



An annual profile of the impacts of simulated oil spills on the Northeast Arctic cod and haddock fisheries

JoLynn Carroll^{a,d,*}, Håvard G. Frøysa^b, Frode Vikebø^b, Ole Jacob Broch^c, Daniel Howell^b, Raymond Nepstad^c, Starrlight Augustine^a, Geir Morten Skeie^a, Mathias Bockwoldt^d

^a Akvaplan-niva, FRAM–High North Research Centre for Climate and the Environment, Hjalmar Johansens Gate 14, 9007 Tromsø, Norway

^b Institute of Marine Research, Box 1870, Nordnes, 5817 Bergen, Norway

^c SINTEF Ocean, Postbox 4762, Torgard, 7465 Trondheim, Norway

^d Research Centre for Arctic Petroleum Exploration (ARCEX), Department of Geosciences, UiT The Arctic University of Norway, 9037 Tromsø, Norway

ARTICLE INFO

Keywords:

Oil spills
Ecosystem modeling
Fishery impacts
Northeast Arctic cod
Northeast Arctic haddock
Seasonal

ABSTRACT

We simulate the combined natural and pollutant-induced survival of early life stages of NEA cod and haddock, and the impact on the adult populations in response to the time of a major oil spill in a single year. Our simulations reveal how dynamic ocean processes, controlling both oil transport and fate and the frequency of interactions of oil with drifting fish eggs and larvae, mediate the magnitude of population losses due to an oil spill. The largest impacts on fish early life stages occurred for spills initiated in Feb–Mar, concomitant with the initial rise in marine productivity and the earliest phase of the spawning season. The reproductive health of the adult fish populations was maintained in all scenarios. The study demonstrates the application of a simulation system that provides managers with information for the planning of development activities and for the protection of fisheries resources from potential impacts.

1. Introduction

Despite the continuing development of alternative energy sources, petroleum is projected to remain among the world's primary energy resources but with ambitions to be partly replaced by renewable energy within the next decades (IEA, 2021; Calverley and Anderson, 2022). By 2050, renewables could be nearing 50 % if countries reach their goals for emission cuts (IEA, 2021). Because extraction and transport of petroleum entails the risk of oil spills in the world's oceans, reducing the numbers and minimizing the effects of oil spills will continue to be a key environmental challenge for the energy sector and society. Scientific knowledge of the impacts of major oil spills on ecosystems and their biological resources has increased substantially in the wake of both the Deepwater Horizon and Exxon Valdez oil spills. These spills serve as bookends of a myriad of possible oil spill scenarios and associated environmental impacts. The Exxon Valdez oil spill resulted from a tanker accident that leaked 10.8 million US gallons (37,000 metric tons) of crude oil for only a few days into the waters of Prince William Sound, a semi-enclosed bay. The Deepwater Horizon oil spill in the Gulf of Mexico resulted from a well blowout at a depth of ~1220 m below the

sea surface releasing ~210 million US gallons (720,000 metric tons) of oil over a period of 87 days. A multitude of scientific investigations in the aftermath of these and other spills have generated valuable knowledge of the specific environments, spill conditions and outcomes of these accidents (Peterson et al., 2003; Shepherd et al., 2016; Kujawinski et al., 2020; Murawski et al., 2021). To decide on tolerable risk and plan for mitigation efforts in case of future spills, it is essential to extrapolate beyond the findings derived from singular events and the outcomes of a few well-studied major oil spills. Such extrapolations will, of course, never be able to simulate all eventualities. However, by synthesising the available state-of-the-art techniques for understanding different processes leading to oil spill impacts on fish populations, in the context of wider ecosystem effects, we can improve the data and knowledge basis for decision-makers to act (Nelson and Grubestic, 2021).

Controlled laboratory experiments provide direct measurements on species-specific sensitivity including genetic, cellular, and organismal toxic thresholds and developmental responses to different types and concentrations of droplets and dissolved oil compounds and/or dispersants. Such studies have revealed effects that include cardiac function, cholesterol biosynthesis, peripheral and central nervous system

* Corresponding author.

E-mail address: jolynnapn@gmail.com (J. Carroll).

<https://doi.org/10.1016/j.marpolbul.2022.114207>

Received 4 July 2022; Received in revised form 27 September 2022; Accepted 29 September 2022

Available online 10 October 2022

0025-326X/© 2022 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

function, the stress response, osmoregulatory acid-base balance processes and photo-induced toxic responses (Barron et al., 2004; Incardona et al., 2013, 2015; Roberts et al., 2017; Grosell and Pasparakis, 2021; Sørhus et al., 2021; Aranguren-Abadía et al., 2022). In the past decade, there has further been an increase in studies focused on behavioral responses to oil exposures and the transfer of toxic substances from parent to offspring (Incardona et al., 2015; Cresci et al., 2020; Bautista et al., 2020). These investigations aid efforts to identify and understand impacts on aquatic life and to support risk management procedures. Yet the complex nature of petroleum substances continues to hinder the consistent characterization of exposures which presents challenges when interpreting results, and further, when comparing results between studies (Bera et al., 2020; Meador and Nahrang, 2019; Redman and Parkerton, 2015; Page et al., 2012; Landrum et al., 2013). And despite our more detailed understanding of oil impacts and affected physiological processes, studies of the effects on fish in natural habitats are highly difficult to conduct, and hence, rare (Incardona et al., 2015; Muhling et al., 2012; Fodrie and Heck, 2011).

Advanced simulation systems are a valuable bridge between the laboratory and real world as they allow us to extrapolate from observations at the cellular, organ, and organismal levels to examine impacts on populations, communities, and ecosystems. These systems are developed by assimilating knowledge from diverse scientific disciplines and distilling this information into mathematical models implemented on high performance computers. The generic value of mathematical models in obtaining more realistic assessments of risk has been well argued (Vlaeminck et al., 2019; Forbes et al., 2011; Thorbek et al., 2009; Galic et al., 2010; Schmolke et al., 2010; Wang and Grimm, 2010). For oil spills, it has been argued that simulations are useful to explore complex interactions and thereby improve our understanding of key

processes and the potential outcomes of a wide variety of realistic oil spill scenarios (Li et al., 2022; Ainsworth et al., 2018; French-McCay, 2003; Buskey et al., 2016; Peterson et al., 2003). Simulation systems can also help to improve and direct laboratory and field studies to test key findings of relevance for the further understanding of realistic oil spill situations. On the other hand, when simulating phenomena in nature, various processes may not be known or understood at the required level of detail. Simulation results only describe the outcome of the scenario and processes that are represented in the model. However, despite this limitation they remain the best available tool to extrapolate toxic effects at the individual to the population level.

In the present work, we conduct simulations to gain valuable insights for future investigations of oil spill impacts on key fish species. The simulation system described here not only estimates likely impacts of a given hypothetical oil spill, but also helps to rank the risk posed by oil activities in different locations and times. We explore the impact of major oil spills occurring at different times throughout a year at a single location in the Lofoten-Vesterålen region of Norway, a key part of the habitat for several commercially important fish species. We use the SYMBIOSES simulation system, a tool designed to evaluate major oil spill impacts at the population level for several fish species (Carroll et al., 2018) (Fig. 1). SYMBIOSES includes an oil fate and transport model, an integrated oceanographic and lower trophic level ecosystem model, a model of fish growth, development, and behaviours, from eggs to larvae, and a multi-species population model for young and mature fish (Fig. 2). The fish early life stages (ELS) model includes a mechanistic model of toxicity processes based on the Dynamic Energy Budget Theory with ecotoxicology (Baas et al., 2018; Ashauer and Jager, 2018; Galic et al., 2017).

Many studies have revealed that mixtures of compounds below their

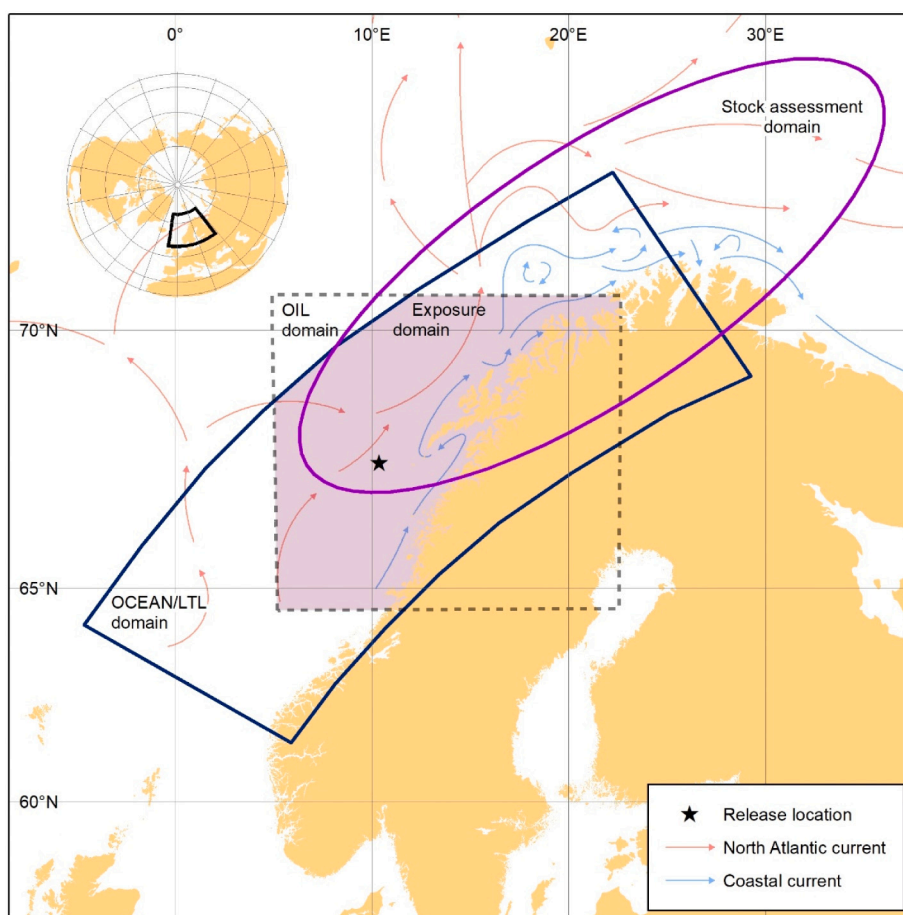


Fig. 1. The SYMBIOSES model domains with the oil release location at 67.700N 10.841E (black star).

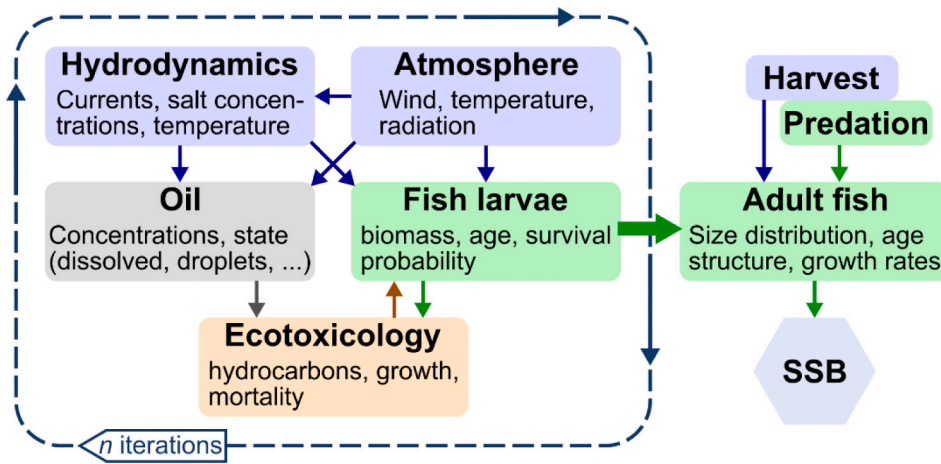


Fig. 2. The model framework predicts the difference in fish population structure (with and without oil) for selected climate, petroleum, predation, and harvesting scenarios. Larvae surviving the effects of petroleum compounds at the end of the pelagic stage are determined from simulations (left). Using a multi-species compartmental model (right), we simulate changes in the spawning stock biomass (SSB) of the juvenile and mature fish populations (>1 year old) for up to 10 years post-spill.

individual effects threshold concentrations (e.g., NOEC, NOEL, LC50) can still show a toxic effect (Drakvik et al., 2020). As the understanding of mixture effects progresses, models are being developed for the assessment of risks from combined exposures to multiple chemicals (Vlaeminck et al., 2020; EFSA Scientific Committee et al., 2019; Bopp et al., 2019; Bopp et al., 2018). To address mixture effects in the SYM-BIOSES simulation system, the DEBtox equations previously described in Carroll et al. (2018) and references therein, have been replaced with a DEBtox mixture toxicity model (Baas et al., 2015; Baas et al., 2009). In Carroll et al. (2018), compounds were independent of one another, and effects occurred only when the NEC value of an individual compound was exceeded. In the present work, all toxic compounds contribute to the NEC. An effect occurs when the NEC value of the mixture of compounds is exceeded.

We aim to investigate the relationship between the time of onset of a severe oil spill throughout a year and the subsequent impacts on two harvestable fish resources — the Northeast Arctic (NEA) cod (hereafter cod) and NEA haddock (hereafter haddock). By initiating identical oil

spills, at a frequency of every two weeks throughout a single year, we investigate how the degree of overlap of a spill with the presence of fish ELS influences their survival percentages and the long-term impact on their stocks. We also present and discuss distribution patterns of *Calanus finmarchicus*, a primary prey species of fish in the North Atlantic, as mismatch between fish larvae and their prey is considered a key cause of mortality and spatiotemporal selective mechanisms for survival along the Norwegian coast (Vikebø et al., 2021; Misund and Olsen, 2013). These results provide valuable insights to further advance the understanding of oil spill impacts on fish populations in support of management.

