impact of an oil spill depends on how survival is regulated locally.

Prospective simulation studies of potential overlap between oil spills and early life stages of fish (e.g., Vikebø et al., 2014; Carroll et al., 2018) typically, due to lack of information, ignore effects of spawning stock size and demographic structure on offspring distribution and exposure. We propose that future studies on NEA cod may assess effects of possible changes in spawning stock size or demographic structure as implemented in our oil spill simulation. Future studies on other stocks that lack long-term egg distribution data may use results in **Fig. 2** to assess how large uncertainty is introduced by ignoring these effects, e.g., quantitatively formalized in a Bayesian Network model (cf. Carroll and Smit, 2011) or as a correction factor. For example, if a study finds a maximal impact of 43 % (Carroll et al., 2018) of a year class assuming average values for $\overline{W}$, we suggest that one can conservatively correct this value based on the results presented here. Based on Fig. 2A, we suggest that adding 0.5 on logit scale would correct for potential increase in impact caused by reduction in $\overline{W}$ from the average value to the minimum observed $\overline{W}$. Hence, we suggest correcting the assessed impact from 43 to 55 % (as logit(0.43) + 0.5 = logit(0.55)) if one wants to account for the potential increased impact caused by a hypothetical future reduction in $\overline{W}$. In principle, hypothetical future changes in *logSSB* can be accounted for similarly, but with a less solid theoretical underpinning than for $\overline{W}$: Our statistical results suggest that the highest proportion of a year class of cod eggs can be lost in years with high *logSSB*, but the causal basis for the distribution changes that drive this result is unclear, as are the implications for long-term cohort loss.

While our results provide quantitative estimates, there are some caveats and limitations. First, we stress that the analysis of potential overlap rate (**Fig. 2**) indicates how $\overline{W}$ or *logSSB* affect “worst-case” effects of oil spills. These “worst-case” effects can be thought of as the upper tails in the probability distribution for overlap rate if an oil spill of a given size hits a random part of the study area: With low $\overline{W}$ this tail is longer. The analysis therefore does not necessarily reflect how the most likely effect of a given oil-spill scenario varies with $\overline{W}$ or *logSSB*, as indeed illustrated by the oil spill simulation.

Further, our calculated potential overlap rate should be interpreted as an index and not as an accurate estimate of maximal overlap between fish offspring and oil for a given oil spill size; for such estimates simulation modelling is needed for obtaining more realistic distributions of oil and appropriately accounting for temporal aspects and small-scale patchiness. To throw more light on the temporal aspect we assessed the spatial distribution of simulated eggs in the oil spill model at a snap-shot in time, finding that eggs having above-threshold oil concentrations at some point in their egg and larval drift trajectory were concentrated in areas of similar size as used in our calculation of potential overlap (**Fig. S5**). We therefore consider that our results are also relevant for oil spills occurring near the drift paths of eggs and larvae over an extended period. We find it unlikely that our simplifying assumption that overlap between fish offspring and oil only depends on the horizontal, and not vertical, locations of fish offspring and oil interferes with our conclusions regarding effects of $\overline{W}$ or *logSSB* on overlap rate. As shown by Vikebø et al. (2014, their Table 5), relaxing this assumption will, in general, reduce the overlap rate by roughly a third, independent of the area affected by oil. In sum, we therefore believe that our estimates are a good approximation, with a clear empirical basis, of how the mean weight of the spawners and spawning stock biomass may influence maximal contact rate between fish offspring and oil.

We conclude that loss of old and large fish from a stock due to high fishing pressure may increase its sensitivity to oil spills. Such a synergistic effect of fishing and oil is both mediated by the potential overlap between offspring and oil (this study) and by age-truncated fish stocks having reduced demographic buffering against recruitment failure (Rouyer et al., 2011; Ohlberger and Langangen, 2015). This conclusion underlines the multiple benefits of good fisheries management, which has contributed to that the biomass of NEA cod now is high and the proportion of old and large fish appears to be on the increase (Kjesbu et al., 2014).

