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The effects of oil spills on marine fish: Implications of spatial variation in natural mortality

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ABSTRACT

The effects of oil spills on marine biological systems are of great concern, especially in regions with high biological production of harvested resources such as in the Northeastern Atlantic. The scientific studies of the impact of oil spills on fish stocks tend to ignore that spatial patterns of natural mortality may influence the magnitude of the impact over time. Here, we first illustrate how spatial variation in natural mortality may affect the population impact by considering a thought experiment. Second, we consider an empirically based example of Northeast Arctic cod to extend the concept to a realistic setting. Finally, we present a scenario-based investigation of how the degree of spatial variation in natural mortality affects the impact over a gradient of oil spill sizes. Including the effects of spatial variations in natural mortality tends to widen the impact distribution, hence increasing the probability of both high and low impact events.

1. Introduction

The risk of large marine oil spills, such as the Exxon Valdez oil spill (Peterson et al., 2003) and the Deepwater Horizon disaster (Crone and Tolstoy, 2010; Kerr et al., 2010), is often perceived as a threat to fish stocks. Very few studies have demonstrated increased mortality of fish as a result of oil spills (Fodrie et al., 2014; Hjermann et al., 2007; IPIECA, 1997). Nevertheless, fish stocks may be especially vulnerable to oil spills close to the spawning grounds or egg and larval drift areas (Hjermann et al., 2007; Rooker et al., 2013). Fish eggs and larvae are typically vulnerable to toxic oil compounds due to their small size, poorly developed membranes and detoxification systems as well as their position in the water column. A number of laboratory studies have shown that oil or oil compounds (mainly polycyclic aromatic hydrocarbons, PAHs) at low concentrations can kill or cause sub-lethal damage to fish eggs and larvae (Carls et al., 1999; Hicken et al., 2011; Meier et al., 2010; Scott and Sloman, 2004; Sørhus et al., 2015). Sub-lethal effects include, e.g., morphological deformities, reduced feeding and growth rates, and are likely to increase vulnerability to predators and starvation. The few existing in situ studies of fish mortality at spill sites indicate sub-lethal effects or elevated mortality of eggs and larvae (deBruyn et al., 2007; Hose et al., 1996; Incardona et al., 2012; McGurk and Brown, 1996).

Studies of biological impacts of oil spills are of two types: retrospective studies investigating the impact of a spill, and, prospective studies estimating the probable outcome of potential future oil spills. In this paper, we focus on the latter. Assuming that an oil spill mainly kills fish at the egg or larval stage (Hjermann et al., 2007), the impact of an oil spill on a fish stock depends on (*i*) the proportion of the eggs and larvae killed by the oil spill, and (*ii*) how early-stage mortality affects cohort survival in subsequent stages. In practice, the availability of methods and data tends to guide assessment of spill impacts. Regarding (*i*), there typically exist data on the spatial distribution of fish eggs and larvae, as well as physical and chemical modeling of advection, spreading, evaporation, dispersion and emulsification of oil (e.g. Hjermann et al., 2007 and references therein). Together with information on which concentrations or exposure (cumulative concentrations over time) to oil are lethal, one can estimate the percentage of eggs or larvae that are killed (French-McCay, 2004; Vikebø et al., 2014). Regarding (*ii*), modelers typically rely on population models (French-McCay et al., 2003; Ohlberger and Langangen, 2015). Further important issues regarding (*ii*), such as spatial variations in vital rates have largely been ignored in impact assessments. There is an appreciation of these matters

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in the scientific community and acknowledgment that the main reasons for leaving these effects out in impact assessments are lack of relevant data and reliable models.

In this study, we focus on the effect of spatial patterns in early-stage natural mortality on cohort survival. In prospective studies, one is concerned with the range of possible outcomes and in particular the probability of adverse effects. Estimating such probability requires an understanding of the combined effect of natural mortality and mortality related to the exposure to oil. Current oil spill risk assessments typically ignore spatial variability in survival, and assume a constant mortality rate across the distribution area or a probability distribution around an average (e.g. Brude and Sverdrup, 2011). However, without empirically based studies it is impossible to estimate effects of spatial variability in mortality.

Here, we first present a hypothetical "thought experiment" to illustrate the concept. Second, we further illustrate the importance of including spatial variations in mortality into the assessment, by considering an example of a spatially bounded mortality event for the stock of Northeast Arctic (NEA) cod (*Gadus morhua*). Third, based on the NEA cod example, we quantify the possible change in impact of an oil spill by considering different scenarios.