2. NEA cod and NEA haddock fisheries

The NEA cod (*Gadus morhua*) fishery in the Barents Sea has existed for at least the past 1000 years. This fishery is arguably among the world’s healthiest commercial fish stocks (Kjesbu et al., 2014), and has a long history of successful management measures to support this fishery

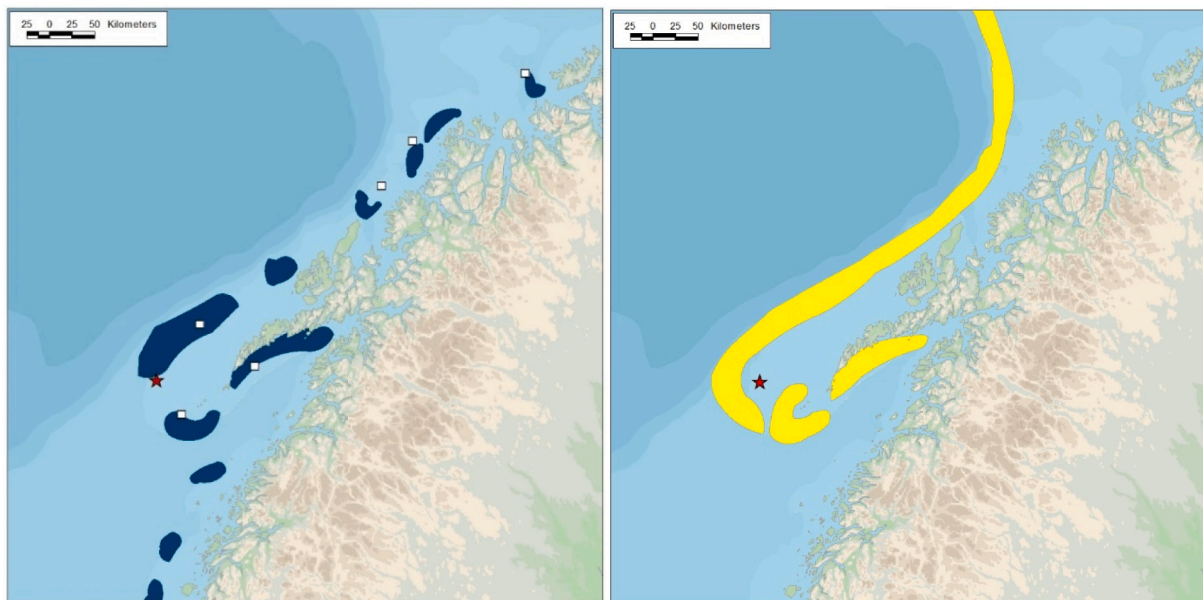


Fig. 3. Spawning areas along the Norwegian coast for Northeast Arctic cod (left panel, blue areas) and Northeast Arctic haddock (right panel, yellow areas). The discharge site is indicated by a red star in both panels. In the fish ELS model, the cod spawning is represented by releasing eggs from nine different spawning grounds indicated by white squares with spawning occurring Mar 1 until Apr 30. For haddock, the spawning is represented by releasing eggs from the entire spawning area with spawning occurring Mar 15 to May 14. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Gullestad et al., 2018). The NEA haddock (*Melanogrammus aeglefinus*) stock has a long record of commercial catches and has been fished following a sustainable management plan since 2009. Annual catches are >150,000 metric tons (ICES, 2021). The main spawning grounds of both fish species are along the Norwegian coast (Fig. 3) and overlap with sea regions containing substantial petroleum resources.

In this region, the spawning of cod occurs from March to late April (Ottersen et al., 2014). Developing eggs, larvae, and juveniles are then transported north and east by near-surface currents towards nursery grounds in the Barents Sea (Yaragina et al., 2011). By around June–July, the cod have mostly gone through metamorphosis becoming pelagic juveniles — young fish. During August, pelagic juveniles begin to settle close to the seabed. Only a tiny fraction of juvenile cod survives in any year (Bogstad et al., 2015). Survivors (age ~ 1 year) enter the Barents Sea as juveniles, grow large enough to enter the fishery at age 3–4, and mature at around 6–7 years. Those that successfully enter the fishery can live for >10 years, depending on fishing pressure. This longevity helps buffer the population from declines during poor spawning years. However, NEA cod also has a relatively high incidence of skipped spawning compared to other cod stocks (Skjæraasen et al., 2012; Rideout and Tomkiewicz, 2011).

NEA haddock is the largest haddock stock in the world, but is rather less well studied than NEA cod. Haddock and cod are closely related, and share similar (although not identical) spawning areas and times in the Northeast Arctic (Olsen et al., 2010). Haddock spawning occurs in Lofoten-Vesterålen and along the northwestern Norwegian continental shelf break up to the Bear Island Trough north of Norway. The timing of spawning varies between years but is within the period from late March to early June (Tronbøl et al., 2022). As with cod, there is a relatively high rate of skipped spawning (up to 40 % in some years) in haddock females (Skjæraasen et al., 2012). Hatched larvae drift into the south and west Barents Sea (Castaño-Primo et al., 2014). Haddock which survive the larval and 0-group (~5–7 months old) stages typically mature between 5 and 7 years of age and typically live to around 10

years. As is common for marine fish stocks, both cod and haddock show considerable variation in recruitment success between years (Fig. 4). However, the recruitment success of haddock is more variable, and occasional good recruitment years are a major factor driving haddock stock dynamics. Individual large year classes give rise to large variations in biomass, with adult biomass more than doubling over 5 years and then returning to more moderate levels (ICES, 2021).

3. Materials and methods

3.1. Model components and features

To determine the response of a fish population to an oil spill requires the integrative understanding of 1) the fate and transport of oil; 2) the transport, behaviour, and interactions of biota in the environment; and 3) species sensitivity linked to the toxicity of oil compounds. We coupled three models to predict the survival of drifting fish ELS exposed to petroleum compounds after an oil spill: a model to simulate oceanographic and atmospheric processes and a lower trophic level ecosystem model (Alver et al., 2016; Slagstad and McClimans, 2005; Wassmann et al., 2006; Broch et al., 2020); an ecological model for the pelagic stages of fish ELS (Vikebø et al., 2007; Vikebø et al., 2021); and an oil transport and fate model (Nordam et al., 2019; Daae et al., 2018; Reed et al., 2004). These models are four-dimensional (three spatial dimensions and time) with domains as shown in Fig. 1. The models are mature models, having undergone individual upgrades and validation exercises throughout the past three decades. The models include the best available information on the life history of NEA cod and haddock early life stages and their primary prey. The models are calibrated with regional data supported by long-term monitoring data sets on the NEA cod and haddock fisheries and wider ecosystems (Bogstad et al., 2015; Jakobsen and Özigin, 2011; ICES, 2021).

The lower trophic level ecological component is fully coupled to the ocean component. It simulates the state of the lower trophic level

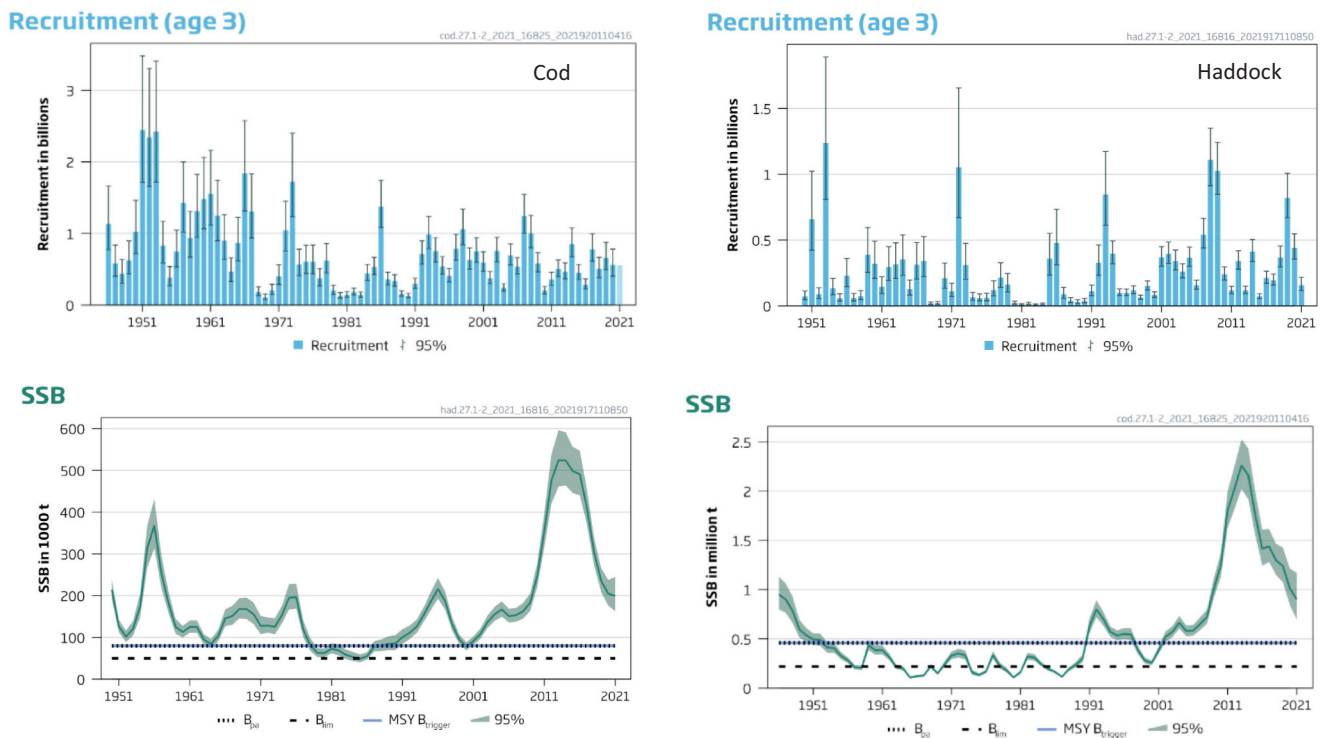


Fig. 4. Recruitment and spawning stock biomass (SSB) for NEA cod (left) and NEA haddock (right) from ICES advice. Note that recruitment is shown at age 3 which corresponds to 4 years after spawning. Also note that the 2003–2006 yearclasses for haddock (2007–2009 at age 3) show multiple adjacent good yearclasses. Source: ICES advice 2021, https://ices-library.figshare.com/collections/ICES_Advice_2021/5796932?q=:category:barents.

ecosystem from nutrients up to mesozooplankton (*C. finmarchicus*) in an Eulerian framework (Wassmann et al., 2006; Alver et al., 2016). It includes egg and nauplii stages, development, spawning, and distribution as functions of ocean currents, food availability and temperature. This model supplies the fish ELS model with current, temperature, salinity, turbulence, and prey concentration fields (Broch et al., 2020). Simulations using the oceanographic model coupled to the lower trophic level ecosystem model generate distributions of *C. finmarchicus*. The ability to investigate the match-mismatch of fish ELS and prey species is essential as it determines what part of the fish ELS that reach the overwintering stage. Vikebø et al. (2021) recently showed that both early and late spawned cod larvae experience slower growth than individuals originating closer to the time of peak spawning in late March/early April due to low temperatures and limitations in the availability of suitable prey, respectively. Also, rapid growth is crucial for survival (Houde, 2008).

The oil transport and fate model simulates the behaviour and fate of oil during a spill as a function of the physico-chemical properties of the oil, environmental weathering processes, and hydrodynamic conditions. The model supplies concentration fields of different oil phases (surface, entrained droplets, and dissolved) for 25 chemical groups (Supplementary material Table S1). The approach assumes that individual hydrocarbon constituents in each group behave similarly (i.e., have similar distributions and fates in the environment). The fish ELS model simulates stage duration and transition, dispersal, diel migration, feeding and growth for different ELS using a particle-tracking model with built-in modules for individual physiological and behavioral responses of eggs and larvae to ambient forcing (Sandvik et al., 2016; Vikebø et al., 2007; Vikebø et al., 2021). The concentration fields of dissolved oil are transferred to the ecotoxicology subroutine within the fish ELS model.

The ecotoxicology subroutine, based on DEBtox equations (Dynamic Energy Budget Theory with ecotoxicology), predicts toxicity for individual fish eggs and larvae using laboratory experimental data and octanol-water coefficients (Kow) for oil compounds (Klok et al., 2014). DEBtox is a widely accepted, generic, and well-tested method that combines knowledge on physiological properties of species (e.g., long, or short lived, big, or small) with sensitivity to different chemical compounds (Ashauer and Jager, 2018; Galic et al., 2017; Teal et al., 2018). DEBtox uses a set of common equations describing key biological and physiological processes. These equations, together with parameter values derived for individual species and substantiated through peer-reviewed scientific investigations, predict the effects of time-varying exposures to chemicals.

Toxic responses are calculated dynamically using simple relationships to describe how chemical substances enter and exit an organism over time (toxicokinetics, TK) and what happens to the organism once the toxicants reach effective doses (toxicodynamics, TD). The magnitude of the response in time is described based on the following three parameters: the no effect concentration (NEC, µg/L), the elimination rate (k_e , 1/d), and the killing rate (b , L/µg/d). The NEC represents the concentration below which no effect occurs. The intensity of the effect is a function of b ; the higher the b value the more toxic the compound (i.e., the faster an organism dies once the NEC is exceeded). The elimination rate integrates both the uptake and elimination processes, driving the speed of the effects. A high k_e value for a toxicant implies that the toxicity level in the organism is reduced faster relative to toxicants with lower k_e values. There is a temperature correction for both k_e and b , and a body length correction for k_e (Klok et al., 2014). The uptake of dissolved oil compounds occurs through water.

In the previous version of SYMBIOSES (Carroll et al., 2018), compounds were treated as independent of one another, and effects occurred only when the threshold concentration of an individual compound was exceeded. In the mixture toxicity model, each compound 'shares' the NEC and an effect is calculated based on contributions of all toxic components in the oil. An effect may occur when the NEC value of the compound mixture is exceeded.

Let C_D be the ambient concentration of an oil component as

experienced by an individual. The scaled internal concentration C_V of this component for the individual is then modelled as

$$\frac{d}{dt}C_V = k_e(C_D - C_V)$$

where k_e is the elimination rate of the component. It is assumed that the ambient concentration is constant within each time step, which gives a closed-form expression for C_V with an exponential approach towards the ambient concentration. For the mixture of all the chemical compounds (components), a dimensionless weighted total concentration is calculated as

$$C_{weighted} = \sum_{components} \frac{C_V}{NEC}$$

where each component is scaled by its own NEC. A toxic effect occurs when the weighted total concentration across all compounds is greater than one. This is represented by the effective concentration C_e of each component, calculated as

$$C_e = \max\left(0, C_V - \frac{NEC}{C_{weighted}}\right)$$

where NEC is the original NEC for the component. C_e is non-zero for all components with a non-zero concentration if the total scaled concentration is greater than one, and zero otherwise. This formulation of the effective concentration corresponds to reversible binding (Baas et al., 2009) and is new compared to Carroll et al., 2018 where the NECs were used directly without scaling. C_e is then used to derive the hazard rate for an individual, given by

$$H(T) = \sum_{components} b \int_0^T C_e(t) dt$$

where the b 's are the killing rates of the individual components. The hazard rate must be calculated by numerical integration within each time step due to the division by the total scaled concentration. It translates directly to the survival probability for the individual as

$$S(t) = \exp\{-H(t)\}$$

where $0 \leq S(t) \leq 1$ since $H(t) \geq 0$. Finally, the overall survival probability s for the population is given by the weighted sum

$$s(t) = \sum_{individuals} w \cdot S(t)$$

where the non-negative weights w are given by the spawning distribution and satisfy

$$\sum_{individuals} w = 1.$$

Each simulation produces a survival percentage for the ELS (to the end of the pelagic stage). We quantify the cumulative difference in survival for identical simulations with and without oil. We then transfer the reduction in larval survival to the fish population model and use this to modify the number of recruits to a fish population model. That is, the estimated recruitment within the fish population model is modified by the overall reduction in survival for the population of fish ELS. This avoids the difficulties that would otherwise arise from the need for a very high level of precision on the ELS estimates.