Supplementary Material

The following figures are available as supplementary online material:

Figure S1. Spawning stock biomass (*logSSB*) and mean weight in the spawning stock ($\overline{W}$) of NEA cod from 1959 to 1993.

Figure S2. Simulated distribution of NEA cod eggs at their locations halfway through the egg development, showing which eggs experience sublethal or lethal oil concentrations for two different oil spill scenarios.

Figure S3. Maximal proportion of the total distribution area of NEA cod eggs contained within areas of 10 000 km^2 or 40 000 km^2 dependent on $\overline{W}$ or *logSSB*.

Figure S4. Maximal proportion of NEA cod eggs contained within areas of 10 000 km^2 or 40 000 km^2 dependent on $\overline{W}$ or *logSSB*, shown for each egg developmental stage.

Figure S5. Simulated distribution of NEA cod eggs at a snap-shot in time (April 10, 1997), showing which eggs experience sublethal or lethal oil concentrations at some part of their egg and larval drift trajectories for two different oil spill scenarios.

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Appendix

Spatiotemporal statistical cod egg distribution model

To quantify the change in spatial distribution of cod eggs under contrasting biomass and size structure in the spawning stock, we fit a variable-coefficient generalized additive model (Hastie and Tibshirani, 1993; Wood, 2006) to the spatiotemporal cod egg data. Following results of time-series analysis by Stige et al. (2017), we included sampling day-of-year (*Day*), sampling location (*Lon*, °N, and *Lat*, °E), *COND*, $\overline{W}$ and *logSSB* as predictor variables. As the survey data contained many stations with no eggs, the data were considered to originate from two different processes: one process determining the probability of a positive tow (i.e., non-zero abundance of eggs of a given stage at a station) and another determining the abundance conditional on a positive tow (see Langangen et al., 2014b). To account for the two processes we used a hurdle model approach (Stefánsson, 1996), whereby a binomial model quantified the probability of a positive tow and a lognormal model quantified abundance in positive tows.

The binomial submodel quantified the probability p of catching at least one egg of a given stage at a station. Each data point represents presence (coded as 1) or absence (coded as 0) of one out of four egg developmental stages at one station in one year. Each station is thus represented by four data points in the analysis, one for each egg stage. This submodel can be written as:

(2) $$logit(p_{s\,ij}) = \alpha_s + f_s(Day_i) + g_s(Lon_i, Lat_i) + \beta\ COND_j + h(Lon_i, Lat_i)\ \overline{W}_j + l(Lon_i, Lat_i)\ logSSB_j$$

where subscripts *s*, *i* and *j* represent stage, station and year, respectively. α_s is a stage-specific intercept. f_s and g_s are stage-specific smooth functions correcting for sampling date and location (g_s being a two-dimensional anisotropic smooth modelled as a tensor-product of two smooth basis functions with maximally 5 knots each). Stage-specific smooths were modelled by using the flag "by=Stage" when specifying the smooth. β is the coefficient for the effect of *COND*. The coefficients for the effects of $\overline{W}$ and *logSSB* were allowed to vary smoothly as functions of location. The smooth function $h(Lon, Lat)$ thus gives a location-dependent coefficient that $\overline{W}$ is multiplied with and $l(Lon, Lat)$ the corresponding function for *logSSB*. The number of samples taken at the station was included as offset. This binomial submodel is similar to a corresponding model with a spatially-variable $\overline{W}$ term used by Stige *et al.* (2017, Fig. 3) to visualize how cod egg distribution varies with $\overline{W}$. We here allowed the effects of both $\overline{W}$ and *logSSB* to vary spatially in order to focus on two factors directly influenced by human activities, while the effect of *COND* was spatially invariable in order to limit the number of parameters in the model.

Furthermore, in contrast to Stige et al. (2017), we also quantified how cod egg abundance within the distribution area varies with $\overline{W}$ and *logSSB*. To do so, we modelled the natural logarithm of cod egg abundance in positive tows, $\log_e(N)$, but using only non-zero counts and assuming a normal error distribution (ε). This submodel can be summarized as:

(3)
$$\log_e(N_{sij}) = \gamma_s + m_s(Day_i) + n_s(Lon_i, Lat_i) + \delta\ COND_j + p(Lon_i, Lat_i)\ \overline{W}_j + q(Lon_i, Lat_i)\ logSSB_j + \varepsilon_{sij} \quad \text{for} \quad N_{sij} > 0$$

The notation is analogous to Eq. 2. For this analysis, the natural logarithm of the number of samples taken at the station was offset.