2. Materials and methods

2.1. Thought experiment to illustrate the concept

A typical example, motivated by the NEA cod, of drift and natural mortality of the planktonic early life stages of a fish is illustrated in Fig. 1. The spawning grounds are at the left side of the figure, and we have assumed spawning to be particularly concentrated in two areas (marked 1 and 2). The eggs develop into larvae and juveniles as they drift along the currents. Due to variation in drift speed, direction, and diffusion, the extent of the distribution of eggs, larvae and juveniles increases with time. If the mortality is uniform in space, drift and diffusion are the primary determinants of the distribution (Fig. 1, thought experiment 1). Here, the two spawning grounds contribute approximately equally to the juvenile abundance (right hand side of Fig. 1, marked 1 and 2). Alternatively, spatial variation in natural mortality may be present. If we assume higher survival close to the mainland (Fig. 1, thought experiment 2), the density in the juvenile stage (right side of Fig. 1) is highest closer to the coast. The cohort impact (proportion affected) of an oil spill at the egg stage (left side of Fig. 1) affecting either area (1 or 2), killing approximately the same amount of eggs, will translate to about the same impact at the juvenile stage in thought experiment 1. In contrast, in the second thought experiment, an oil spill affecting the egg stage will have a considerable impact at the juvenile stage if area 2 is affected, and an insignificant impact at the juvenile stage if area 1 is affected. The concept may also generalize to any spatially bounded event resulting in elevated mortality, e.g. extreme weather events such as storms (Lough et al., 1996) and predatory species invasions (Nentwig, 2007). We here define the *effective density* as the density weighted with the future survival probabilities. Thus, two regions with the same actual density of eggs have different effective density if the currents transport the eggs and larvae into areas with different natural mortality. To determine the significance of spatial variability in natural mortality on the assessed impact of an oil spill, empirical examples must be considered.

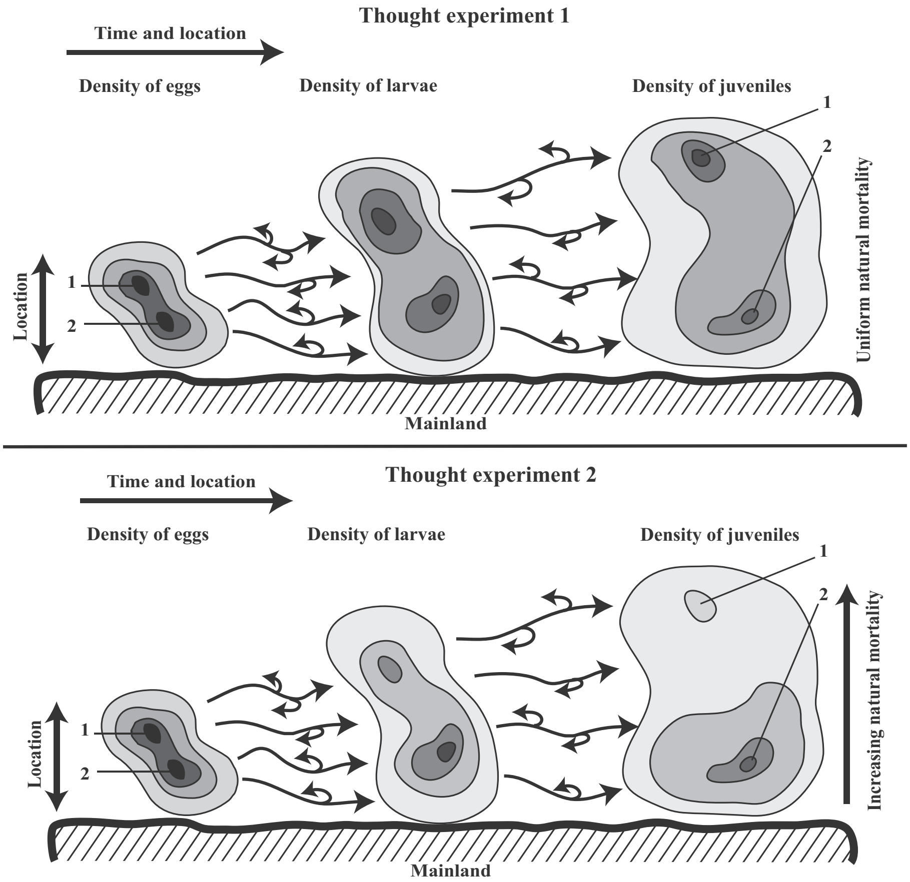

Fig. 1. Conceptual model of effective density. The changes in density (darker shade = higher density) of early life stages of a fish with pelagic eggs and larvae drifting in a current (indicated by arrows, from left to right) are illustrated. The changes in density are due to advection and diffusion (Thought experiment 1) and also spatial differentiated natural mortality (Thought experiment 2, with mortality for illustration purposes assumed to be increasing with distance from the mainland). See main text for further details.