A general limitation of toxicity models is the availability of experimental data that supports modeling (De Laender et al., 2011; Olsen et al., 2013; Klok et al., 2014). Due to the limitations of data and current knowledge on the effects of exposure to petroleum compounds, we apply four toxicity parameter sets (Supplementary material Table S2), producing four survival probabilities for each simulation. This is a recognized procedure to estimate uncertainty by exploring a range of

simulated model outcomes associated with different parameters sets (Bassis, 2021). Briefly, parameter set P1 is based on empirically supported linear relationships between log Kow and the NEC for individual compounds, k_e and b that were estimated for juvenile fathead minnow (Klok et al., 2014) with the addition of an assessment factor (AF) of 50 to account for higher sensitivity at younger development stages (ELS) than in adults. For parameter set P2, an assessment factor of 500 was applied to polyaromatics (including naphthalenes) to account for uncertainties in the toxicity mechanisms for marine fish eggs and larvae exposed to PAHs. The NECs for naphthalenes 1 and 2 and PAH 1 and 2 for parameter set P1 are 92.1, 18.1, 13.1, and 2.26 $\mu\text{g/L}$; for parameter set P2 the values are 9.21, 1.81, 1.31, and 0.226 $\mu\text{g/L}$ (SI Table 2). Uptake kinematics slow down with decreasing threshold for effect (NEC) as reflected in the corresponding k_e for the four polyaromatic groups equal to 3.82, 1.14, 0.87 and 0.23 day^{-1} . Parameter sets P3 and P4 have threshold levels for the four polyaromatic groups at 1.0 and 0.1 $\mu\text{g/L}$, respectively. Lethality is instantaneous when the exposure concentration of the sum of the four polyaromatic groups exceed these threshold levels.

There are two important distinctions between P1/P2 and P3/P4. First, acute lethality occurs only in response to the outcome of the time varying uptake and elimination (TK) processes for P1 and P2 while for P3 and P4, lethality is instantaneous when the exposure concentrations of the sum of the four polyaromatic groups exceed the selected threshold values. Second, for P1 and P2, the NECs for the four polyaromatic groups are based on the temperate freshwater fish fathead minnow (Klok et al., 2014) while the P3 and P4 NEC values are based on published studies of toxic effects (lethal and sublethal) performed on a variety of marine cold water fish species. These four parameter sets encompass a wide range of uncertainty in both threshold levels and effects for petroleum compounds (Carroll et al., 2018). For context, the lowest reported effect concentration for haddock is 10 $\mu\text{g/L}$ of oil (0.1 $\mu\text{g/L}$ $\sum\text{PAH}$) (Cresci et al., 2020). For cod, the lowest nominal crude oil concentration is 140 $\mu\text{g/L}$ (Nordtug et al., 2022). The lowest $\sum\text{PAH}$ effect concentration is 1.34 $\mu\text{g/L}$ $\sum\text{PAH}$ (Hansen et al., 2016).

A fish population model run (right side of Fig. 2) quantifies the impact on the spawning stock biomass (SSB) of fish (from age 1+) (Howell and Bogstad, 2010; Lindström et al., 2009). This model performs forward simulations of biological processes (growth, predation, maturation, etc.), including both bottom-up and top-down effects and spatial and temporal variations in species interactions (Guldbrandsen Frøysa et al., 2002). It simulates whole populations of a given species. The main state variables are the number and mean weight of individuals in each age/length group for a given population and area. Model parameters are derived by tuning the model to the available fisheries and survey data.

For cod, we apply a density-dependent mortality function on the late larval stage (often called the “0-group”) to adjust our abundance estimates during this period (Carroll et al., 2018). In addition, there is density dependence among juvenile and small adult cod because of cod cannibalism, which is included in the model. The inclusion of density dependence ensures that the mature cod model does not over-estimate the abundance of juveniles recruited to the fish population. Although 0-group mortality is accounted for in the haddock, this is not modelled as density dependent. This may result in an over-estimate when translating the oil-induced mortalities on ELS on the adult fish population. However, the presence of extremely large yearclasses of haddock indicates that, at least given ideal conditions, the density dependent portion of mortality must be rather small. Haddock are not cannibalistic. Instead, haddock mortality varies according to cod predation, particularly at age 3, but also at ages 4 and 5. This variable mortality is accounted for in the modeling. There is evidence of density-dependent growth in haddock after the 0group stage, with smaller size at age in the occasional very large year class.

We assess the impact and track recovery for the harvestable fish populations post-spill. In all simulations, oil is assumed to have no

impact after one year and all surviving fish are healthy. We quantify the change in the aggregated weight of mature fish in the stock, termed the spawning stock biomass (SSB). The population structure is modulated by the Harvest Rule (regulated fishing quotas) and predation (loss of fish due to predator/prey interactions) for each year. We assume that the fishing intensity (i.e., the fraction of the stock caught) is the same for identical scenarios, with and without oil, although absolute number of fish caught will vary as the stock size responds to oil mortality.

We note that the fish population model is much faster to run computationally than the ocean simulations on the ELS. Therefore, to increase the range of possible stock states to examine, we apply the oil-induced mortality (fraction) from the oil spill year (2001) to each recruitment year in the fish model (1990–2010). Oil-induced mortalities on cod and haddock depend on the oceanographic and feeding conditions in each year. However, the impact of those mortalities on the overall stock development will depend on the degree to which the adult stock is dominated by recruits from that year. This implies that the overall stock impact depends not only on recruitment within a given year, but also the relative strength of that recruitment compared to the years before and after. For this reason, we apply the oil-induced mortalities from a given year to all potential years within the adult fish population model. Here we report the impacts of an oil spill in 2001 oceanographic conditions to the stock conditions which would have shown the maximum impact (Tables 1 and 2). For cod this is the 2004 yearclass. For haddock, the recruitment peak in 2004–2006 arose from several good adjacent yearclasses while most other recruitment peaks in this haddock stock have occurred as single good yearclasses (Fig. 4). Applying oil mortality to a single year of the 2004–2006 peak is therefore a good representation of an oil spill affecting that recruitment period (or something similar in the future) but is an underestimate of the oil impact on a recruitment peak consisting of a single good yearclass. We therefore run two scenarios to estimate likely impacts on both a single-year and a multi-year recruitment peak. In scenario one of the two scenarios, we assume that the 2004–2006 recruitment period represents a single year and apply the oil mortality to the entire recruitment spike. In scenario 2, the recruitment values for each year are independent and

Table 1
Percent survival of early life stages (to the end of the pelagic stage) of Northeast Arctic cod and Northeast Arctic Haddock for oil releases starting on selected dates (column 2). The discharge rate was 4500 m^3/day for 90 days at a single location on the Lofoten-Vesterålen shelf (67.700N 10.841E). Four toxicity parameter sets were applied (P1–P4) representing different threshold levels of effects from petroleum compounds. The values given in the columns P1–P4 represents the survival relative to that of the non-exposed population, e.g., 100 means that the survival for both exposed and non-exposed populations are the same, 98 means that the survival of the exposed population is 2 % lower than for the non-exposed population. Lower numbers indicate higher impacts on survival.

| Scenario | Oil start | Cod early life stages | | | | Haddock early life stages | | | |
|----------|-----------|-----------------------|-----|-----|----|---------------------------|-----|-----|----|
| | | P1 | P2 | P3 | P4 | P1 | P2 | P3 | P4 |
| 1 | 1 Jan | 100 | 100 | 91 | 72 | 100 | 100 | 98 | 87 |
| 2 | 16 Jan | 100 | 100 | 89 | 66 | 100 | 100 | 96 | 74 |
| 3 | 1 Feb | 100 | 100 | 85 | 59 | 100 | 100 | 92 | 64 |
| 4 | 15 Feb | 100 | 100 | 84 | 56 | 100 | 99 | 91 | 62 |
| 5 | 1 Mar | 100 | 100 | 84 | 53 | 100 | 99 | 90 | 63 |
| 6 | 16 Mar | 100 | 100 | 84 | 60 | 100 | 99 | 90 | 66 |
| 7 | 1 Apr | 100 | 100 | 89 | 69 | 100 | 99 | 92 | 76 |
| 8 | 16 Apr | 100 | 100 | 91 | 76 | 100 | 100 | 93 | 84 |
| 9 | 1 May | 100 | 100 | 93 | 79 | 100 | 100 | 97 | 90 |
| 10 | 16 May | 100 | 100 | 96 | 84 | 100 | 100 | 98 | 94 |
| 11 | 1 Jun | 100 | 100 | 96 | 88 | 100 | 100 | 99 | 96 |
| 12 | 16 Jun | 100 | 100 | 97 | 87 | 100 | 100 | 99 | 96 |
| 13 | 1 Jul | 100 | 100 | 97 | 90 | 100 | 100 | 99 | 97 |
| 14 | 16 Jul | 100 | 100 | 97 | 91 | 100 | 100 | 99 | 97 |
| 15 | 1 Aug | 100 | 100 | 98 | 93 | 100 | 100 | 99 | 98 |
| 16 | 16 Aug | 100 | 100 | 98 | 94 | 100 | 100 | 99 | 98 |
| 17 | 1 Oct | 100 | 100 | 100 | 98 | 100 | 100 | 100 | 99 |

Table 2

Assessment of spawning stock biomass (SSB) of Northeast Arctic cod and Northeast Arctic haddock for oil releases starting on selected dates (column 2). The discharge rate was 4500 m³/day for 90 days at a single location on the Lofoten-Vesterålen shelf (67.700N 10.841E). Four toxicity parameter sets were applied (P1–P4) representing different threshold levels of effects from petroleum compounds. The values given in the columns P1–P4 represent the SSB value relative to the SSB value for the non-exposed population, for example, 100 means that the SSB's for both exposed and non-exposed populations are the same, 98 means that the SSB of the exposed population is 2 % lower than the non-exposed population. Lower numbers indicate higher impacts on the spawning stock biomass (SSB). Results are for the post oil spill year with the largest impact on the SSB. For haddock SSB, the impact is given for a 3-year recruitment peak and a 1-year peak. See text for further details.

| Scenario | Oil Start | Cod SSB | | | | Haddock SSB 3 yr recruitment peak | | | | Haddock SSB 1 yr recruitment peak | | | |
|----------|-----------|---------|-----|-----|----|--------------------------------------|-----|-----|----|--------------------------------------|-----|-----|-----|
| | | P1 | P2 | P3 | P4 | P1 | P2 | P3 | P4 | P1 | P2 | P3 | P4 |
| 1 | 1 Jan | 100 | 100 | 96 | 89 | 100 | 100 | 98 | 89 | 100 | 100 | 99 | 95 |
| 2 | 16 Jan | 100 | 100 | 96 | 86 | 100 | 100 | 97 | 78 | 100 | 100 | 99 | 90 |
| 3 | 1 Feb | 100 | 100 | 94 | 84 | 100 | 100 | 93 | 70 | 100 | 100 | 97 | 87 |
| 4 | 15 Feb | 100 | 100 | 94 | 82 | 100 | 99 | 93 | 68 | 100 | 100 | 97 | 86 |
| 5 | 1 Mar | 100 | 100 | 94 | 81 | 100 | 99 | 92 | 69 | 100 | 100 | 96 | 86 |
| 6 | 16 Mar | 100 | 100 | 94 | 84 | 100 | 99 | 92 | 72 | 100 | 100 | 96 | 88 |
| 7 | 1 Apr | 100 | 100 | 96 | 88 | 100 | 99 | 93 | 80 | 100 | 100 | 97 | 91 |
| 8 | 16 Apr | 100 | 100 | 96 | 90 | 100 | 100 | 94 | 87 | 100 | 100 | 97 | 94 |
| 9 | 1 May | 100 | 100 | 97 | 92 | 100 | 100 | 98 | 92 | 100 | 100 | 99 | 96 |
| 10 | 16 May | 100 | 100 | 98 | 94 | 100 | 100 | 98 | 95 | 100 | 100 | 99 | 98 |
| 11 | 1 Jun | 100 | 100 | 98 | 95 | 100 | 100 | 99 | 97 | 100 | 100 | 100 | 99 |
| 12 | 16 Jun | 100 | 100 | 99 | 95 | 100 | 100 | 99 | 97 | 100 | 100 | 100 | 99 |
| 13 | 1 Jul | 100 | 100 | 99 | 96 | 100 | 100 | 99 | 98 | 100 | 100 | 100 | 99 |
| 14 | 16 Jul | 100 | 100 | 99 | 96 | 100 | 100 | 99 | 98 | 100 | 100 | 100 | 99 |
| 15 | 1 Aug | 100 | 100 | 99 | 97 | 100 | 100 | 99 | 98 | 100 | 100 | 100 | 99 |
| 16 | 16 Aug | 100 | 100 | 99 | 98 | 100 | 100 | 99 | 98 | 100 | 100 | 100 | 99 |
| 17 | 1 Oct | 100 | 100 | 100 | 99 | 100 | 100 | 100 | 99 | 100 | 100 | 100 | 100 |

the oil spill impacts one year of the recruitment peak.

3.2. Simulations

We initiated 17 simulations, each with a different start date for an oil release but for the same model year 2001. In the first simulation, the oil spill release started on 1 January. Oil releases in subsequent scenarios were initiated ~15 days later until 16 August. A final scenario was run with an oil release on 1 October. All releases occurred at a single location on the Lofoten-Vesterålen shelf (67.700N 10.841E) (Fig. 1). We selected this location because it resulted in the largest areal coverage in the marine environment for a selected group of oil spill scenario simulations commissioned to support the update of the Integrated Management Plan for the Marine Environment of the Barents Sea–Lofoten Area (Det Norske Veritas, 2010). It is also located in key areas of the spawning grounds for both fish species under investigation (Fig. 3).

We simulate a topside release (ocean surface) with the oil type Balder Blend 2010 and a release rate of 4500 m³/day lasting 90 days. This oil type is a combination of Balder (40 %, asphaltenic) and Ringhorne oils (60 %, wax-rich), resulting in a medium-high paraffinic blend (Sørheim and Leirvik, 2010; NOAA, n.d. ADIOS oil database¹). The selected rate aligns with expert knowledge of the reservoir characteristics of our study location which exerts physical control of oil flow rates and discharge volumes (Dimmen and Syversen, 2010). For context, the volume of oil released in our simulations is approximately half the volume of the Deepwater Horizon oil spill and 11 times the Exxon Valdez spill.

The obtained temporally varying concentration fields of dissolved oil are transferred from the oil model to the ecotoxicology sub-routine within the fish ELS model. The ambient concentrations of bioavailable oil compounds in the dissolved phase are then taken up by drifting fish ELS as described in Section 3.1. These bioavailable oil compounds are in the chemical groups: saturates (C1–C9), monoaromatics (benzenes, C10 saturates), and polyaromatics (naphthalenes, PAH-1, PAH-2) (Table S1 Supplementary Information). Based on the derived losses in the early life stage cohorts after each oil spill, we evaluate the associated impact on the biomass (SSB) of the adult fish populations. All simulations are stored in a permanent electronic library. NetCDF files are available upon

request.

4. Results

4.1. Oil in the environment

For our 4500 m³/day oil release scenario for 90 days, the total volume of discharged oil was 349 × 10³ metric tons with 8–13 % of discharged oil lost through the process of biodegradation, 26–35 % lost through evaporation and 9–44 % through advection outside the oil spill model domain (Fig. 5). These processes vary throughout the year depending on weather and ocean conditions with, for instance, more evaporation in the summer months. During summer months there is also a relative increase in surface oil, while submerged oil is largest during winter and autumn months (Fig. 5b, upper panels). The volume of oil exceeding concentrations of 1.0 and 0.1 µg/L also varies throughout the year in response to changes in the relative predominance of the underlying processes, as listed above. The largest volumes to exceed these limits were observed during winter and autumn (Fig. 5b, bottom panels.)