This hurdle model was used to map the expected total egg abundance as function of $\overline{W}$ and *logSSB*. Specifically, we calculated total egg abundance (sum of all stages) by multiplying predicted probabilities from Eq. 2 with predicted conditional abundances from Eq. 3 (taking into account that expected *N* from Eq. 3 is the exponent of the expected $\log_e(N)$ + ½ variance of $\log_e(N)$).

Table 1. Overlap of NEA cod eggs and larvae with oil as function of mean weight in the spawning stock ($\overline{W}$) and spawning stock biomass (*logSSB*) for two oil spill scenarios in year 1997 and alternative threshold concentrations of oil compounds.

	Percentage overlap [Overlap relative to baseline]				
Scenario / threshold	Baseline	Low $\overline{W}$	High $\overline{W}$	Low *logSSB*	High *logSSB*
Oil spill scenario 1 / 0.1 ppb	20.3 [1]	21.3 [1.05]	19.6 [0.97]	21.0 [1.03]	19.6 [0.97]
Oil spill scenario 1 / 1.0 ppb	5.7 [1]	5.9 [1.05]	5.4 [0.96]	5.8 [1.06]	5.5 [0.96]
Oil spill scenario 2 / 0.1 ppb	29.8 [1]	31.3 [1.05]	28.6 [0.96]	31.5 [1.02]	28.4 [0.96]
Oil spill scenario 2 / 1.0 ppb	11.1 [1]	11.8 [1.06]	10.6 [0.96]	12.0 [1.07]	10.5 [0.95]

Baseline: $\overline{W}$ = 5.5 kg and *logSSB* = 12.4, low $\overline{W}$: 3.8 kg, high $\overline{W}$: 6.9 kg, low *logSSB*: 11.7, high *logSSB*: 13.0