2.2. Study system

We use NEA cod situated in the Lofoten-Barents Sea region outside northern Norway and northwestern Russia (Fig. 2) to illustrate the concept of effective density. In addition, we analyze a set of scenarios based on the NEA cod to quantify how spatial variation in natural mortality may alter the effects of an oil spill. We are primarily motivated by prospective assessments of how commercial fish stocks may be impacted by possible future oil spills in the region, which is still partly closed to petroleum development, but may be opened for oil exploration in the future (Blanchard et al., 2014; Hjermann et al., 2007; Olsen et al., 2007). The debate about opening for oil exploration has especially revolved around the susceptibility to a hypothetical oil spill on the two large and economically important stocks that spawn in or upstream of this area: NEA cod and Norwegian Spring-spawning herring (NSS herring, *Clupea harengus*). The fisheries for these species are valuable and economically important to Norway, Russia, and other countries. For example, in 2015, the economic value of the Norwegian catch (constituting about half the total catch) of NEA cod and NSS herring amounted to >0.6 billion US dollars (Institute of Marine Research, 2016). The spawning grounds of NEA cod are distributed along the coast of mid- and northern-Norway and the primary spawning season is from mid-February to mid-May (Sundby and Nakken, 2008). The eggs and larvae of the NEA cod drift pelagically with the Norwegian Atlantic and the Norwegian Coastal Currents through the areas of possible oil activities (e.g. Misund and Olsen, 2013) towards the nursery area in the Barents Sea (Hjermann et al., 2007; Olsen et al., 2010). The natural mortality experienced during the egg and larval stages is on average high (Langangen et al., 2014b) and is likely to vary considerably over the study area (Langangen et al., 2014a), see Fig. 2. Defining the relevant oil spill scenarios used in the risk assessments has been highly debated, especially in relation to the likely size of a spill and the biological realism of the risk-assessment methods employed (Hauge et al., 2014; Misund and Olsen, 2013). A lack of biological realism in accounting for spatio-temporal variability in fish-larvae survival has been identified as a core knowledge gap, and an important reason to invoke the precautionary approach and refrain from opening the Lofoten spawning areas for petroleum activities.

2.3. Drift modeling and egg and larval mortalities

The present study is based on an individual-based coupled physical-biological drift model (Ådlandsvik and Sundby, 1994; Langangen et al., 2014a; Opdal et al., 2011; Vikebø et al., 2007). The model simulated the drift and development of the early life stages of NEA cod from spring to summer for the years 1959 to 1993. This period is chosen because of availability of abundance data of cod eggs and larvae from two annual spring and summer surveys. For each year, >100,000 particles each representing several eggs and larvae (Scheffer et al., 1995) at different developmental stages were released at 10th of May according to the observed spatial patterns of cod eggs (four stages) and larvae (two length classes) in spring of the same years (see Langangen et al., 2014a for details). The ocean currents and temperature were estimated by using the Regional Ocean Modeling system for the North Atlantic (ROMS, e.g., Lien et al., 2014; Shchepetkin and McWilliams, 2005). Observation-based atmospheric reanalysis (Reistad et al., 2011) provided winds and heat fluxes. The eggs and larvae develop and grow according to temperature and the larvae migrate vertically according to light and larval size. We