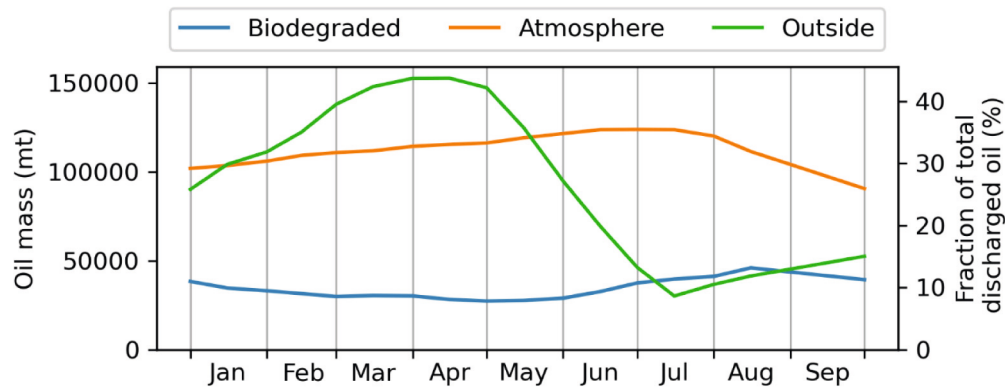
4.2. Prey concentration fields

The appearance of *C. finmarchicus* in the region of study is driven by the dynamics of the spring bloom period. This period initiates with the light and temperature driven growth of phytoplankton. The increase in primary production begins earlier along the coast and in the stratified Norwegian coastal current relative to deeper waters farther offshore and beyond the shelf break (Fig. 6A and B). Early in the year phytoplankton concentrations are generally lower in regions influenced by Atlantic water masses with a deeper mixing layer (Fig. 6A). In late summer/autumn as nutrients become depleted in the surface layers, the region of highest primary production shifts to nutrient-rich waters located in deeper waters, further away from the continental shelf (Fig. 6B).

The seasonal pattern of *C. finmarchicus* in the Lofoten-Vesterålen region, begins with the ascent of adult females from diapause in late winter. At the start of the spring phytoplankton bloom, the biomass on the shelf and along the shore is relatively low and the *Calanus* population mostly consists of early copepodite stages and nauplii (Fig. 6C). By late summer/autumn (Fig. 6D), the biomass concentration is higher but a

¹ <https://adios.orr.noaa.gov/oils/NO00008>.

a



b

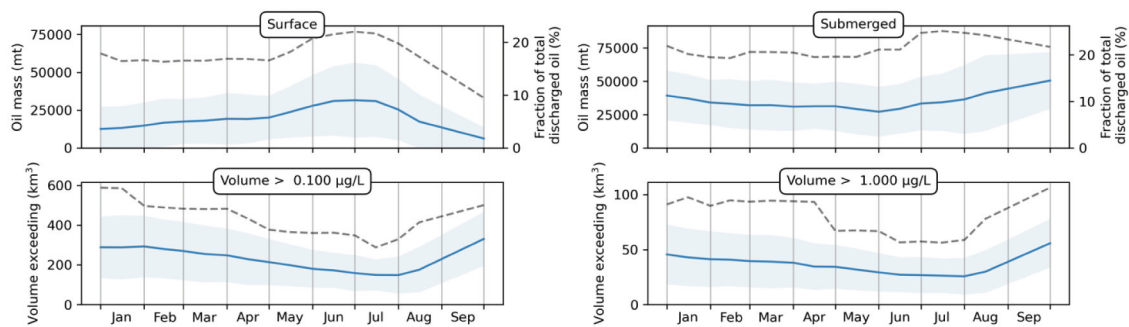


Fig. 5. a. Oil-related endpoints for all scenarios, as a function of scenario start date. These are cumulative, in the sense that they only increase during an individual simulation. Thus, the final (maximum) values are shown. The fraction (in %) is given relative to the total amount of discharged oil in each simulation. Biodegraded: oil mass removed by bacterial degradation (metric tons). Atmosphere: oil mass removed by evaporation (metric tons). Outside: oil mass advected outside the domain of the oil spill model (metric tons).

b. Oil-related endpoints for all scenarios, as a function of scenario start date. The black dashed line shows time-maximum values, light blue area shows time-mean \pm time-standard deviation, while the full blue line shows time-mean values. The fraction (in %) is given relative to the total amount of discharged oil in each simulation. Surface: oil mass on the surface (metric tons). Submerged: oil mass dispersed in the water column (metric tons). Volume > 0.100 $\mu\text{g/L}$: Volume of water where dissolved oil concentration exceeds 0.1 $\mu\text{g/L}$ (km^3). Volume > 1.000 $\mu\text{g/L}$: Volume of water where dissolved oil concentration exceeds 1.0 $\mu\text{g/L}$ (km^3). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

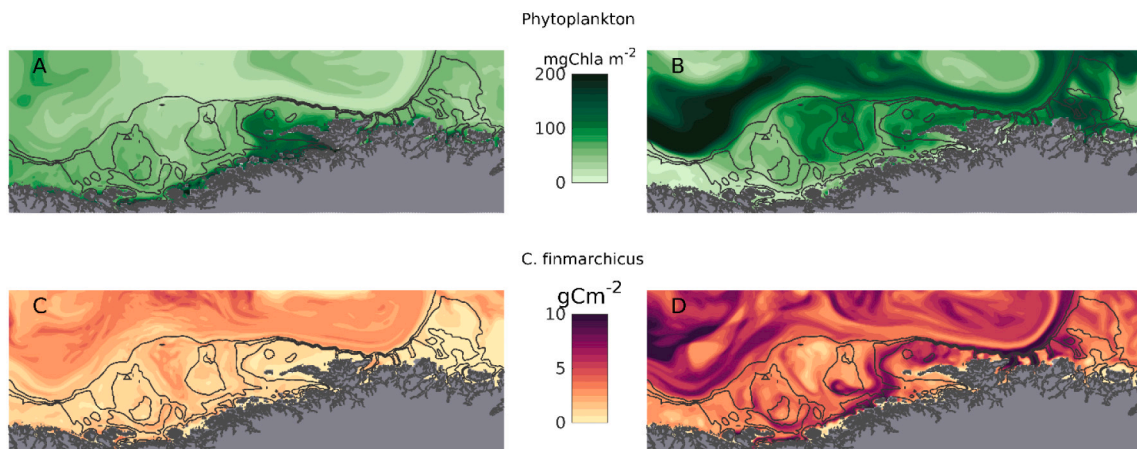


Fig. 6. Simulated, depth-integrated phytoplankton (0–50 m) given as Chlorophyll A content (mg Chla m^{-2}) averaged over the period March 17–May 17 (A) and August 1–October 1 (B), 2001. Simulated, depth-integrated (0–50 m) *C. finmarchicus* concentrations shown as carbon content (g C m^{-2}) averaged over the period March 17–May 17 (C) and August 1–October 1 (D), 2001. The black curves indicate 200, 300, and 500 m isobaths. The shelf break approximately follows the 500 m isobath.

The colormaps used are described in Thyng et al. (2016).

large part of the biomass consists of late stage copepodites in diapause at deeper water levels (Fig. 7A). The optimal size range of *C. finmarchicus* for fish larvae to capture is Nauplii stages NIII to NIV. These stages coincide with the presence of larvae on the shelf in spring-early summer (Fig. 7B and C). By late August, the productivity of *C. finmarchicus* on the shelf is close to zero and is negative along the shelf break.

4.3. Fish early life stages

We simulated temporally varying ambient concentrations of dissolved oil compounds and their uptake by drifting fish ELS. There was no impact on fish early life stage survival relative to a simulation without oil for any of the modelled oil discharge scenarios when applying toxicity parameter sets P1 and P2 (Table 1). Parameter sets P1 and P2 include TKTD factors (the elimination rate (k_e , 1/d), and the killing rate (b , L/ $\mu\text{g}/\text{d}$) and with assessment factors (50 and 500, respectively) applied to the individual NEC values for each compound group (see methods section).

Parameter sets P3 and P4 invoke instantaneous lethality when the exposure concentrations of the sum of the four polyaromatic groups exceeds the selected threshold values. For toxicity parameter set P4, the highest and lowest survival for the early life stages of cod as a response to oil exposure is 98 % (1 Oct) and 53 % (1 Mar) (Fig. 8A). For parameter set P3, the highest survival is 100 % (1 Oct) and the lowest 84 % (15 Feb; 1 Mar; 16 Mar). For haddock (P4), the highest survival is 99 % (1 Oct) and the lowest 62 % (15 Feb) (Fig. 8C). For parameter set P3, the highest survival is 100 % (1 Oct) and the lowest 90 % (1 Mar; 16 Mar). These minimums in survival for oil releases coincide with the early part of the fish spawning seasons. After this period, survival increases for both fish species for all subsequent simulation start dates through to the final simulation start date of 1 Oct.

A first prototype version of a simulation visualization tool was developed to aid the comprehension of results. Four example videos using the visualization tool are available for viewing at <https://drive.google.com/drive/folders/1gz3Ia0W8vZqAJVzd1wnPdbboK6ChbEqz?usp=sharing>. These videos are for Scenario 5 (cod) and Scenario 5 (haddock) presenting oil spills starting on 1 March, and Scenario 13 (cod) and Scenario 13 (haddock) presenting oil spills starting on 1 August. All four videos present the results for fish early life stages and the ecotoxicology parameter set P4 (Supplementary Videos S1–S4). The color legend used in these videos is: Grey = oil concentrations $<0.1 \mu\text{g}/\text{L}$; Blue = oil concentrations $<1 \mu\text{g}/\text{L}$; Green = 100 % survival probability; and Red = 0 % survival probability.

4.4. Spawning stock biomass (SSB)

There is no identifiable impact on cod or haddock survival relative to a simulation without oil for any of the modelled oil discharge scenarios when applying toxicity parameter sets P1 and P2 (Table 2). For cod (P4), the highest SSB is 99 % (1 Oct) and the lowest is 81 % (1 Mar) (Fig. 8B). For parameter set P3, the highest SSB is 100 % (1 Oct) and the lowest is 94 % (1 Feb–16 Mar). In both cases, the consequences of cod ELS loss due to oil exposure is dampened due to i) density-dependence (see Section 3.1) and ii) the fact that SSB consists of multiple year classes whereof only one is assumed affected by the spill.

In scenario one of the two scenarios simulated for haddock, we assume that the recruitment in the period 2004–2006 represents a single year and apply the oil mortality to the entire recruitment spike. This approximates the situation where a single good yearclass occurs. In this scenario with P4, the highest SSB values are 99 % (1 Oct) and the lowest is 68 % (15 Feb) (Table 2 and Fig. 8D). For parameter set P3, the highest SSB value is 100 % (1 Oct) and the lowest is 92 % (1 Mar–16 Mar). In scenario 2 the recruitment values for each year are independent and the oil only impacts part of the recruitment peak. In this scenario with P4, the highest SSB values are 100 % (1 Oct) and the lowest is 86 % (15 Feb–1 Mar) (Fig. 8E). For parameter set P3, the highest SSB value is 100

% (1 June–1 Oct) and the lowest is 96 % (1 Mar–16 Mar). As expected, the temporal patterns in SSB values are similar for cod and haddock. These SSB patterns mirror the trends in ELS survival for their respective fish species, albeit with a smaller range of variation.

5. Discussion

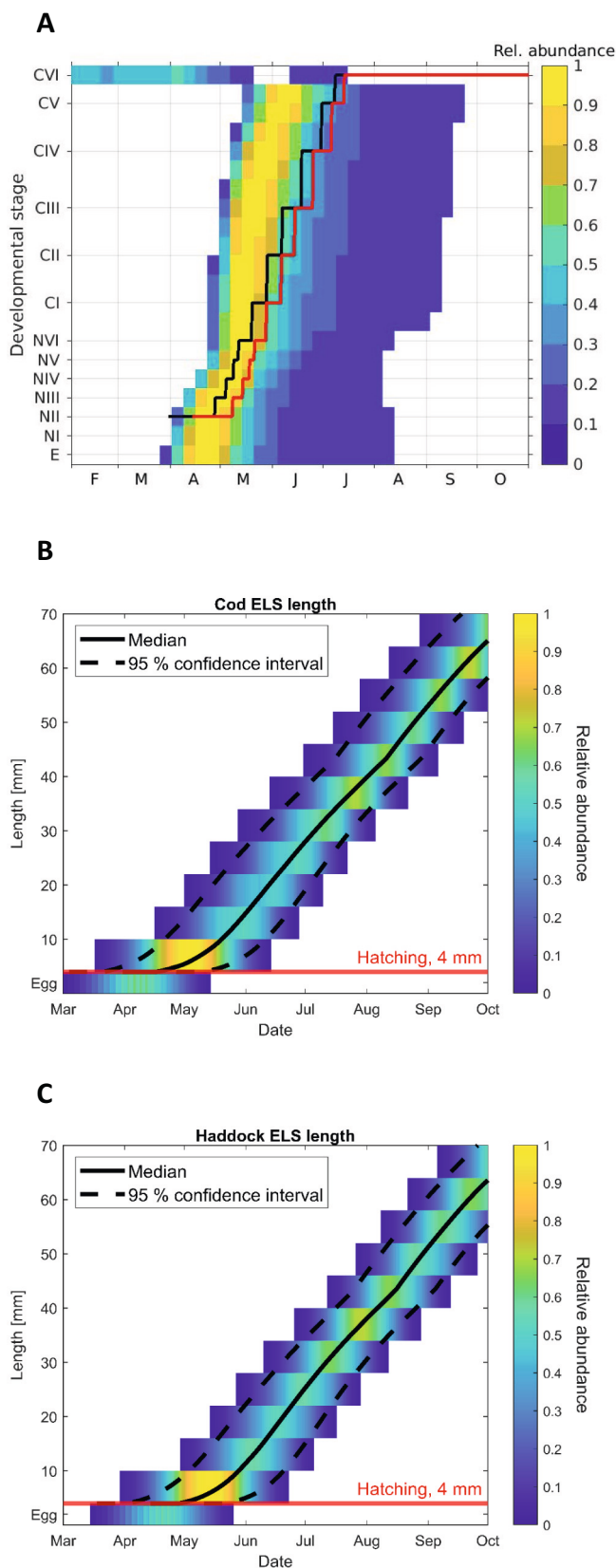
We have examined how the time of an oil spill event in a year impacts two commercial fish species. Through simulations, the overlapping influences of fish life history and oil transport and fate are shown to result in encounters with oil in the marine environment that result in variable exposures and effects on fish ELS and reductions to fish SSB. We first present and discuss the distribution patterns of a key prey species for cod and haddock larvae, the zooplankton species *C. finmarchicus*. This species is a primary cause of mortality and spatiotemporal selective mechanisms for the survival of fish larvae along the Norwegian coast. Next, we discuss insights obtained by applying a toxic effects model that predicts the time-varying effects of exposures to chemicals and treats oil as a dynamic mixture of compounds. We then discuss our general findings on the relationships between the time of an oil spill and key events in the life history of developing fish and the resulting responses of the population of juvenile and mature fish. This includes an examination of recruitment variability in haddock and how this factor influences the outcome of an oil spill at the population level. The study findings demonstrate the value of using simulation systems to provide insights on fish life history and oil spills which is essential for developing sound management strategies to achieve the goals of sustainable resource development.