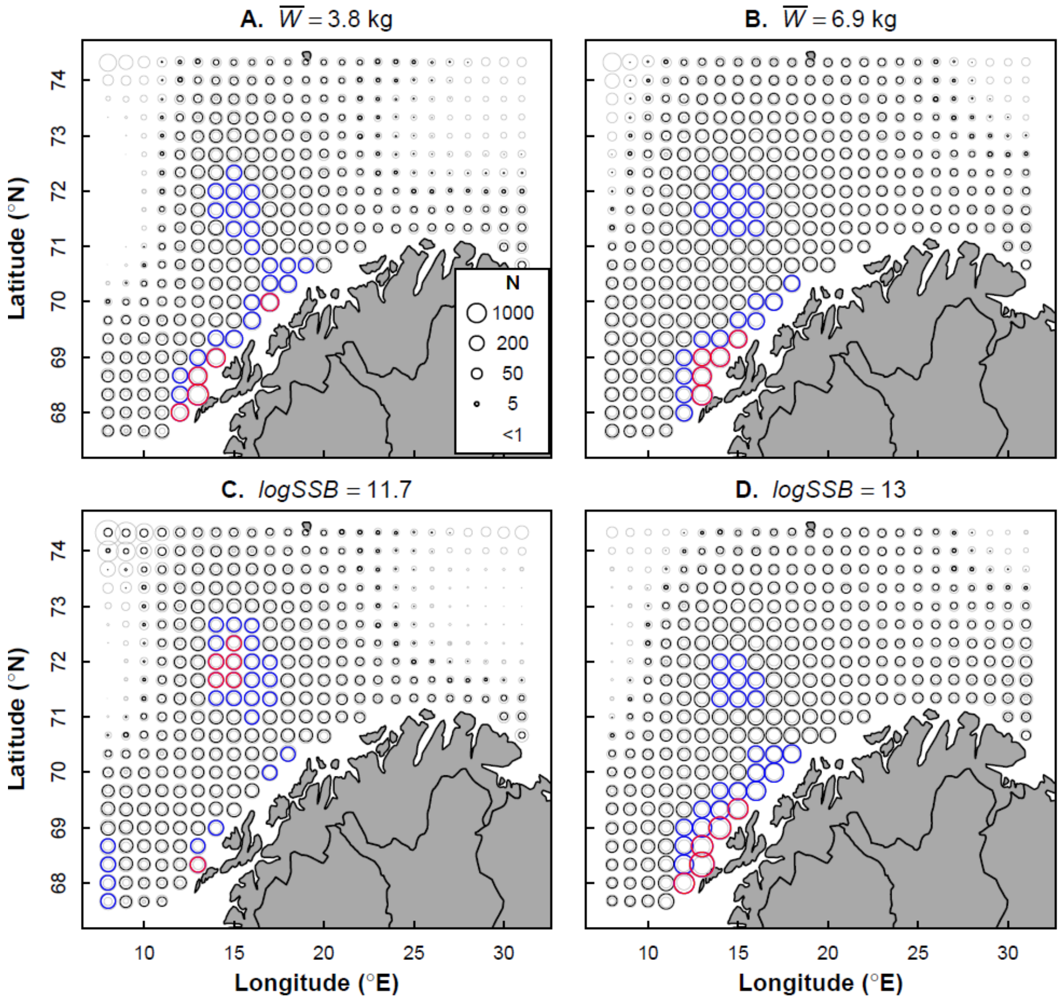

Figure 1. Expected distribution of Northeast Arctic (NEA) cod eggs at different combinations of mean weight in the spawning stock, $\overline{W}$, and spawning stock biomass, *logSSB*. Panels A and B represent 10th and 90th percentile of $\overline{W}$ and mean *logSSB*. Panels C and D represent 10th and 90th percentile of *logSSB* and mean $\overline{W}$. Sizes of circles scale with total expected egg abundance per net haul, with grey circles representing 95 % bootstrap confidence intervals. Red and blue circles show the grid cells representing, respectively, the 10 000 km^2 and 40 000 km^2 with highest egg abundance.

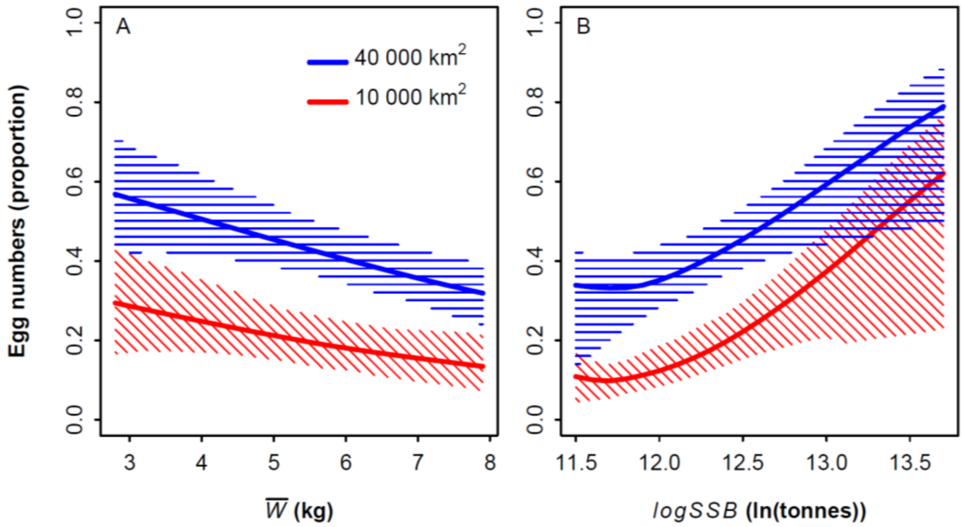

Figure 2. Maximal proportion of NEA cod eggs contained within areas of 10 000 km^2 or 40 000 km^2 dependent on (A) mean weight in the spawning stock, $\overline{W}$, or (B) spawning stock biomass, *logSSB*. Hatched lines represent 95 % confidence intervals (horizontal blue lines for 40 000 km^2, oblique red lines for 10 000 km^2).