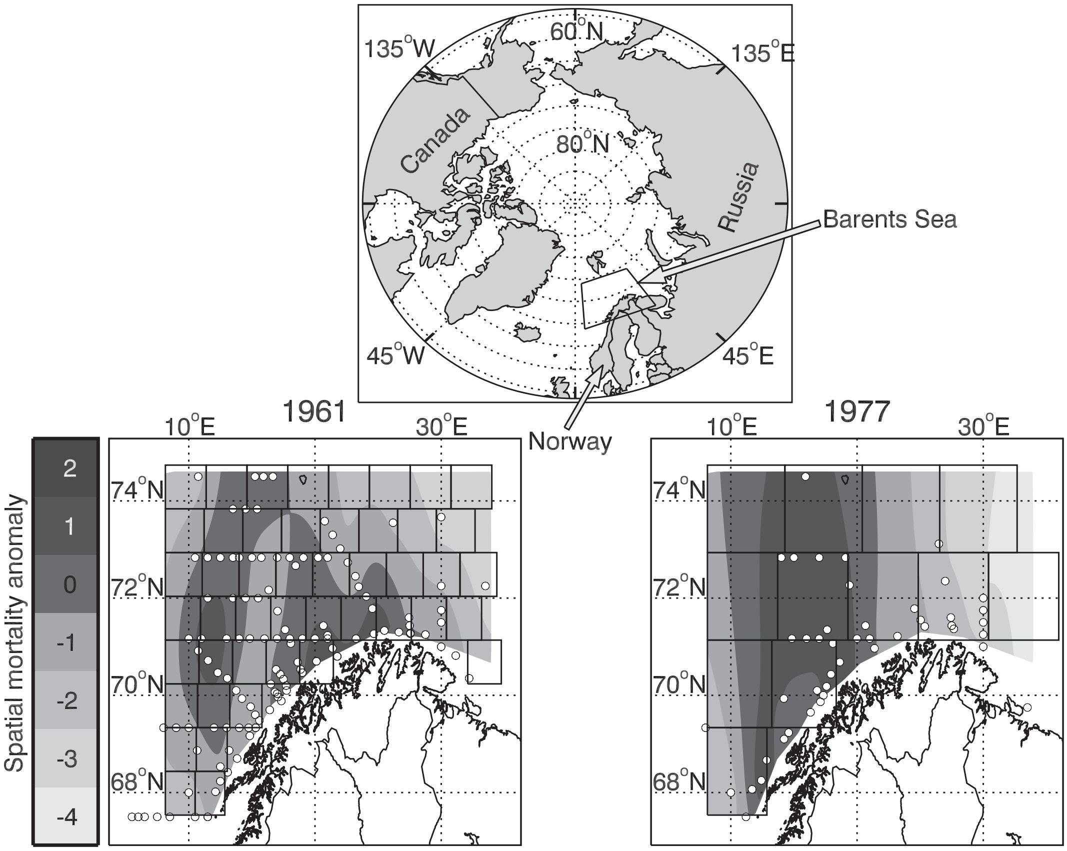

Fig. 2. The area of interest outside the coast of northern Norway is outlined by the box in the upper map. The detailed maps of spatially resolved mortality fields in the egg and larval stages of NEA cod in the study area for two representative years (Langangen et al., 2014a) are shown as grey scaled contours in the two lower panels. Contour colors show the level of spatial anomaly in mortality experienced by particles over a drift time of 45 days. Positive values mean higher than average mortality. The mortality anomalies were scaled to zero averaged over the observations (indicated with *white circles*, see (Langangen et al., 2014a)) each year. Grid cells of different sizes are shown (1961: 10,000 km^2, 1977: 40,000 km^2) as examples of the grids used in the analysis.

apply a daily stage-dependent mortality to the eggs (0.169 day^{-1}) and larvae (0.075 day^{-1}, values are based on Langangen et al., 2014b). In addition, we apply a scenario-dependent (see below) correction for the spatially variable mortality, based on estimated mortality fields (Langangen et al., 2014a) in the study area (Fig. 2). The mortality fields are interpreted as anomalies in total mortality over the drift period between Spring and Summer surveys (Mukhina et al., 2003), about 45 days of drift. For example, an anomaly of 2 corresponds to an increased daily instantaneous mortality of about 0.045 day^{-1} over the 45-day period (see Langangen et al., 2014a). The average instantaneous mortality for a simulated particle, not accounting for spatial anomalies, for 45 days of drift (10 days as eggs and 35 days as larvae) is about 0.096 day^{-1}.

Note that there are several sources of uncertainty associated with these estimates (see Langangen et al., 2014a and the *Electronic Supplement* for a summary). One important possible source of error is the likely slight downward bias in drift speed in the hydrographic archive (Lien et al., 2013). The bias in drift speed may lead to an overestimation of mortality in areas with high density (i.e. apparent compensatory density dependence, see *Electronic Supplement*). For the empirical examples and the scenarios, we assume that the spatial variation in natural mortality varies in space according to the estimated fields (empirical examples and scenario 2) or a multiple of these (scenario 3).

2.4. Empirically based illustration of the effective density

The distribution of larvae in the summer in the absence of an oil spill was predicted by tracking particles from the empirically estimated egg and larval distributions in the spring (10th of May, Langangen et al., 2014a).

The estimated effective density (as defined in the "Thought experiment" section) on 20th of May (after 10 days of drift) was mapped by summing up the number of particles weighted with the year specific (spatially variable) survival prospects until the median date of the Summer survey (roughly the end of the larval stage; usually occurring between July and August) within square grid cells of 6.3 × 6.3 km, roughly covering 66 N to 75 N and 5 E to 30 E. To reduce the noise and make the maps of effective densities easier to interpret we smoothed the resulting maps by convolution with a two-dimensional isotropic Gaussian kernel with a standard deviation of 7 km. The effective density of the eggs and larvae could be estimated for all possible days after the release of the particles. Fig. 3 illustrates the resulting effective densities (20th of May) with respect to the end of the larval stage for 1961 and 1977 – two example years with highly different egg and larval distributions. As an illustration of potential effects of oil spills based on empirically estimated effective egg and larval densities, we investigate three selected regions (corresponding to oil regions; Fig. 3) for where an oil spill would lead to different impacts depending on the year and if the spatial structure in the natural mortality is included in the calculation. Note that all eggs and larvae that spatially overlap with the oil spill in the horizontal dimension were assumed to die. Hence, we have assumed that eggs and larvae at all depths are affected (see *Electronic Supplement* for a discussion of this assumption). In addition, we assume that the oil spill does not affect the structure of the mortality field. More specifically this means that we assume that predators and prey are not affected by the oil spill to an extent that impacts the survival of cod eggs and larvae survival outside the oil spill region.

2.5. Scenarios to quantify potential impacts of an oil spill

To quantify the probability of accentuation or alleviation of effects due to spatially heterogeneous mortality, we constructed three scenarios for spatial mortality combined with three hypothetical oil spills of different sizes.