5.1. Prey availability for fish early life stages

The natural survival of an individual fish larva depends on many environmental factors, primarily temporal and spatial variations in sea temperatures, larval advection and dispersal, ambient light conditions, ocean turbulence, prey availability, and predation. These processes are inextricably linked to the annual cycle of marine productivity. In northern temperate waters, most of the annual primary production, Chlorophyll A content up to 400 mg m^{-2} , is supplied during the spring bloom with gross primary production ranging from 80 to $180 \text{ g m}^{-2} \text{ y}^{-1}$ (Rey, 1981; Oziel et al., 2017). Each spring the dominant herbivorous copepod species in this region (*Calanus finmarchicus*) migrate from the deep basins of the North Atlantic to the food-rich epipelagic zone to feed, grow, and reproduce (Conover, 1988). The magnitude of zooplankton production is triggered by the timing and strength of the spring bloom which depends on sunlight, nutrient concentration, and vertical mixing/stratification, over the length of the year. These copepods are advected along the north Norwegian shelf break where they feed on the abundant concentrations of phytoplankton that consists mainly of diatoms (Slagstad et al., 1999; Wassmann et al., 1999; Henson et al., 2009).

The biomass of *C. finmarchicus* starts low in March–April and increases, peaking along the shelf break of the Norwegian Sea in May–June (carbon content of 10 – 12 g m^{-2}) (Fig. 6). At the same time, the larvae of cod and haddock are being hatched from eggs released by females in their spawning areas. These newly hatched larvae are prone to starvation. The presence and high biomass of herbivorous copepod species along the shelf break is essential to their survival as they serve as the primary food resource for developing larvae.

A recent modeling investigation demonstrates that water temperature, food availability and growth performance are inextricably linked for cod larvae drifting along the Norwegian coast (Vikebø et al., 2021). These authors show a clear difference in performance for early and late spawned cod larvae. Larvae hatched early in the season achieve growth close to their size- and temperature-dependent potential, while late spawned larvae do not achieve optimal growth. The results in the present investigation (Figs. 6 and 7) further highlight the critical role of the timing of the presence of fish larvae and their prey on the shelf. The early



(caption on next column)

Fig. 7. *Calanus finmarchicus* relative abundance of copepodite stages throughout a season (A) and changes in the length of Northeast Arctic cod (B) and Northeast Arctic haddock (C) larvae from hatching to settlement. In A, *C. finmarchicus* stage development is in accordance with water temperatures and available food. The simulation data from SINMOD are averaged over the shelf in the Lofoten-Vesterålen region (depth < 300 m) and represent the combined result of local production and advection into the area. The black line represents the *C. finmarchicus* stage available as prey to the median cod larva in the region at that time, while the red line represents the stage available for the median haddock. Only the values above 0.1 are displayed to highlight the periods of the highest abundances. In B and C, fish weight is calculated using growth models by Folkvord (2005) and Björnsson et al. (2007) based on temperatures from SINMOD at the individual larval positions. The weight is then converted to length using the formula for standard length in Folkvord (2005). All individuals are initiated as eggs throughout the spawning period and hatched after roughly 14 days (Geffen et al., 2006) at a length of 4 mm (Folkvord, 2005). The growth model is developed for cod and is also applied to haddock. Only values of relative abundances above 0.01 are shown. The lines show the 2.5 % percentile, the median and the 97.5 % percentile of all the individuals, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

spawned cod and haddock larvae are feeding and developing during the optimal time window of the presence of *C. finmarchicus* nauplii stages NIII to NIV on the shelf (Fig. 7). By late August, *C. finmarchicus* nauplii no longer serve as the primary prey for cod and haddock that are developing into juveniles.

It is interesting that Färber et al. (2018) investigated the costs and benefits of long-distance spawning migration in fish. These authors hypothesized that to elicit an advantage of long-distance spawning to individual fish, the energetic costs must be counterbalanced by benefits. By looking at the fitness tradeoffs associated with the migration of NEA cod, these authors concluded that the additional energy expenditure of long-distance migration benefited the cod because it resulted in increased growth of the early life stages. This growth increase was attributed to warmer waters and higher food availability which ultimately resulted in increased survival during the first year of life. Our results exemplify this optimal overlap between the presence of NEA cod and haddock fish ELS and prey availability during early spawning period of March–April. What is still uncertain is the extent to which the precise location (rather than timing) of spawning relates to the final recruitment success.

It should be noted that Broch et al. (2020) simulated bioaccumulation and the lethal and sublethal effects of dissolved oil in *C. finmarchicus* for a subset of the scenarios investigated in the present study. These authors showed that copepod body burden levels vary as a function of spill type (surface spill, blowout) and timing (March, August). The highest body burden levels (up to 100 mg kg⁻¹ wet weight) were detected in the immediate vicinity of the discharge point. However, the effect of oil bioaccumulation on the population was small due to limited spatial and temporal overlap between copepods and oil in the environment.

However, oil droplets represent an additional exposure pathway for *Calanus* species. A 4-day exposure/3-day depuration study on *C. hyperboreus* with two crude oil model compounds, dodecane and phenanthrene, showed that the depuration of these compounds was non-significant (Agersted et al., 2018). The authors concluded that short-term exposure of lipid rich high-Arctic copepods may result in long-term bioaccumulation. The study by Toxvard et al. (2019), found that direct exposure to pyrene did not reduce survival and egg production but reduced hatching success for *C. hyperboreus*. These authors also documented delayed effects on faecal pellet production and the recovery of lipid reserves. Further, Nordtug et al. (2015) investigated the accumulation and effects of oil droplet ingestion in *C. finmarchicus* exposed to mechanically and chemically dispersed crude oil. They demonstrated that the filtration rates of this copepod species as well as accumulation of oil droplets decreased with increasing exposure concentration. At

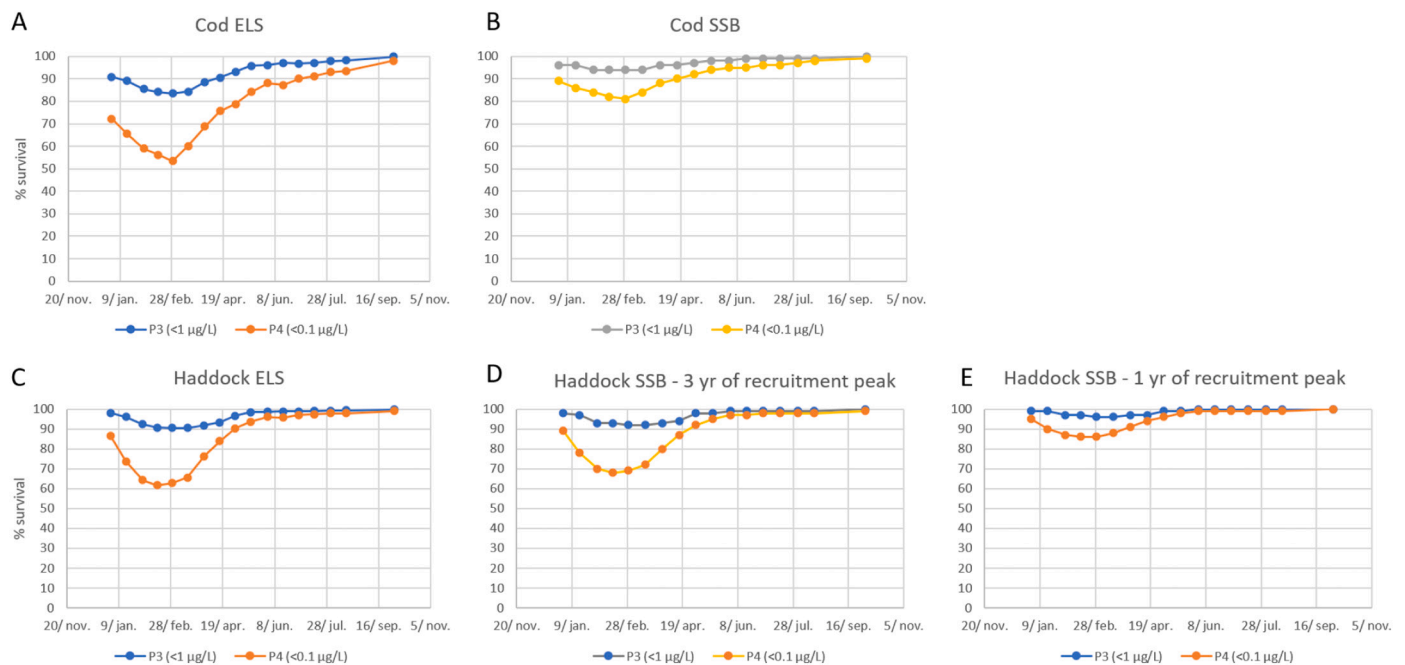


Fig. 8. Temporal variations in percent survival of early life stages (to the end of the pelagic stage) and spawning stock biomass (SSB) of NEA cod on selected dates (A & B). Survival percentages and SSB values are relative to that of the non-exposed population. Lower numbers indicate higher impacts. Only the two most conservative toxicity parameter sets are presented. These parameter sets assume instantaneous mortality for ELS exposed to concentrations above 1.0 µg/L (P3) and 0.1 µg/L (P4). The lower three plots present temporal variations in percent survival of early life stages (C) and SSB (D-E) for NEA haddock. For haddock SSB, we show two scenarios, one where all year classes in the recruitment spike (2004–2006) are impacted and one where only the 2005 spike is impacted. Results are for the post-spill with the largest impact on the SSB, typically 5–8 years post-spill. These data are also presented in [Tables 1 and 2](#).

present, oil droplets are not included as an exposure pathway in our model system, but the evidence from laboratory investigations is sufficient to warrant the investigation of oil droplets in future simulations.

5.2. Interactions between drifting larvae and petroleum compounds in an ocean setting

In the aftermath of an oil spill both the transport and fate of oil and the movements and spreading of drifting organisms into and away from a spill site are influenced by ocean circulation processes. Oil initially concentrates at the sea surface which facilitates evaporation of the most volatile compounds (French-McCay, 2004). In subsequent days, oil disperses through wind, turbulent mixing, and currents, and is broken down via photo-oxidation and biodegradation processes (French-McCay, 2002; Reddy et al., 2012). For our study region on the Norwegian shelf, the circulation features of the North Atlantic are dominated by topographic steering with currents aligned with depth isobaths and a general northward transport direction. Varying winds, depending on duration and strength, can cause upwelling or downwelling and wave-generation with subsequent mixing. In our simulation study, 349×10^3 metric tons were discharged to the sea. Between 37 and 47 % of the oil was removed via evaporation and biodegradation, with the percentage increasing from January through August (Fig. 5). These percentages are comparable to estimates obtained in several marine accidents (Passow and Overton, 2021; French-McCay, 2003, 2004). Detailed investigations of the Deepwater Horizon oil spill revealed that the surface oil expression changed daily. A large fraction of discharged oil was removed from the environment through a variety of physical, chemical, and biological mechanisms. Biodegradation removed up to 60 % of the oil in the intrusion layer but was less efficient in the surface slick, due to nutrient limitation. Photochemical processes altered up to 50 % (by mass) of the floating oil (Passow and Overton, 2021).

The exposure of drifting fish larvae to the remaining bioavailable oil compounds depends on the proximity of patchy spawning areas to a spill

location (Fig. 3) and the prevailing oceanographic conditions at the time of the spill. In the present study, the outcome of exposures to oil compounds for cod and haddock ELS drifting in the simulated ocean are assessed by applying the physiology-based modelling framework DEBtox with the mixture approach to improve the evaluation of biological effects. The approach explicitly addresses and thereby facilitates examination of the toxicokinetics (TK) of chemical uptake and elimination in an organism. This is an advantage when assessing the impacts of oil spills whose composition and distribution in the environment are constantly in flux as previously discussed. However, to apply the DEBtox method we must have sufficient data generated in laboratory ecotoxicology investigations for parameters needed to simulate the dynamics of chemical uptake, depuration, and the effects of exposures. In this study, our results are derived from the application of 2 parameter sets with comparatively low threshold values and no toxicokinetics and 2 sets with higher threshold values and kinetics to describe time varying exposure concentrations in cod and haddock ELS. The application of parameter sets P1 and P2 resulted in minor reductions in survival relative to the comparable no oil scenario (Table 1). However, when applying parameter sets P3 and P4, significant reductions in survival were observed. These alternative approaches, based on the available knowledge generated from laboratory exposure studies, exemplify the acute need for well-constrained values for the species of interest, both NEC values and experimental data on the effects of time varying exposure concentrations. Ashauer et al. (2016) previously demonstrated that when toxicity is assessed for time-variable concentrations, species differ in their responses as a function of the exposure profile. This results in different species sensitivity rankings and safe levels.

Our simulation study clearly demonstrates that there is further need for investigations of the interplay of exposure pattern and species sensitivity. These efforts should include ecotoxicology studies that address the requirements for developing and testing simulation systems. Namely, laboratory ecotoxicology investigations that generate time-series data on chemical uptake, depuration, and the effects of

exposures of target species to individual oil compounds are needed. Only then, can we determine with greater certainty the relative roles of thresholds and kinematics associated with the advection and dispersion of oil and fish ELS in the ocean. In the next two sections, we will discuss the simulation results for the most sensitive parameter sets, P3 and P4.

5.3. Annual profiles of ELS survival

The perceived highest risk to fish populations from oil spills are those that coincide in space and time with spawning events, when the most sensitive life stages of a single year's juvenile recruitment cohort are present. The inability of drifting fish eggs and larvae to avoid contaminated waters near an oil spill discharge point is a key factor making them susceptible to oil spill impacts compared to other fish life stages (Carls et al., 1999; Heintz et al., 1999). By initiating oil spills at a frequency of every two weeks throughout a single year, we can investigate how the degree of overlap of an oil spill with the presence of fish ELS influences their survival percentages and the long-term resiliency of their stocks.

We report the lowest survival percentages of cod and haddock ELS for oil spills initiated on 1 March and 15 February, respectively. Discharges with start dates after June resulted in notably higher survival percentages (Table 1 and Fig. 8). The temporal patterns in survival percentages illustrate the key relationships that have come to light through our analysis. In general, major oil spills that occur early in the productivity cycle coincide with the presence of the earliest life stages of cod and haddock, primarily eggs and larvae in the Lofoten-Vesterålen region. Oil spills occurring late in the productivity cycle coincide with late-stage larvae and juveniles (Fig. 7B and C). These older life stages are advected towards nursery grounds in the Barents Sea and dispersed across a wide geographic domain relative to their former early life stages.