Supplementary Information

This online supplementary information file accompanies the paper:

Stige, L.C., Ottersen, G., Yaragina, N.A., Frode B. Vikebø, Stenseth, N.C., and Langangen, Ø., 2018. Combined effects of fishing and oil spills on marine fish: role of stock demographic structure for offspring overlap with oil. Marine Pollution Bulletin.

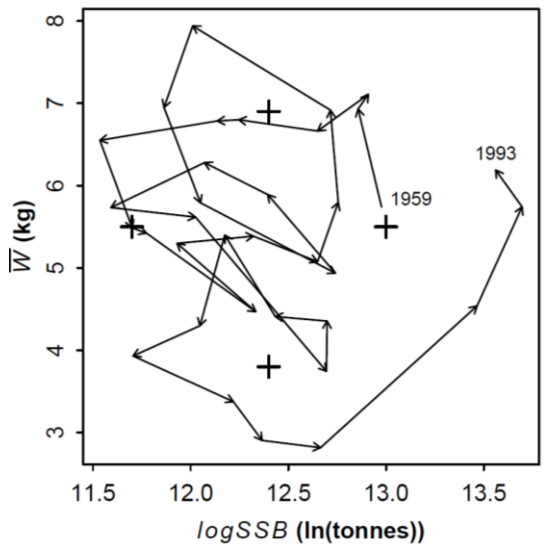

Figure S1. Spawning stock biomass (*logSSB*) and mean weight in the spawning stock ($\overline{W}$) of Northeast Arctic cod from 1959 to 1993. Crosses are at 10th percentile, mean and 90th percentile of variables.