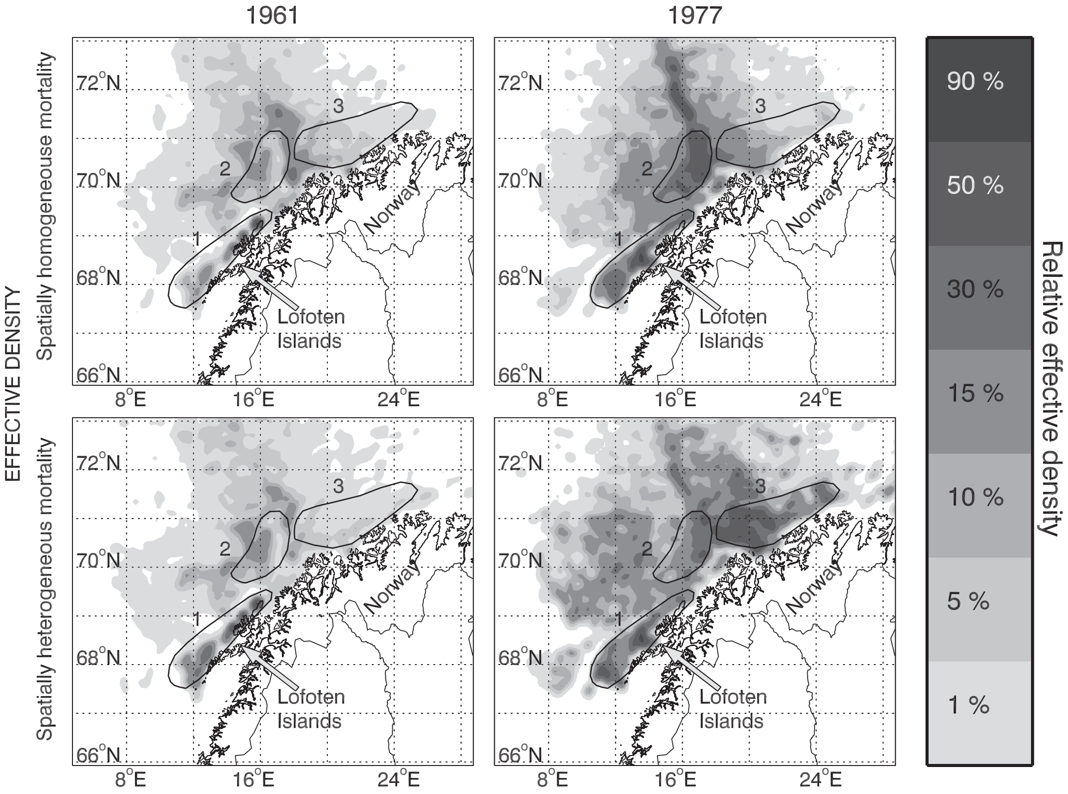

Fig. 3. The effective densities calculated with spatially homogeneous mortality (upper panels) and spatially heterogeneous mortality (lower panels) for two example years (1961 and 1977). The contour grey scales indicate the relative effective density with respect to the maximum density of the given year. Three different example regions (marked by 1, 2 and 3, see Table 1) where an oil spill could affect different proportions of the eggs and larvae are also shown.

The following three scenarios on spatial variation in natural mortality were considered:

Scenario 1 – Spatially homogenous mortality.

Scenario 2 – Spatially heterogeneous mortality based on the estimated mortality fields (Fig. 2).

Scenario 3 – Spatially heterogeneous mortality 2 times larger than the estimated mortality fields.

With these three scenarios, we investigate how the effect of an oil spill may change with increasing spatial variation in natural mortality. To simulate the effect of an oil spill, we divided the study area (grey scaled areas in lower panels in Fig. 2) into a grid of squares. We considered three alternative grid sizes (small: 10,000 km^2, medium: 25,000 km^2 and large: 40,000 km^2, see Fig. 2), where each grid cell is considered to represent hypothetical extents of a large oil spill (see *Electronic Supplement* for a discussion of oil spill size). For simplicity, we assume equal probability of an oil spill occurring in a cell for all scenarios.

For scenario 2 and 3, we apply the years-specific anomaly in natural mortality averaged over each grid cell. In addition, we calculated the cell-specific larval densities at the median day of the Summer survey (on average about 45 days after 10th of May), assuming spatially homogeneous natural mortality. The procedure was applied to the 20 years with sufficient data coverage (1959, 1961–63, 1969–74, 1977–79, 1982–83, 1985, 1990–93, see Langangen et al., 2014a for details). As a proxy for cohort loss due to an oil-spill affecting a cell, we estimated the percentage of eggs and larvae in the cell relative to the total egg and larval in the study area at the median day of the Summer survey.

For scenarios 2 and 3, we resampled the mortality field in space (12, 18 and 47 cells for the large, medium and small oil spills respectively) and alternatively in time (20 years), for each scenario. By resampling in time, we retain the spatial correlation structure in the mortality field, while resampling in space ignores this correlation structure. By resampling the mortality fields, we quantify how the impact probability distribution is widened when the spatial structure in the mortality is accounted for. We quantify the scenario specific impacts at different quantiles of the distributions of cohort loss. Finally, to quantify the changes in median and width of the impact distribution (in fractions), we estimated the location and scale parameters of a logit-normal impact distribution.