The survival percentages obtained for cod and haddock, after 90-day spills initiated at consecutive times throughout the year, help to illustrate how fish life history dynamics influence survival, recruitment potential, and ultimately, the long-term health of the fish stock. By plotting the percentages of fish eggs and larvae inside the oil domain over time, we show how advection and dispersion plays a key role in determining the fraction of surviving ELS (Fig. 9). These data were taken from 2001

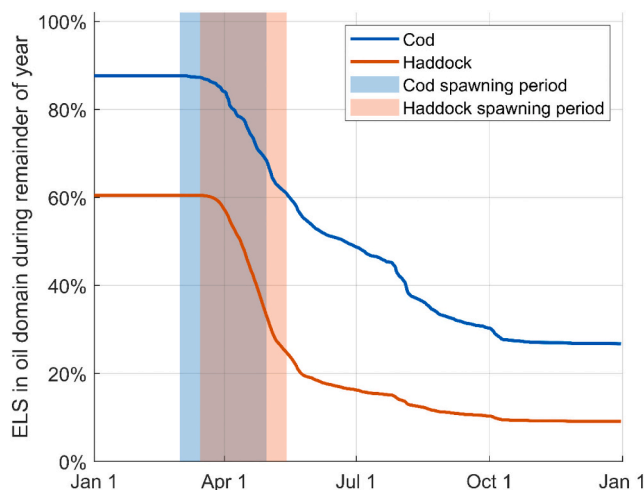


Fig. 9. The percentage of Northeast Arctic cod eggs and larvae (blue line) and Northeast Arctic haddock eggs and larvae (red line) that are in the oil domain (Fig. 1) at some time during the remainder of the year. These percentages of the two populations of eggs and larvae have the potential to encounter oil during a 90-day oil release. The spawning periods for the species are given in the shaded regions and correspond to the periods of lowest survival identified in Fig. 7. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and are independent of the oil spill scenario. At the start of the simulation on Mar 1, 88 % of cod eggs and larvae are inside the oil domain at some time point until the simulation ends on Dec 1. But by Aug 1, only 42 % of cod eggs and larvae are inside the oil domain at some time during the remaining simulation. Similarly, at the start of the simulation on Mar 1, 61 % of haddock eggs and larvae are inside the oil domain at some time during the remaining simulation. But by Aug 1, only 14 % of haddock eggs and larvae are inside the oil domain during the remaining time of the simulation. These percentages of ELS that are inside the oil domain are vulnerable to oil exposure. The other fraction of the ELS has already been advected and dispersed to outside the region of influence from the oil spill. This leads to considerably higher survival percentages for the oil spill simulations started on 1 August compared to 1 March.

These survival percentages indicate that the population of haddock ELS is less impacted by an oil spill relative to cod. However, due to a lack of mathematical algorithms and associated parameter values there are processes that are not accounted for in these simulations, despite having been identified in experimental studies. In the case of haddock embryos, oil droplet adhesion has been identified as an additional toxic exposure route (Sørhus et al., 2015; Sørensen et al., 2017). A mathematical algorithm and parameters are required to simulate oil droplet adhesion to haddock eggs. An additional loss of eggs because of oil droplets does not change the main finding of this study. Namely that the impacts of major oil spills on fish populations are greatest during the spring spawning season. Of course, there are other exposure mechanisms (e.g., unknown toxic compounds in oil, photo-induced toxicity, etc.) that may lead to additional effects on fish ELS (e.g., Whitehead et al., 2012; Meador and Nahrgang, 2019; Pasparakis et al., 2019; Roberts et al., 2017; Barron et al., 2004; Aranguren-Abadía et al., 2022). Their impact on survival will depend on the interplay between oil transport and fate, the movements and spreading of drifting eggs into and away from a spill site, and the time-dependent processes controlling toxic responses.

5.4. Annual profiles of SSB

The historical assessment of cod and haddock stock and recruitment trends is presented in Fig. 4. Note that recruitment is shown at age 3, as this is the age at which the species enter the fishery and the assessment models begin. Both cod and haddock show variability in recruitment and stock size, with recent high peak adult biomasses arising from a combination of high recruitment and moderate fishing pressure (Kjesbu et al., 2014). Stock sizes below Blim (the dashed line on the figure) result in reduced reproductive capacity and should be avoided. Reduced fishing pressure in the last two decades has resulted in the stocks being well above this critical level, giving them more resilience to any additional mortality relative to a situation of lower stock levels. However, the haddock shows considerably higher variability in stock sizes, driven by the presence of occasional extremely good yearclasses. In principle this reliance for stock development on such individual years makes the stock more vulnerable to any reduction in recruitment success in a single year. Most good haddock recruitment events arise from a single good yearclass, while the major peak in 2012–2016 arises from 2 to 3 adjacent good yearclasses. To simulate the impacts of future oil spills we modelled this recruitment event with two simulations as discussed in Section 4.4. In this way, we develop an awareness of the maximum plausible outcome of an oil spill on the haddock SSB.

Comparing the impact of an oil spill on a single large recruitment peak versus on part of a recruitment peak, it is not surprising that there is not much difference between the two scenarios for oil spills occurring after June. However, for earlier in the year, the difference in survival percentages between scenario one and scenario two is as high as 18 percentage points (P4). This variability in recruitment translates into an additional source of uncertainty for the understanding of oil spill impacts on fish stocks that must be evaluated on a case-by-case basis.

While the annual patterns for juvenile and mature cod and haddock populations (Fig. 8B, D, E) are like those obtained for the ELS, the impact

on SSB is less. This is because oil spills impact a single year-class of fish larvae, while the adult populations of both cod and haddock consist of fish from multiple year-classes. Species that have several year-classes are less likely to be impacted by severe mortality events to a single generation of individuals (e.g., [Ohlberger and Langangen, 2015](#)). These results reveal that impacts of major oil spills on cod and haddock populations are greater during the spring spawning season compared to oil spills of similar magnitude occurring near the end of the productivity season in late summer. Of course, any additional losses of haddock ELS due to oil droplet adhesion would propagate into an additional loss of haddock SSB.

The cumulative effect of interactions between oil and fish ELS of both cod and haddock simulated in this study did not compromise the reproductive health of the adult populations. Similar findings were obtained in field investigations of the Gulf of Mexico after the Deepwater Horizon accident ([Fodrie and Heck, 2011](#); [Muhling et al., 2012](#)). [Muhling et al. \(2012\)](#) used satellite-derived estimates of oil coverage and compared these with spawning habitat models. They estimated that <12 % of larval fish were in contaminated waters in the northern Gulf of Mexico on a weekly basis. They concluded that only a small fraction of eggs and larvae were likely impacted by oil contaminated waters. [Fodrie and Heck \(2011\)](#) showed that species by species catch rates were notably higher at the end of their study with no significant impacts on the strength of juvenile cohorts within seagrass habitats. These authors postulated that this was due to the retention of a large proportion of spilled oil at depth, limiting the impacts on shallow-water, coastal ecosystems.

6. Summary

The Lofoten-Vesterålen region has been the subject of considerable debate regarding the environmental risks versus societal benefits of the exploration and development of the region's petroleum resources. At the center of this debate is the potential damage to harvestable fish populations that may result from an oil spill. The Norwegian Government's regulatory framework for the region is based on the principles of Ecosystem-based Management ([Anon, 2006](#)) with the governing principle of resource utilization based on a balance between environmental protection and sustainable development. In this context there is a recognized need for increased scientific understanding of the potential impacts of major oil spills in a complex region with multi-sectoral interests and a government seeking to balance industrial development and environmental resource protection.

The scientific assessments following both the Exxon Valdez and Deepwater Horizon oil spills called for the development of numerical simulation tools to aid the assessment of changes in the structure, function and variability of ecosystems following spills ([Murawski et al., 2021](#); [Peterson et al., 2003](#)). The advantage of using a simulation system is that we can address important natural factors, i.e., ocean processes and variability, fish behaviour and life history traits, in concert with the biological effects of oil on individuals and extrapolate these to examine the outcomes to the fish populations. Our simulations demonstrate the importance of advection and dispersion of both oil and organisms in the environment in determining the exposure dynamics of petroleum-related compounds and the resulting survival percentages for the ELS of cod and haddock. The inclusion of a mechanistic methodology to simulate and quantify the time-varying effects of sublethal and lethal exposures to chemicals and that treats oil as a mixture is a key advancement.

The presented annual profiles of the impacts of simulated oil spills on two important Northeast Arctic fisheries provides valuable input to the management of resources and in the planning of development activities to protect fisheries from potential impacts. Spatial and temporal dynamic interactions between oil and fish ELS drifting in a simulated ocean affect survival and the reproductive health of the fish populations after a major oil spill. For the region of investigation and the selected oil spill

scenario, the impacts on two fish stocks were greatest during the spring spawning season compared to an oil spill of similar magnitude in late summer, near the end of the productivity season. About 88 % (cod) and 61 % (haddock) of fish ELS, present during the start of the spawning season, were inside the oil model domain at some time during a 90-day simulation. These percentages declined throughout the remainder of the year and thereby reduced the fraction of individuals in the population of fish ELS to encounter oil.

This highlights the importance of integrated analysis of the different potential mortalities, rather than considering individual risks separately. The differing impacts of relatively similar oil mortalities on cod and haddock stock development result from their differences in stock dynamics. This indicates the need for studies on specific species of interest rather than relying on "borrowing strength" from similar species. It also highlights the need to study and understand stock dynamics as part of any risk assessment. In this study the effects of the higher susceptibility of haddock eggs to oil droplets were not included, and therefore the oil-induced mortalities on haddock are likely underestimated. All of this confirms the importance of basing risk assessments on data from the specific species of concern, both on the ecotoxicology and the stock dynamics, as well as looking at the uncertainties around this data.

The cumulative effect of interactions between oil and fish ELS of both cod and haddock did not compromise the reproductive health of the adult populations. We would stress that both the cod and haddock stock are managed sustainably and are at good stock status. This gives the stocks resilience to any additional pressures (such as from oil) — stocks that were overfished would likely be more vulnerable to additional oil-induced mortalities. This resilience to the simulated oil impacts of both cod and haddock is predicated on the stocks being substantially above the level at which reproductive capacity would be impaired (the so-called Blim).

While our results provide valuable insights, additional knowledge is of course warranted. This includes advancing the understanding of the interplay and role of species sensitivity to oil and spatio-temporal variations in environmental factors. The importance of the timing of spawning highlights the need for detailed and mechanistic simulations to evaluate and rank the risks from different oil activities. New oceanographic observational studies are needed to reduce uncertainties in risk assessment models. Ocean data are needed for evaluating the capacity of general circulation models to capture ocean dynamics at a range of scales responsible for the overlap and duration of contaminants and vulnerable marine species. Improvements in the methods used to integrate earth observations into simulation systems (e.g., [Li et al., 2022](#)) is also a much-needed priority. Further, there is a need to improve the design of laboratory experiments to ensure that experimental studies provide information on effects that are relatable to the time-varying environmental processes controlling exposures of organisms to chemicals.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2022.114207>.

Funding sources and role of the funding sources

The simulations were performed on resources provided by UNINETT Sigma2 — the National Infrastructure for High Performance Computing and Data Storage in Norway (NN9295K and NS9295K). Financial support was also provided by the Research Council of Norway (project #228107). Some RCN grant programs are contingent upon additional financial contributions from industry. The following companies provided additional financial contributions: Equinor Energy, ConocoPhillips Skandinavia, Wintershall Dea Norge, Vår Energi, OMF, Lundin, and Aker BP. The findings presented in this manuscript are those of the coauthors and associated researchers listed in acknowledgments. Industry investors received no censorship rights in the analysis, interpretation, or reporting of these research results.

CRedit authorship contribution statement

JC was responsible for funding acquisition, project administration, and writing of the original manuscript draft. All coauthors participated in the conceptualization, analysis, investigation, methodology, validation, as well as review and editing of the manuscript. HF, FV, OJB, DH, RN, MB, and SA were responsible for model resources, software, and data curation. GMS was responsible for data curation.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: JoLynn Carroll reports financial support was provided by Equinor Energy. JoLynn Carroll reports financial support was provided by ConocoPhillips Skandinavia. JoLynn Carroll reports financial support was provided by Wintershall Dea Norge AS. JoLynn Carroll reports financial support was provided by Vår Energi. JoLynn Carroll reports financial support was provided by OMV. JoLynn Carroll reports financial support was provided by Lundin Energy Norway AS. JoLynn Carroll reports financial support was provided by Aker BP ASA.

Data availability

Data will be made available on request.

Acknowledgments

We thank Anna Franziska Horne (anna.franziska.horne@gmail.com) for developing a first prototype version of a tool for the visualization of SYMBIOSES III results. The following additional persons provided knowledge in support of the development of the model system: Jonas Juselius, Radovan Bast, Morten Omholt Alver, Martin Biuw, Bjarte Bogstad, Katrin Bluhm, Ute Brønner, Raoul-Marie Couture, Frederik de Laender, Lisette de Hoop, Bjørn Einar Grøsvik, A. Jan Hendriks, Chris Klok, Øystein Langangen, Jannicke Moe, Mark Reed, Dag Slagstad, Petter Rønningen, Karel Viaene, Magnus Aune, Lindsay Wilson, Maj Arnberg and Gro Harlaug Refseth.