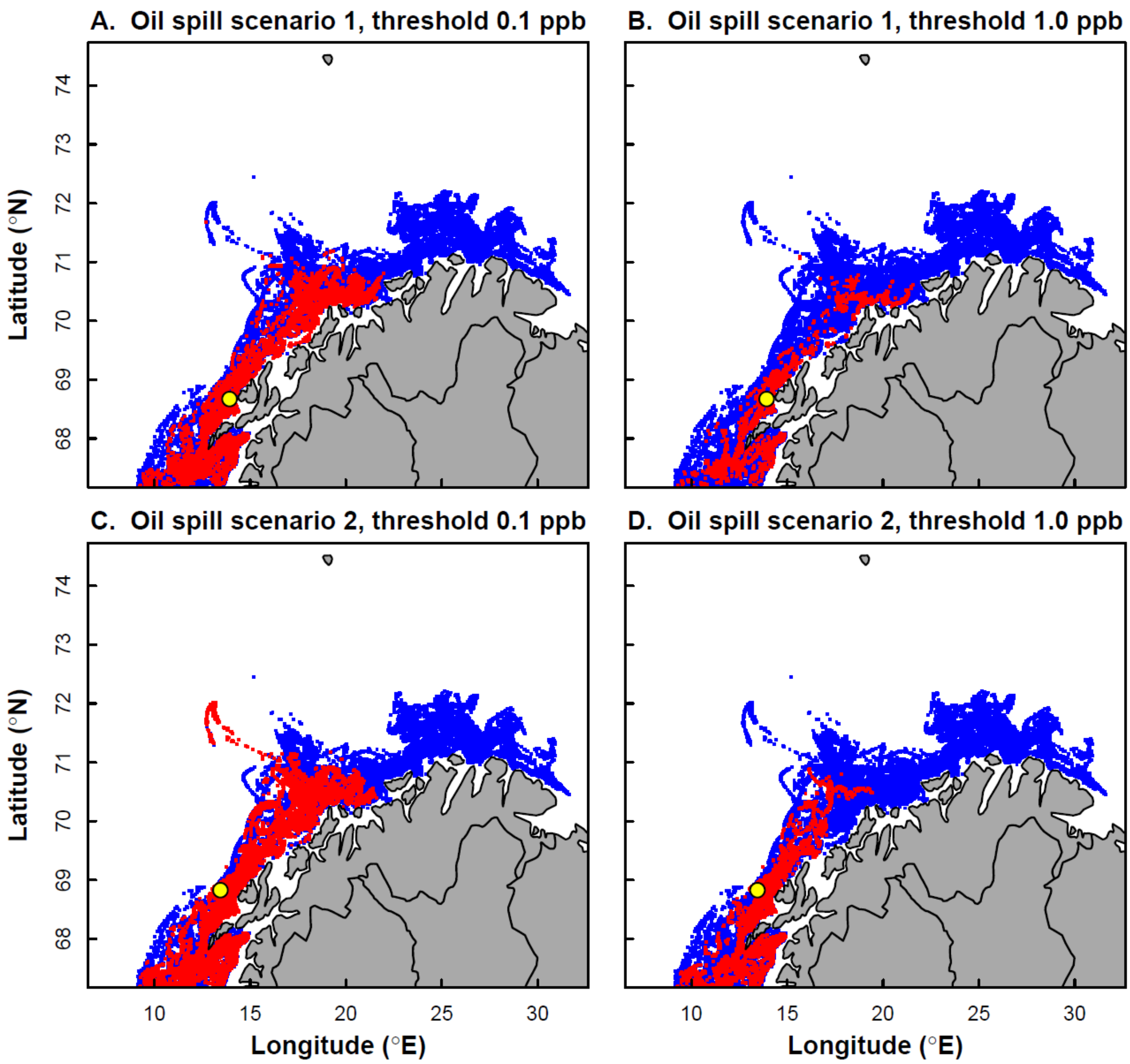

Figure S2. Simulated distribution of Northeast Arctic cod eggs at their locations halfway through the egg development. Red points in each panel represent eggs that experience oil concentrations above a threshold concentration of 0.1 ppb (left column) or 1.0 ppb (right column) at some point in their egg and larval life. Blue points (partly overlaid by the red points) represent remaining eggs. Upper and lower rows represent two different oil spill scenarios with filled yellow circles showing the release location.

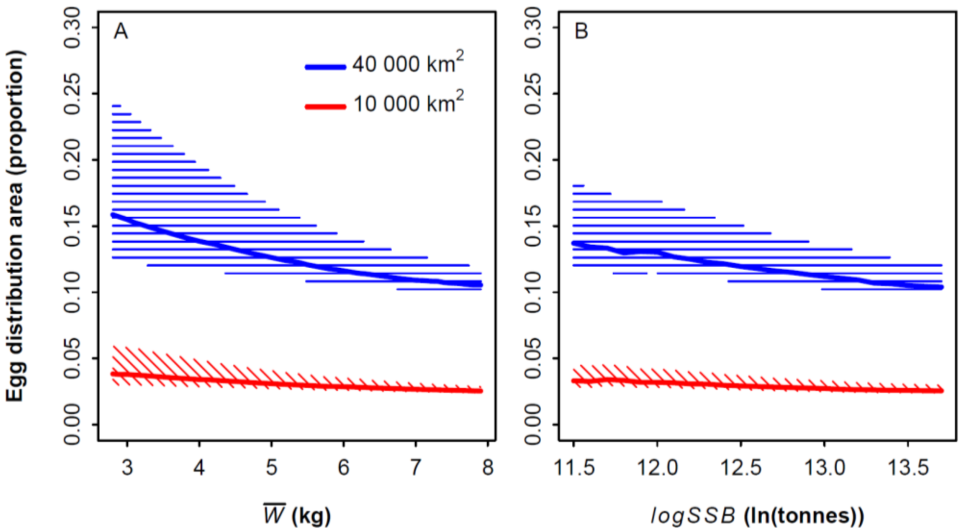

Figure S3. Maximal proportion of the total distribution area of Northeast Arctic cod eggs contained within areas of 10 000 km^2 or 40 000 km^2 dependent on (A) $\overline{W}$ or (B) *logSSB*. Hatched lines represent 95 % confidence intervals.