3. Results

3.1. Illustration of the effective density

We have estimated the effective densities (i.e. density weighted by future survival) with respect to the end of the larval stage of NEA cod eggs and larvae, also accounting for spatial variations in natural mortality, for 20 years between 1959 and 1993. Examples of the effective density on 20th of May for two years, 1961 and 1977, are shown in Fig. 3. We find that the effective densities calculated based on spatially homogeneous mortality (i.e., effective density is proportional to actual density) is significantly different, at both small and large scales, from the effective densities where the variation in natural mortality is taken into account (Fig. 3). In particular, there are shifts in both the spatial location and size of peaks in density between the two estimated effective densities for each year. These size and spatial shifts in density may lead to a different outcome should an oil spill occur, see Table 1 for details. For example, an oil spill in 1961 in region 1 in Fig. 3 (and Table 1) affects a higher proportion of the population when the spatial variation in natural mortality is accounted for. The situation is opposite for the same region in 1977: a lower proportion is affected when the spatial variation in natural mortality is accounted for. In region 2 the difference in population impact between the two calculated effective densities is relatively small (11 and 12%) in 1961. This contrasts to 1977, when there is quite a strong alleviation of the affected proportion with a reduction from 19% to 8%. In this year, the alleviation is mainly due to an eastward shift in the estimated effective density. This eastwards shift results in an opposite effect in the more eastern region 3, where there is an accentuation in the affected fraction from 9% to 20%.

Table 1
The percentage affected eggs and larvae (of total abundance) for the example regions for the two example years as shown in Fig. 3. The surface areas of the example regions are shown in parenthesis. The affected percentages refer to effective densities calculated with either spatially homogeneous or heterogeneous natural mortality.

	Spatial natural mortality	1961	1977
Region 1	Homogeneous	13%	15%
(20,000 km^2)	Heterogeneous	19%	11%
Region 2	Homogeneous	12%	19%
(13,000 km^2)	Heterogeneous	11%	8%
Region 3	Homogeneous	10%	9%
(22,000 km^2)	Heterogeneous	7%	20%

3.2. Scenario results

The estimated scenario specific impact probabilities based on resampling in space at some example quantiles are shown in Table 2. Impacts are typically only very high at high quantiles (95% and 97.5%). This table also shows that the probability that a very small (<1%) or very large (>50%) proportion of the population is affected increases as the spatial variability of natural mortality increases from Scenario 1 to 3. Note that the probability distributions do not follow a normal distribution. The widening and shift of the probability distributions are summarized in Fig. 4, which shows how the location and scale parameter (parameters in the logit-normal distribution describing the median and width of the distribution) of the impact distribution change with scenario. The median (location parameter) impact tends to increase and the width (scale parameter) of the distribution tends to decrease with the size of the oil spill (Fig. 4, left panel). In contrast, the median impact tends to decrease and the width of the distribution tends to increase with increasing variability in the spatial mortality field (Fig. 4, left panel). On logit-scale, the difference in location (-0.95 and -3.0 for Scenario 2 and 3 respectively) and scale (0.73 and 2.2 for Scenario 2 and 3 respectively) parameters between scenarios 2 and 3 and the spatial heterogeneous case (scenario 1) are fairly constant across spill sizes (Fig. 4, right panel). A more extensive summary of impact probabilities for the resampling in time and space is shown in Tables S1–2. These results demonstrate that both alleviation and accentuation of the impact of an oil spill on the fish cohort are associated with significant probability when accounting for the spatial variations in natural mortality. However, alleviation is more likely than accentuation (Table 2).

Table 2
Summary of impacts (reduction in cohort strength in percent) at different quantiles for the three scenarios. Results are based on resampling in space.

				Impact quantile			
				50%	90%	95%	97.5%
Mortality scenario	3	Oil spill size	10,000 km^2	0.0	4.2	12.8	24.8
			25,000 km^2	0.1	16.9	39.4	59.6
			40,000 km^2	0.3	30.1	61.8	81.0
	2	Oil spill size	10,000 km^2	0.3	5.6	11.3	18.2
			25,000 km^2	3.5	12.9	18.0	23.8
			40,000 km^2	2.1	26.1	44.0	58.5
	1	Oil spill size	10,000 km^2	1.1	5.8	6.7	7.7
			25,000 km^2	3.6	14.6	16.9	18.2
			40,000 km^2	7.4	19.3	22.4	26.7