References

- Agersted, M.D., Møller, E.F., Gustavson, K., 2018. Bioaccumulation of oil compounds in the high-Arctic copepod *Calanus hyperboreus*. *Aquat. Toxicol.* 195, 8–14. <https://doi.org/10.1016/j.aquatox.2017.12.001>.
- Ainsworth, C.H., Paris, C.B., Perlin, N., Dornberger, L.N., Patterson 3rd, W.F., Chancellor, E., Murawski, S., Hollander, D., Daly, K., Romero, I.C., Coleman, F., Perryman, H., 2018. Impacts of the Deepwater Horizon oil spill evaluated using an end-to-end ecosystem model. *PLoS One* 13. <https://doi.org/10.1371/journal.pone.0190840> e0190840-e0190840.
- Alver, M.O., Broch, O.J., Melle, W., Bagoien, E., Slagstad, D., 2016. Validation of an eulerian population model for the marine copepod *Calanus finmarchicus* in the Norwegian Sea. *J. Mar. Syst.* 160, 81–93. <https://doi.org/10.1016/j.jmarsys.2016.04.004>.
- Anon, 2006. St.meld.nr. 8 (2005–2006) Helhetlig forvaltning av det marinemiljø i Barentshavet og havområdene utenfor Lofoten (forvaltningsplan). Ministry of Environment, Oslo.
- Aranguren-Abadía, L., Yadette, F., Donald, C.E., Sørhus, E., Myklatun, L.E., Zhang, X., Lie, K.K., Perrichon, P., Nakken, C.L., Durif, C., Shema, S., 2022. Photo-enhanced toxicity of crude oil on early developmental stages of Atlantic cod (*Gadus morhua*). *Sci. Total Environ.* 807, 150697. <https://doi.org/10.1016/j.scitotenv.2021.150697>.
- Ashauer, R., Jager, T., 2018. Physiological modes of action across species and toxicants: the key to predictive ecotoxicology. *Environ. Sci.: Processes Impacts* 20, 48–57. <https://doi.org/10.1039/C7EM00328E>.
- Ashauer, R., Albert, C., Augustine, S., Cedergreen, N., Charles, S., Ducrot, V., Focks, A., Gabsi, F., Gergs, A., Goussen, B., Jager, T., Kramer, N.I., Nyman, A.-M., Poulsen, V., Reichenberger, S., Schäfer, R.B., Van den Brink, P.J., Veltman, K., Vogel, S., Zimmer, E.I., Preuss, T.G., 2016. Modelling survival: exposure pattern, species sensitivity and uncertainty. *Sci. Rep.* 6, 29178. <https://doi.org/10.1038/srep29178>.
- Baas, J., Jager, T., Kooijman, S.A.L.M., 2009. A model to analyze effects of complex mixtures on survival. *Ecotoxicol. Environ. Saf.* 72, 669–676. <https://doi.org/10.1016/j.ecoenv.2008.09.003>.
- Baas, J., Spurgeon, D., Broerse, M., 2015. A simple mechanistic model to interpret the effects of narcotics. *SAR QSAR Environ. Res.* 26 (3), 165–180. <https://doi.org/10.1080/1062936X.2015.1018940>.
- Baas, J., Augustine, S., Marques, G.M., Dorne, J.-L., 2018. Dynamic energy budget models in ecological risk assessment: from principles to applications. *Sci. Total Environ.* 628–629, 249–260. <https://doi.org/10.1016/j.scitotenv.2018.02.058>.
- Baron, M.G., Carls, M.G., Heintz, R., Rice, S.D., 2004. Evaluation of fish early life-stage toxicity models of chronic embryonic exposures to complex polycyclic aromatic hydrocarbon mixtures. *Toxicol. Sci.* 78, 60–67. <https://doi.org/10.1093/toxsci/kfh051>.
- Bassis, J., 2021. Quit worrying about uncertainty in sea level projections. <https://eos.org/opinions/quit-worrying-about-uncertainty-in-sea-level-projections>.
- Bautista, N.M., Crespel, A., Crossley, J., Padilla, P., Burggren, W., 2020. Parental transgenerational epigenetic inheritance related to dietary crude oil exposure in Danio rerio. *J Exp Biol* 223 (Pt 16), jeb222224. <https://doi.org/10.1242/jeb.222224>. PMID: 32620709.
- Bera, G., Doyle, S., Passow, U., Kamalanathan, M., Wade, T.L., Sylvan, J.B., Sericano, J. L., Gold, G., Quigg, A., Knap, A.H., 2020. Biological response to dissolved versus dispersed oil. *Mar. Pollut. Bull.* 150, 110713. <https://doi.org/10.1016/j.marpolbul.2019.110713>.
- Björnsson, B., Steinarrson, A., Árnason, T., 2007. Growth model for Atlantic cod (*Gadus morhua*): effects of temperature and body weight on growth rate. *Aquaculture* 271, 216–226. <https://doi.org/10.1016/j.aquaculture.2007.06.026>.
- Bogstad, B., Yaragina, N.A., Nash, R.D.M., 2015. The early life-history dynamics of Northeast Arctic cod: levels of natural mortality and abundance during the first 3 years of life. *Can. J. Fish. Aquat. Sci.* 73, 246–256. <https://doi.org/10.1139/cjfas-2015-0093>.
- Bopp, S.K., Kienzler, A., Richarz, A.-N., van der Linden, S.C., Paini, A., Parissis, N., Worth, A.P., 2019. Regulatory assessment and risk management of chemical mixtures: challenges and ways forward. *Critical Reviews in Toxicology* 49 (2), 174–189. <https://doi.org/10.1080/10408444.2019.1579169>.
- Bopp, Stephanie K., Barouki, Robert, Brack, Werner, Costa, Silvia Dalla, Dorne, Jean-Lou C.M., Drakvik, Paula E., Faust, Michael, et al., 2018. Current EU research activities on combined exposure to multiple chemicals. *Environ. Int.* 120 (November), 544–562. <https://doi.org/10.1016/j.envint.2018.07.037>.
- Broch, O.J., Nepstad, R., Ellingsen, I., Bast, R., Skeie, G.M., Carroll, J., 2020. Simulating crude oil exposure and uptake in North Atlantic *Calanus finmarchicus* populations. *J. Mar. Environ. Res.* <https://doi.org/10.1016/j.marenvres.2020.105184>.
- Buskey, E.J., Esbaugh, A.J., White, H.K., 2016. Impact of oil spills on marine life in the Gulf of Mexico: effects on plankton, nekton, and deep-sea benthos. *Oceanography* 29, 174–181. <https://doi.org/10.5670/oceanog.2016.81>.
- Calverley, D., Anderson, K., 2022. Phaseout Pathways for Fossil Fuel Production Within Paris-compliant Carbon Budgets, 2022. Tyndall Centre, University of Manchester, 817 pp. <https://www.manchester.ac.uk/>.
- Carls, M.G., Rice, S.D., Hose, J.E., 1999. Sensitivity of fish embryos to weathered crude oil: part I. Low-level exposure during incubation causes malformations, genetic damage, and mortality in larval pacific herring (*Clupea pallasii*). *Environ. Toxicol. Chem.* 18, 481–493. <https://doi.org/10.1002/etc.5620180317>.
- Carroll, J., Vikebo, F., Howell, D., Broch, O.J., Nepstad, R., Augustine, S., Skeie, G.M., Bast, R., Juselius, J., 2018. Assessing impacts of simulated oil spills on the Northeast Arctic cod fishery. *Mar. Pollut. Bull.* 126, 63–73. <https://doi.org/10.1016/j.marpolbul.2017.10.069>.
- Castañero-Primo, R., et al., 2014. A model approach to identify the spawning grounds and describing the early life history of Northeast Arctic haddock (*Melanogrammus aeglefinus*). *ICES J. Mar. Sci.* 71 (9), 2505–2514. <https://doi.org/10.1093/icesjms/fsu078>.
- Conover, R.J., 1988. Comparative life histories in the genera *calanus* and *neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia* 167, 127–142. <https://doi.org/10.1007/BF00026299>.
- Cresci, A., Paris, C.B., Browman, H.I., Skiftesvik, A.B., Shema, S., Bjelland, R., Durif, C.M.F., Foretich, M., Di Persia, C., Lucchese, V., Vikebo, F.B., Sørhus, E., 2020. Effects of exposure to low concentrations of oil on the expression of cytochrome P4501a and routine swimming speed of Atlantic haddock (*Melanogrammus aeglefinus*) larvae in situ. *Environ. Sci. Technol.* 54, 13879–13887. <https://doi.org/10.1021/acs.est.0c04889>.
- Daae, R.L., Skancke, J., Brandvik, P.J., Faksness, L.G., 2018. The sensitivity of the surface oil signature to subsurface dispersant injection and weather conditions. *Mar. Pollut. Bull.* 127, 175–181.
- De Laender, F., Olsen, G.H., Grøsvik, B.E., Grung, M., Hansen, B.H., Hendriks, A.J., Janssen, C.R., Klok, C., Nortug, T., Smit, M., Carroll, J., Camus, L., 2011. Ecotoxicological mechanisms and models in an impact analysis tool for oil spills. *J. Toxicol. Environ. Health* 74, 605–619. <https://doi.org/10.1080/15287394.2011.550567>.
- Det Norske Veritas, 2010. Foundation report. Update of the knowledge basis for the management plan for the Barents Sea and the areas outside of Lofoten (HFB). In: *Oil Spill Modeling, OS3D. Report Nr. 2010-0241 in Norwegian*.
- Drakvik, E., Altenburger, R., Aoki, Y., Backhaus, T., Bahadori, T., Barouki, R., Brack, W., Cronin, M.T.D., Demeneix, B., Hougaard Bennekou, S., van Klaveren, J., Kneuer, C., Kolossa-Gehring, M., Lebret, E., Posthuma, L., Reiber, L., Rider, C., Rüegg, J., Testa, G., van der Burg, B., van der Voet, H., Warhurst, A.M., van de Water, B., Yamazaki, K., Öberg, M., Bergman, Å., 2020. Statement on advancing the assessment of chemical mixtures and their risks for human health and the environment. *Environ. Int.* 134, 105267. <https://doi.org/10.1016/j.envint.2019.105267>.
- Dimmen, A., Syversen, U., 2010. In: *The Accident in the Gulf of Mexico - The Risk Group's Assessment Forum for Cooperation on Risk. The Risk Group*, p. 79.

- EFSA Scientific Committee, More, Simon John, Bampidis, Vasileios, Benford, Diane, Bennekou, Susanne Hougard, Bragard, Claude, Halldorsson, Thorhallur Ingi, et al., 2019. Guidance on harmonised methodologies for human health, animal health and ecological risk assessment of combined exposure to multiple chemicals. EFSA Journal 17 (3). <https://doi.org/10.2903/j.efsa.2019.5634>.
- Färber, L., Durant, J.M., Vindenes, Y., Langangen, Ø., 2018. Increased early offspring growth can offset the costs of long-distance spawning migration in fish. Mar. Ecol. Prog. Ser. 600, 141–150. <https://doi.org/10.3354/meps12662>.
- Fodrie, F.J., Heck Jr., K.L., 2011. Response of coastal fishes to the Gulf of Mexico oil disaster. PLoS One 6, e21609. <https://doi.org/10.1371/journal.pone.0021609>.
- French-McCay, D.P., 2002. Development and application of an oil toxicity and exposure model, OilToxEx. Environ. Toxicol. Chem. 21, 2080–2094. <https://doi.org/10.1002/etc.5620211011>.
- French-McCay, D.P., 2003. Development and application of damage assessment modeling: example assessment for the north cape oil spill. Mar. Pollut. Bull. 47, 341–359. [https://doi.org/10.1016/S0025-326X\(03\)00208-X](https://doi.org/10.1016/S0025-326X(03)00208-X).
- French-McCay, D.P., 2004. Oil spill impact modeling: development and validation. Environ. Toxicol. Chem. 23, 2441–2456. <https://doi.org/10.1897/03-382>.
- Folkvord, A., 2005. Comparison of size-at-age of larval Atlantic cod (*Gadus morhua*) from different populations based on size- and temperature-dependent growth models. Can. J. Fish. Aquat. Sci. 62, 1037–1052. <https://doi.org/10.1139/f05-008>.
- Forbes, V.E., Calow, P., Sibly, R.M., 2011. Are current species extrapolation models a good basis for ecological risk assessment? Environ. Toxicol. Chem. 20, 442–447.
- Galic, N., Grimm, V., Forbes, V.E., 2017. Impaired ecosystem process despite little effects on populations: modeling combined effects of warming and toxicants. Glob. Chang. Biol. 23, 2973–2989. <https://doi.org/10.1111/gcb.13581>.
- Galic, N., Hommen, U., Baveco, J.M., Van Den Brink, P.J., 2010. Potential application of population models in the European ecological risk assessment of chemicals II: review of models and their potential to address environmental protection aims. Integr. Environ. Assess. Manag. 6, 338–360.
- Geffen, A.J., Fox, C.J., Nash, R.D.M., 2006. Temperature-dependent development rates of cod *Gadus morhua* eggs. J. Fish Biol. 69 (4), 1060–1080. <https://doi.org/10.1111/j.1095-8649.2006.01181.x>.
- Grossell, M., Pasparakis, C., 2021. Physiological responses of fish to oil spills. Annual Review of Marine Science 13 (1), 137–160. <https://doi.org/10.1146/annurev-marine-040120-094802>, 2021.
- Guldbrandsen Frøysa, K., Bogstad, B., Skagen, D.W., 2002. Fleksibest—an age-length structured fish stock assessment model. Fisheries Research 55, 87–101. [https://doi.org/10.1016/S0165-7836\(01\)00307-1](https://doi.org/10.1016/S0165-7836(01)00307-1).
- Gullestad, P., Howell, D., Stenevik, E.K., Sandberg, P., Bakke, G., 2018. Management and rebuilding of herring and cod in the Northeast Atlantic. 2018. In: Garcia, S.M., Ye, Y. (Eds.), Rebuilding of marine fisheries. Part 2. Case studies, FAO Fisheries and Aquaculture Technical Paper No. 630/2. FAO, Rome, 234 pp.
- Hansen, B.H., Lie, K.K., Størseth, T.R., Nordtug, T., Altin, D., Olsvik, P.A., 2016. Exposure of first-feeding cod larvae to dispersed crude oil results in similar transcriptional and metabolic responses as food deprivation. Journal of Toxicology and Environmental Health, Part A 79 (13–15), 558–571. <https://doi.org/10.1080/07317131.2016.1171985>.
- Heintz, R.A., Short, J.W., Rice, S.D., 1999. Sensitivity of fish embryos to weathered crude oil: part II. Increased mortality of pink salmon (*Oncorhynchus gorbuscha*) embryos incubating downstream from weathered Exxon Valdez crude oil. Environ. Toxicol. Chem. 18, 494–503. <https://doi.org/10.1002/etc.5620180318>.
- Henson, S.A., Dunne, J.P., Sarmiento, J.L., 2009. Decadal variability in North Atlantic phytoplankton blooms. J. Geophys. Res. Oceans 114. <https://doi.org/10.1029/2008jc005139>.
- Houde, E., 2008. Emerging from Hjort's shadow. Fish. Sci. J. Northw. Atl. Fish. Sci. 41, 53–70. <https://doi.org/10.2960/J.v41.m634>.
- Howell, D., Bogstad, B., 2010. A combined Gadget/FLR model for management strategy evaluations of the Barents Sea fisheries. ICES J. Mar. Sci. 67, 1998–2004. <https://doi.org/10.1093/icesjms/fsq135>.
- IEA, 2021. World Energy Outlook 2021. IEA, Paris. <https://www.iea.org/reports/world-energy-outlook-2021>.
- ICES, 2021. In: ICES Scientific Reports, 3. Arctic Fisheries Working Group (AFWG), p. 58. <https://doi.org/10.17895/ices.pub.8196>, 817 pp.
- Incardona, J.P., Carls, M.G., Holland, L., Linbo, T.L., Baldwin, D.H., Myers, M.S., Peck, K.A., Tagal, M., Rice, S.D., Scholz, N.L., 2015. Very low embryonic crude oil exposures cause lasting cardiac defects in salmon and herring. Sci. Rep. 5, 13499. <https://doi.org/10.1038/srep13499>.
- Incardona, J.P., Swarts, T.L., Edmunds, R.C., Linbo, T.L., Aquilina-Beck, A., Gardner, L.D., Block, B.A., Sloan, C.A., Scholz, N.L., 2013. Exxon Valdez to Deepwater Horizon: Comparable toxicity of both crude oils to fish early life stages. Aquatic Toxicology 142–143, 303–316. <https://doi.org/10.1016/j.aquatox.2013.08.011>.
- Jakobsen, T., Ozigin, V.K., 2011. The Barents Sea: Ecosystem, Resources, Management: Half a Century of Russian-Norwegian cooperation. Tapir Academic Press, Trondheim.
- Kjesbu, O.S., Bogstad, B., Devine, J.A., Gjøseter, H., Howell, D., Ingvaldsen, R.B., Nash, R.D.M., Skjæraasen, J.E., 2014. Synergies between climate and management for Atlantic cod fisheries at high latitudes. Proc. Natl. Acad. Sci. 111, 3478–3483. <https://doi.org/10.1073/pnas.1316342111>.
- Klok, C., Nordtug, T., Tamis, J.E., 2014. Estimating the impact of petroleum substances on survival in early life stages of cod (*Gadus morhua*) using the dynamic energy budget theory. Mar. Environ. Res. 101, 60–68. <https://doi.org/10.1016/j.marenvres.2014.09.002>.
- Kujawinski, E.B., Reddy, C.M., Rodgers, R.P., et al., 2020. The first decade of scientific insights from the Deepwater horizon oil release. Nat. Rev. Earth Environ. 1, 237–250. <https://doi.org/10.1038/s43017-020-0046-x>.
- Landrum, P.F., Chapman, P.M., Neff, J., Page, D.S., 2013. Influence of exposure and toxicokinetics on measures of aquatic toxicity for organic contaminants: a case study review. Integr. Environ. Assess. Manag. 9 (2), 196–210. <https://doi.org/10.1002/ieam.1388>.
- Li, Y., Huang, W., Lyu, X., Liu, S., Zhao, Z., Ren, P., 2022. An adversarial learning approach to forecasted wind field correction with an application to oil spill drift prediction. Int. J. Appl. Earth Obs. Geoinf. 112, 102924. <https://doi.org/10.1016/j.jag.2022.102924>.
- Lindström, U., Smout, S., Howell, D., Bogstad, B., 2009. Modelling multi-species interactions in the Barents Sea ecosystem with special emphasis on minke whales and their interactions with cod, herring and capelin. Deep-Sea Res. II Top. Stud. Oceanogr. 56, 2068–2079. <https://doi.org/10.1016/j.dsr2.2008.11.017>.
- Meador, J.P., Nahrgang, J., 2019. Characterizing crude oil toxicity to early-life stage fish based on a complex mixture: are we making unsupported assumptions? Environ. Sci. Technol. 53, 11080–11092. <https://doi.org/10.1021/acs.est.9b02889>.
- Misund, O.A., Olsen, E., 2013. Lofoten-Vesterålen: for cod and cod fisheries, but not for oil? ICES J. Mar. Sci. 70, 722–725. <https://doi.org/10.1093/icesjms/fst086>.
- Muhling, B.A., Roffer, M.A., Lamkin, J.T., Ingram, G.W., Upton, M.A., Gawlikowski, G., Muller-Karger, F., Habtes, S., Richards, W.J., 2012. Overlap between Atlantic bluefin tuna spawning grounds and observed Deepwater horizon surface oil in the northern Gulf of Mexico. Mar. Pollut. Bull. 64, 679–687. <https://doi.org/10.1016/j.marpolbul.2012.01.034>.
- Murawski, S.A., Grossell, M., Smith, C., Sutton, T., Halanych, K.M., Shaw, R.F., Wilson, C.A., 2021. Impacts of petroleum, petroleum components, and dispersants on organisms and populations. Oceanography 34 (1), 136–151. <https://www.jstor.org/stable/27020066>.
- Nelson, J.R., Grubestic, T.H., 2021. A spatiotemporal analysis of oil spill severity using a multi-criteria decision framework. Ocean Coast. Manag. 199, 105410. <https://doi.org/10.1016/j.ocecoaman.2020.105410>.
- NOAA. ADIOS Oil Database. <https://adios.orr.noaa.gov/oils/NO000008>.
- Nordam, T., Beegle-Krause, C.J., Skancke, J., Nepstad, R., Reed, M., 2019. Improving oil spill trajectory modelling in the Arctic. Mar. Pollut. Bull. 140, 65–74.
- Nordtug, T., Olsen, A.J., Wold, P.-A., Salaberria, I., Øverjordet, I.B., Altin, D., Kjorsvik, E., Hansen, B.H., 2022. The impact of exposure timing on embryo mortality and the partitioning of PAHs when cod eggs are exposed to dispersed and dissolved crude oil. Ecotoxicol. Environ. Saf. 229, 113100. <https://doi.org/10.1016/j.ecoenv.2021.113100>.
- Nordtug, T., Olsen, A.J., Salaberria, I., Øverjordet, I.B., Altin, D., Størdal, I.F., Hansen, B.H., 2015. Oil droplet ingestion and oil fouling in the copepod *Calanus finmarchicus* exposed to mechanically and chemically dispersed crude oil. Environmental Toxicology and Chemistry 34 (8), 1899–1906, 2015 Aug.
- Ohlberger, J., Langanen, Ø., 2015. Population resilience to catastrophic mortality events during early life stages. Ecol. Appl. 25, 1348–1356. <https://doi.org/10.1890/14-1534.1>.
- Olsen, G.H., Klok, C., Hendriks, A.J., Geraudie, P., De Hoop, L., De Laender, F., Farmen, E., Grøsvik, B.E., Hansen, B.H., Hjorth, M., Jansen, C.R., Nordtug, T., Ravagnan, E., Viaene, K., Carroll, J., 2013. Toxicity data for modeling impacts of oil components in an Arctic ecosystem. Mar. Environ. Res. 90, 9–17. <https://doi.org/10.1016/j.marenvres.2013.05.007>.
- Olsen, E., Aanes, S., Mehl, S., Holst, J.C., Aglen, A., Gjøseter, H., 2010. Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the biological value of the area. – ICES J. Mar. Sci. 67, 87–101. <https://doi.org/10.1093/icesjms/fsp229>.
- Ottersen, G., Bogstad, B., Yaragina, N.A., Stige, L.C., Vikebø, F.B., Dalpadado, P., 2014. A review of early life history dynamics of Barents Sea cod (*Gadus morhua*). ICES J. Mar. Sci. 71, 2064–2087. <https://doi.org/10.1093/icesjms/fsu037>.
- Oziel, L., Neukermans, G., Ardyna, M., Lancelot, C., Tison, J.-L., Wassmann, P., Sirven, J., Ruiz-Pino, D., Gascard, J.-C., 2017. Role for Atlantic inflows and sea ice loss on shifting phytoplankton blooms in the Barents Sea. J. Geophys. Res. Oceans 122, 5121–5139. <https://doi.org/10.1002/2016jc012582>.
- Page, D.S., Chapman, P.M., Landrum, P.F., Neff, J., Elston, R., 2012. A perspective on the toxicity of low concentrations of petroleum-derived polycyclic aromatic hydrocarbons to early life stages of herring and salmon. Hum. Ecol. Risk Assess. 18 (2), 229–260. <https://doi.org/10.1080/10807039.2012.650569>.
- Passow, U., Overton, E.B., 2021. The complexity of spills: the fate of the Deepwater horizon oil. Annu. Rev. Mar. Sci. 13 (1), 109–136. <https://doi.org/10.1146/annurev-marine-032320-095153>.
- Pasparakis, C., Esbaugh, A.J., Burggren, W., Grossell, M., 2019. Physiological impacts of Deepwater horizon oil on fish. Comp. Biochem. Physiol., Part C: Toxicol. Pharmacol. 224, 108558. <https://doi.org/10.1016/j.cbpc.2019.06.002>.
- Peterson, C.H., Rice, S.D., Short, J.W., Esler, D., Bodkin, J.L., Ballachey, B.E., Irons, D.B., 2003. Long-term ecosystem response to the Exxon Valdez oil spill. Science 302, 2082–2086. <https://doi.org/10.1126/science.1084282>.
- Reed, M., Daling, P., Lewis, A., Ditlevsen, M.K., Brørs, B., Clark, J., Aurand, D., 2004. Modelling of dispersant application to oil spills in shallow coastal waters. Environ. Model Softw. 19, 681–690. <https://doi.org/10.1016/j.envsoft.2003.08.014>.
- Reddy, C.M., Arey, J.S., Seewald, J.S., Sylva, S.P., Lemkau, K.L., Nelson, R.K., Carmichael, C.A., McIntyre, C.P., Fenwick, J., Ventura, G.T., Van Mooy, B.A.S., Camilli, R., 2012. Composition and fate of gas and oil released to the water column during the Deepwater horizon oil spill. Proc. Natl. Acad. Sci. 109, 20229–20234. <https://doi.org/10.1073/pnas.1101242108>.
- Redman, A.D., Parkerton, T.F., 2015. Guidance for improving comparability and relevance of oil toxicity tests. Mar. Pollut. Bull. 98, 156–170. <https://doi.org/10.1016/j.marpolbul.2015.06.053>.
- Rey, F., 1981. The development of the spring phytoplankton outburst at selected sites off the Norwegian coast. In: The Norwegian coastal current, 2, pp. 649–680.