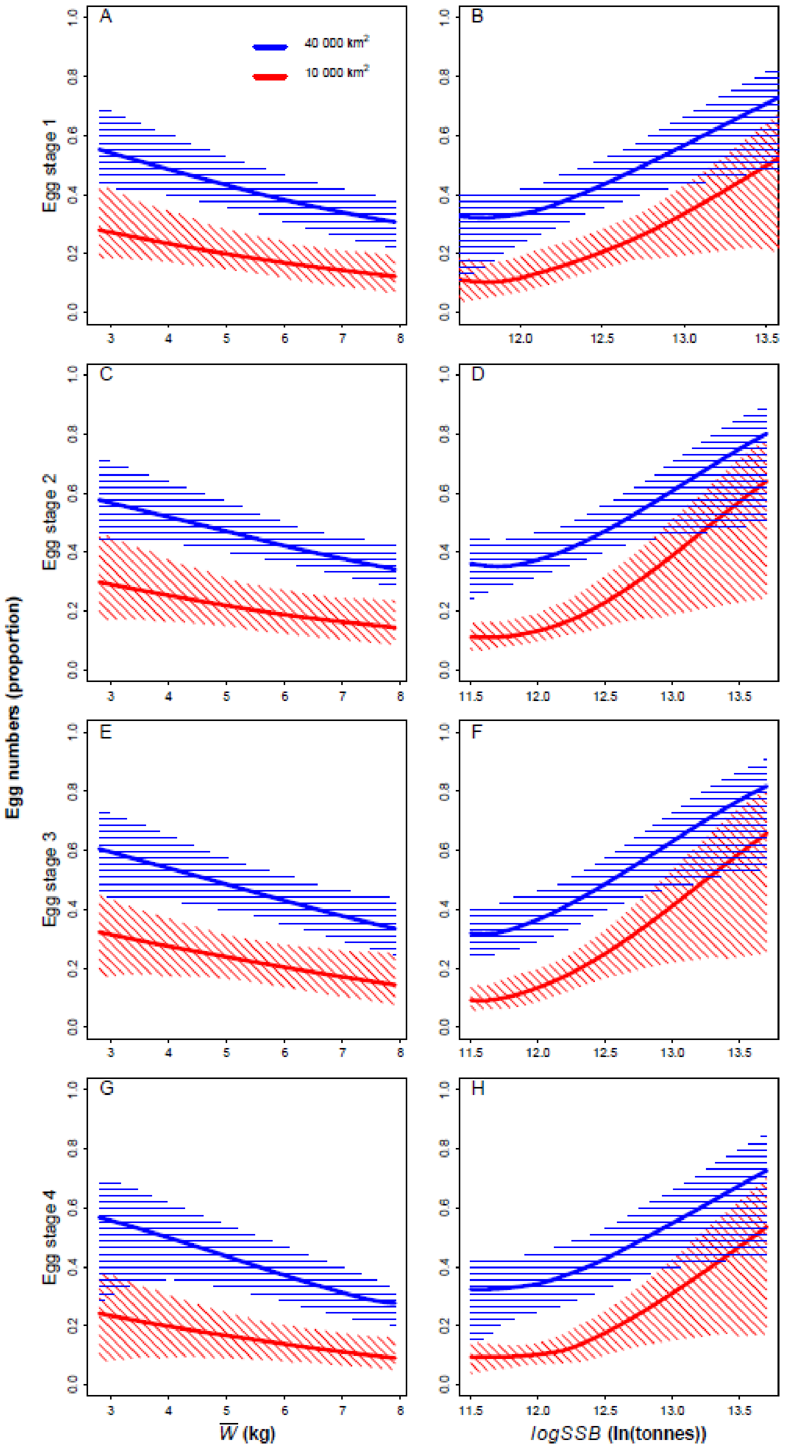

Figure S4. Maximal proportion of Northeast Arctic cod eggs contained within areas of 10 000 km^2 or 40 000 km^2 dependent on (A, C, E, G) mean weight in the spawning stock, $\overline{W}$, or (B, D, F, H) spawning stock biomass, *logSSB*. Each row shows results for one egg developmental stage. Hatched lines represent 95 % confidence intervals (horizontal blue lines for 40 000 km^2, oblique red lines for 10 000 km^2).