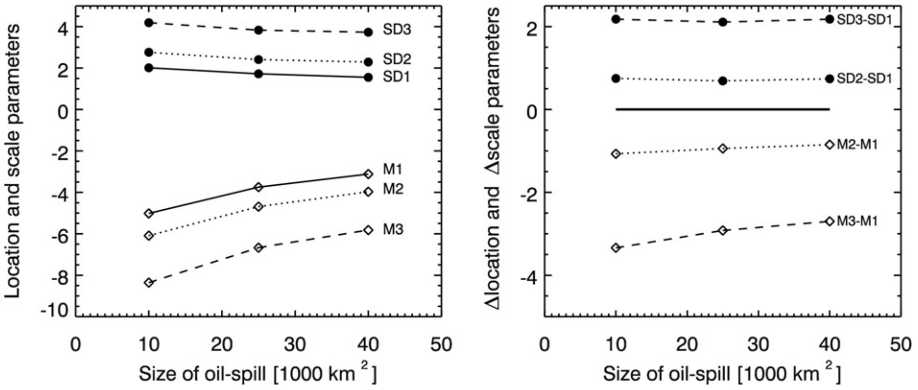

Fig. 4. The location (mean [M] of the logit-transformed impact distribution [in fractions], diamonds) and scale (standard deviation [SD] of the logit-transformed impact distribution [in fractions], filled circles) is shown (left panel) for the three scenarios (Scenario 1, no spatial variation in mortality: solid lines. Scenario 2, medium spatial variations in mortality: dotted lines. Scenario 3, high spatial variations in mortality: dashed lines.) as a function of oil spill size. The differences in location and scale parameters with respect to parameters from Scenario 1 are shown as a function of oil spill size (right panel).

4. Discussion

The empirical examples emphasize how accounting for spatial variations in natural mortality may affect the estimated effective density in a variety of ways. Based on these results, we conclude that spatial variation in natural mortality can be very important when assessing the impact of oil pollution on pelagic fish eggs and larvae. In particular, we have demonstrated how spatial variation in natural mortality in NEA cod eggs and larvae may affect the assessed impact of a possible oil spill in the region off northern Norway and northwestern Russia. The spatial structure in effective density and the exact location of the oil spill may interact to accentuate or alleviate the impact (Fig. 3 and Table 1). We find that spatial structure in natural mortality has a tendency to alleviate the impacts of oil spills. This is partly due to a skewed spatial distribution of the mortality anomalies and partly due to the negative correlation between density and survival. However, accentuation also occurs in a significant proportion of cases (Table 1). The spatial structure of natural mortality is a major source of uncertainty in prospective studies (Hjermann et al., 2007; Vikebø et al., 2014) and it cannot currently be reliably predicted. Other important sources of uncertainty include timing and location of spawning, vertical swimming behavior of the fish larvae, physical conditions such as current speed and direction, location of the oil spill, toxicity of the different oil-components and variations in toxic sensitivity among species and life stages. To avoid an underestimation of possible oil spill effects, ecosystem management should attempt to account for all sources of uncertainty, including spatial structure in natural mortality.

To quantify, at least partially, the uncertainty introduced by spatial variations in natural mortality, we ran multiple scenarios. Our results demonstrate how explicitly including the spatial variability in mortality tends to widen the probability distribution and hence increase the predicted probability of an extreme impact of an oil spill (Fig. 4, Table 2). Note that there will be an increased probability for both significant and insignificant impacts (Table 2). When assessing the possible outcomes of an oil spill, a precautionary approach is often recommended due to the potentially expansive and long-lasting environmental effects. For example the UN World Charter for Nature of 1982 states "… *when potential adverse effects are not fully understood, the activities should not proceed*". As a result, we give a particular focus on the probability and impact of adverse effects. However, what degree of risk is considered acceptable, is a political decision outside the realm of science. Severe cohort loss (e.g. >50%) is only present in the upper quantiles (Table 2), but the consequences of these less likely events may be substantial (cf. Ohlberger and Langangen, 2015). Our results may also be directly used as input in a risk based environmental impact assessment for example by adding a probability distribution to the expected effect level (Brude and Sverdrup, 2011) or by including the conditional probability tables (Tables S1–2) in a Bayesian Network model (Caroll and Smit, 2011). For other ecologically similar stocks with little or no information on how mortality varies in space, we suggest that our results may be used as an alternative to assuming spatial heterogeneous mortality. We suggest that, as a an approximation, other studies may use an additive constant for the location and scale factors (-0.95 and 0.73 for Scenario 2 and -3.0 and 2.2 for Scenario 3) on the same parameters obtained assuming no spatial variations in mortality (cf. Brude and Sverdrup, 2011). For example, if a study finds that the median impact may be 10% (i.e. a fraction of 0.10 corresponding to location parameter $\mu = -2.20$) with a logit-normal scale parameter (standard deviation of the logit-transformed impact distribution) of $\sigma = 0.8$, one could alternatively assume (based on Scenario 2) that spatial mortality may change the location parameter to -3.2 and the scale parameter to 1.5. Hence, the median impact would change from 10% to 4%, while the 95% impact quantile would change from 35% to 48% when accounting for spatial variations in natural mortality.

In this study, we have assumed that eggs and larvae at all depths are affected if there is horizontal overlap with the oil spill. As shown by Vikebø et al. (2014, their Tables 1–5), relaxing this assumption will, in general, reduce the effect by roughly a third, independent of the area affected by oil. The sizes of the theoretical oil spill regions (Table 1) are similar to the sizes found in more detailed oil spill simulations. Based on the oil spill simulations of a large oil spill from Vikebø et al. (2014), we estimated an area covering up to 28,000 km^2 will have lethal PAH concentrations in the water column (1.0 ppb, and an area up to 150,000 km^2 will have sub-lethal effects 0.1 ppb PAH concentration in the water column, see *Electronic Supplement*). The simulations represent a large oil spill with a release of 4500 tons of oil per day for 30 days. Nevertheless, it is smaller than what is considered the "worst case scenario" in the management plan for the Lofoten-Barents Sea area, which has been taken as 4500 tons of oil per day for 50 days (Brude and Sverdrup, 2011). We here note that our assumption regarding oil toxicity is simplified. The toxicity of oil can be complex and may depend on the specific composition of organic and inorganic substances that varies between oil type, the degree of weathering and the use of dispersants (Hjermann et al., 2007, but see Vikebø et al., 2015).