- Rideout, R.M., Tomkiewicz, J., 2011. Skipped spawning in fishes: more common than you might think. *Mar. Coast. Fish.* 3, 176–189. <https://doi.org/10.1080/19425120.2011.556943>.
- Roberts, A., Alloy, M.M., Oris, J.T., 2017. A review of the photo-induced toxicity of environmental contaminants. *Comp. Biochem. Physiol. A* 191, 160–167.
- Sandvik, H., Barrett, R.T., Erikstad, K.E., Mykssvoll, M.S., Vikebø, F., Yoccoz, N.G., Anker-Nilssen, T., Lorentsen, S.-H., Reierson, T.K., Skarðhamar, J., Skern-Mauritzen, M., Systad, G.H., 2016. Modelled drift patterns of fish larvae link coastal morphology to seabird colony distribution. *Nat. Commun.* 7, 11599. <https://doi.org/10.1038/ncomms11599>.
- Schmolke, A., Thorbek, P., DeAngelis, D.L., Grimm, V., 2010. Ecological models supporting environmental decision making: a strategy for the future. *Trends Ecol. Evol.* 25, 479–486.
- Shepherd, J., Benoit, D.S., Halanynch, K.M., Carron, M., Shaw, R., Wilson, C., 2016. Introduction to the special issue: an overview of the Gulf of Mexico research initiative. *Oceanography* 29, 26–32. <https://doi.org/10.5670/oceanog.2016.58>.
- Skjæraasen, J., Nash, R., Korsbrette, K., Fonn, M., Nilsen, T., Kennedy, J., Nedreaas, K., Thorsen, A., Withames, P., Geffen, A., Høie, H., Kjesbu, O., 2012. Frequent skipped spawning in the world's largest cod population. *Proc. Natl. Acad. Sci. U. S. A.* 109, 8995–8999. <https://doi.org/10.1073/pnas.1200223109>.
- Slagstad, D., McClimans, T.A., 2005. Modeling the ecosystem dynamics of the Barents Sea including the marginal ice zone: I. Physical and chemical oceanography. *J. Mar. Syst.* 58, 1–18. <https://doi.org/10.1016/j.jmarsys.2005.05.005>.
- Slagstad, D., Tande, K.S., Wassman, P., 1999. Modelled carbon fluxes as validated by field data on the north Norwegian shelf during the productive period in 1994. *Sarsia* 84, 303–317. <https://doi.org/10.1080/00364827.1999.10420434>.
- Sørheim, K.R., Leirvik, F., 2010. Kartlegging av forvitringsegenskaper, fargekode og spredningsegenskaper for Balder Blend. In: SINTEF report A16789 (in Norwegian).
- Sørensen, L., Sørhus, E., Nordtug, T., Incardona, J.P., Linbo, T.L., et al., 2017. Oil droplet fouling and differential toxicokinetics of polycyclic aromatic hydrocarbons in embryos of Atlantic haddock and cod. *PLOS ONE* 12 (7), e0180048. <https://doi.org/10.1371/journal.pone.0180048>.
- Sørhus, E., Edvardsen, R., Karlsen, Ø., Nordtug, T., van der Meeren, T., Thorsen, A., Harman, C., Jentoft, S., Meier, S., 2015. Unexpected interaction with dispersed crude oil droplets drives severe toxicity in Atlantic Haddock embryos. *PLOS ONE* 10 (4). <https://doi.org/10.1371/journal.pone.0124376>.
- Sørhus, E., Donald, C.E., da Silva, D., Thorsen, A., Karlsen, Ø., Meier, S., 2021. Untangling mechanisms of crude oil toxicity: linking gene expression, morphology and PAHs at two developmental stages in a cold-water fish. *Sci. Total Environ.* 757, 143896. <https://doi.org/10.1016/j.scitotenv.2020.143896>.
- Teal, L.R., Marras, S., Peck, M.A., Domenici, P., 2018. Physiology-based modelling approaches to characterize fish habitat suitability: their usefulness and limitations. *Estuar. Coast. Shelf Sci.* 201, 56–63. <https://doi.org/10.1016/j.ecss.2015.11.014>.
- Thorbek, P., Forbes, V., Heimbach, F., Hommen, U., Thulke, H.H., Van Den Brink, P., et al., 2009. Ecological Models for Regulatory Risk Assessments of Pesticides: Developing a Strategy for the Future. Society for Environmental Toxicology and Chemistry and CRC Press, Pensacola, Florida, US.
- Thyng, K.M., Greene, C.A., Hetland, R.S., Zimmerle, H.M., DiMarco, S.F., 2016. True colors of oceanography: guidelines for effective and accurate colormap selection. *Oceanography* 29, 9–13. <https://doi.org/10.5670/oceanog.2016.66>.
- Toxværd, K., Dinh, K.V., Henriksen, O., Hjorth, M., Nielsen, T.G., 2019. Delayed effects of pyrene exposure during overwintering on the Arctic copepod *Calanus hyperboreus*. *Aquat. Toxicol.* 217, 105332. <https://doi.org/10.1016/j.aquatox.2019.105332>.
- Tronbøl, F., Johannessen, E., Alix, M., dos Santos Schmidt, T.C., Charionidou, K., Folkvord, A., Kjesbu, O.S., 2022. Tracking oocyte development and the timing of skipped spawning for northeast Arctic haddock (*Melanogrammus aeglefinus*). *Journal of Fish Biology* 1–11. <https://doi.org/10.1111/jfb.15057>. *Journal of Fish Biology*.
- Vikebø, F., Broch, O.J., Endo, C.A.K., Frøysa, H.G., Carroll, J., Juselius, J., Langangen, Ø., 2021. Northeast Arctic cod and prey match-mismatch in a high-latitude spring-bloom system. *Front. Mar. Sci.* <https://doi.org/10.3389/fmars.2021.767191>.
- Vikebø, F., Jørgensen, C., Kristiansen, T., Fiksen, Ø., 2007. Drift, growth, and survival of larval Northeast Arctic cod with simple rules of behaviour. *Mar. Ecol. Prog. Ser.* 347, 207–219. <https://doi.org/10.3354/meps06979>.
- Vlaeminck, K., Viaene, K.P., Van Sprang, P.A., De Schampelaere, K.A., 2020. Development and validation of a mixture toxicity implementation in DED-IBM: effects of copper and zinc on *Daphnia magna* populations. *Environ. Toxicol. Chem.* <https://doi.org/10.1002/etc.4946>.
- Vlaeminck, K., Viaene, K.P.J., Van Sprang, P., Baken, S., De Schampelaere, K., 2019. The use of mechanistic population models in metal risk assessment: combined effects of copper and food source on *lymnaea stagnalis* populations. *Environ. Toxicol. Chem.* 38, 1104–1119. <https://doi.org/10.1002/etc.4391>.
- Wang, M., Grimm, V., 2010. Population models in pesticide risk assessment: lessons for assessing population-level effects, recovery, and alternative exposure scenarios from modeling a small mammal. *Environ. Toxicol. Chem.* 29, 1292–1300.
- Wassmann, P., Andreassen, L.J., Rey, F., Høisæter, T., 1999. Seasonal variation of nutrients and suspended biomass on a transect across Nordvestbasken, north Norwegian shelf, in 1994. *Sarsia* 84, 199–212. <https://doi.org/10.1080/00364827.1999.10420426>.
- Wassmann, P., Slagstad, D., Riser, C.W., Reigstad, M., 2006. Modelling the ecosystem dynamics of the Barents Sea including the marginal ice zone: II. Carbon flux and interannual variability. *J. Mar. Syst.* 59, 1–24. <https://doi.org/10.1016/j.jmarsys.2005.05.006>.
- Whitehead, A., Dubansky, B., Bodinier, C., Garcia, T.I., Miles, S., Pilley, C., Raghunathan, V., Roach, J.L., Walker, N., Walter, R.B., Rice, C.D., Galvez, F., 2012. Genomic and physiological footprint of the Deepwater horizon oil spill on resident marsh fishes. *Proc. Natl. Acad. Sci.* 109, 20298–20302. <https://doi.org/10.1073/pnas.1109545108>.
- Yaragina, N.A., Aglen, A., Sokolov, K.M., 2011. Chapter 5.4. Fish. Cod. In: Jakobsen, T., Ozhigin, V.K. (Eds.), *The Barents Sea: Ecosystem, Resources, Management, Half a Century of Russian-Norwegian Cooperation*. Tapir Academic Press, Trondheim.