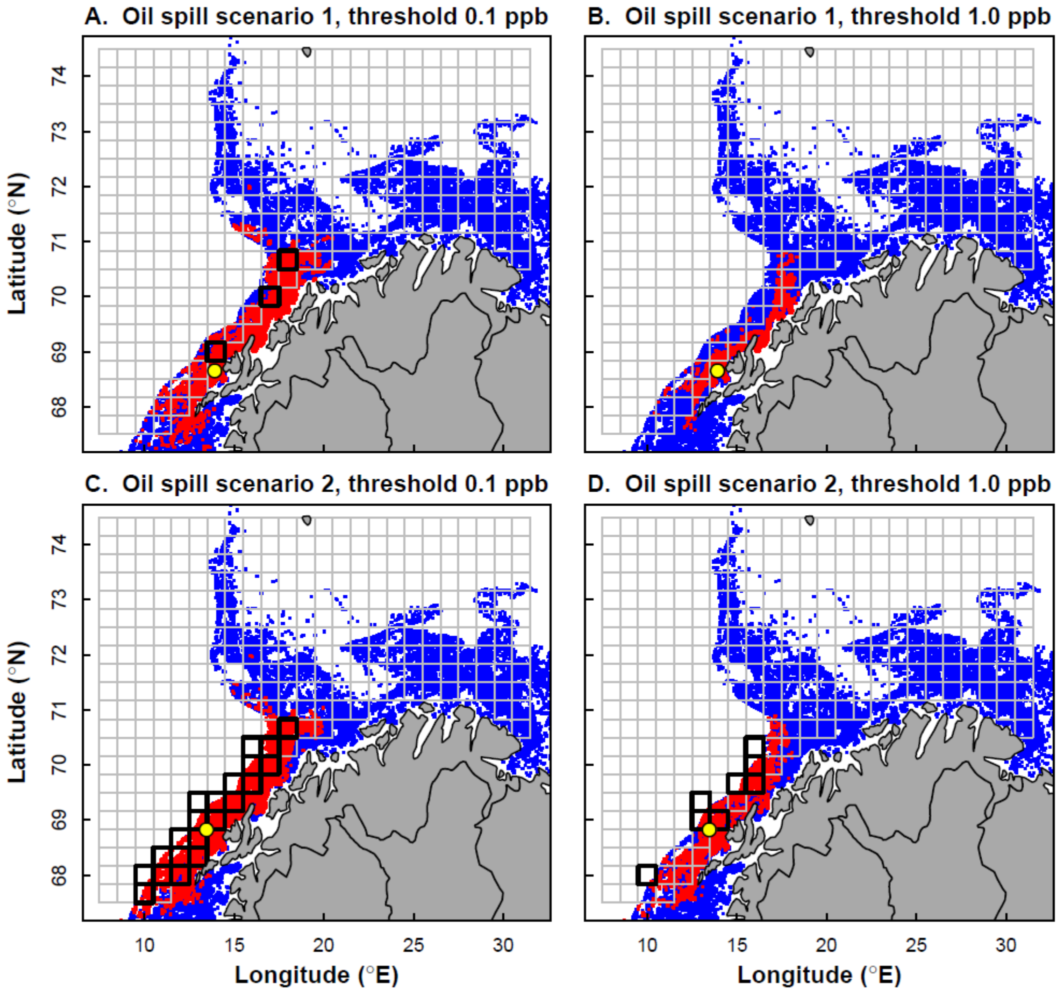

Figure S5. Simulated distribution of Northeast Arctic cod eggs at their locations at 10th April 1997. Red points in each panel represent eggs that experience oil concentrations above a threshold concentration of 0.1 ppb (left column) or 1.0 ppb (right column) at some point in their egg and larval life. Blue points (partly overlaid by the red points) represent remaining eggs. Upper and lower rows represent two different oil spill scenarios with filled yellow circles showing the release location. Grey lines represent the grid used to predict egg distribution from the statistical model (**Fig. 1**). Grid cells with >50 % of particles experiencing above-threshold oil concentrations are shown in black.