The outcome of an oil spill may be significantly altered by spatial variation in natural mortality if at least the following three conditions are fulfilled. First, only part of the egg and larval distribution must be affected by the pollution. This is true if the spatial extent of the distributions is much larger than the oil spill or if the oil spill only partially overlaps with the eggs and larval distributions. The spatial extent of larval distribution of fish is in general large compared to the typical extent of an oil spill, also because many fish have protracted spawning periods compared with the duration of a typical oil spill. Winemiller and Rose (1992) found that species with small clutch sizes tend to have long spawning seasons, and thereby a smaller part of the larval population is likely to be affected by an oil spill. Second, mortality during the early life-stages must be potentially important for population dynamics. This is typically the case for fish stocks experiencing high mortality during the early life stages, which is common (Winemiller and Rose, 1992). In the highly fecund NEA cod >99% of the individuals die during the first 3 months, from the egg to the early juvenile stage (Bogstad et al., 2016; Langangen et al., 2014b; Sundby et al., 1989). The third condition is that the expected natural mortality of eggs or early larvae has a large degree of spatial variation. In NEA cod, spatial variations in natural mortality is likely present (Langangen et al., 2014a) to a degree that has ecological relevance, e.g. potentially affecting the spawning ground use over time (Langangen et al., 2016). Such variations are possibly present for many marine fish stocks, but this has to be further empirically investigated. For many stocks, eggs and/or larvae are carried with currents between separate spawning and nursery grounds. The individual eggs and larvae will usually encounter a varying environment en route. While it is debated whether natural mortality of larvae is mainly shaped by food availability, predation, abiotic factors, or a combination of these factors (Fiksen et al., 2007; Leggett and Deblois, 1994), it is highly likely that natural mortality, in a given year, varies for different parts of the larval distribution. Furthermore, the within season temporal variations in natural mortality may also similarly affect the impact of an oil spill if e.g. early-hatched larvae survive better than late-hatched ones.

We have illustrated how spatial variation in natural mortality may significantly alter the effect of an oil spill at the cohort level until the end of the larval stage for NEA cod. Taking a precautionary approach and focusing on attenuation, we have demonstrated a potentially dramatic increase in the effects, e.g. >50% for a large oil spill (Table 2). This illustrates that spatial variability in mortality can accentuate the impact of oil spills to levels that may result in significant ecological and socioeconomic effects (Ohlberger and Langangen, 2015) and that spatial variations in natural mortality may have direct relevance to managers and decision-makers. Spatial variations in natural mortality will, however, often alleviate the impact of an oil spill. In addition, the life stages ensuing the larval stage may further affect the outcome of an oil spill at the cohort level. For instance, depth appears to have a negative effect on survival of NEA cod juveniles over the first winter (Hjort, 1926); cod juveniles switch to benthic habitats in the autumn, and individuals that have been carried to areas with unsuitable depth may not find a suitable habitat to settle in (Ciannelli et al., 2007). Such spatial effects on natural mortality in later life stages may further alleviate or accentuate the cohort effect of an oil spill. Compensatory density dependence is not expected to be strong in the pelagic life stages of cod (see e.g. Fig. 4 in Langangen et al., 2014b). Nevertheless, at low density the natural mortality is expected to be reduced during the subsequent life stages (Hjermann et al., 2004; Ohlberger et al., 2014). Indeed, Ohlberger and Langangen (2015) demonstrate how density dependence combined with a broad population age structure in cod can dampen the effects of a catastrophic mortality event occurring during the early life stages. However, is it conceivable that the opposite (*depensation*) may occur at very low abundances (Keith and Hutchings, 2012). The available data on NEA cod do however not include years with very low total abundances. Finally, we note that an oil spill may also affect prey or predators of the focal species, which may not only propagate through the food web (Langangen et al., 2017; Stige et al., 2011), but may as well have the potential to affect the spatial mortality field assumed to be unaltered outside the oil spill region in this work. However, we expect the error introduced by ignoring the dynamic feedback on the mortality field to be small compared to the error introduced by ignoring spatial variations in mortality altogether.

5. Conclusion

Spatial variation in natural mortality may significantly alter the effect of an oil spill on the recruitment of marine fish. In prospective studies of possible population impacts of oil spills, this has up until now largely been ignored. Our results demonstrate that the probability of extreme effects might be underestimated. At the same time, our results show that there is a higher probability for a decrease in impact than for an increase – indicating that the risks are skewed and not normally distributed. Thus, our results strongly indicate a general need for explicitly including spatial mortality in oil spill assessments to better capture the risk of accentuation of oil spill effects over time.

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Appendix A. Supplementary data

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