Effects of an aquaculture pesticide (diflubenzuron) on non-target shrimp populations: Extrapolation from laboratory experiments to the risk of population decline

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ABSTRACT

Marine aquaculture production has lately experienced high economic growth, but also concerns related to production and environmental contamination. For the Atlantic salmon aquaculture industry, the ectoparasitic crustacean salmon louse (*Lepeophtheirus salmonis*) has become a major problem. A common method to control populations of salmon lice within farm cages is treatment by various pharmaceuticals. One of the pesticides used in medicated feed for salmon is diflubenzuron (DFB), which acts as a chitin synthesis inhibitor and thereby interferes with the moulting stages during the development of this crustacean. However, DFB from fish feed may also affect non-target crustaceans such as the northern shrimp (*Pandalus borealis*), which is an economically and ecologically important species. Nevertheless, the actual risk posed by this chemical to shrimp populations in nature is largely unknown. Laboratory experiments have demonstrated that both larval and adult shrimp exposed to DFB through medicated fish feed have reduced survival compared to control. Moreover, the effects of DFB exposure are more severe under conditions of higher temperature and reduced pH (ocean acidification), which can be expected in a future environment. The aim of this study is to make the individual-level information from laboratory studies more relevant for risk assessment at the population level. We have developed a density-dependent age-structured population model representing a northern shrimp population located in a hypothetical Norwegian fjord containing a fish farm, under both ambient and future environments. Our model is based on thorough documentation of shrimp biology and toxicological effects from the laboratory experiments. Nevertheless, extrapolating the reported individual-level effects of DFB to the population level poses several challenges. Relevant information on shrimp populations in Norwegian fjords is sparse (such as abundances, survival and reproductive rates, and density-dependent processes). The degree of exposure to DFB at different distances from aquaculture farms is also uncertain. We have therefore developed a set of model scenarios representing different DFB application schemes and different degrees of exposure for the shrimp populations. The model predicts effects of DFB exposure on population-level endpoints such as long-term abundance, age structure and the probability of population decline below threshold abundances. These model predictions demonstrate how the risk of DFB to shrimp populations can be enhanced by factors such as the timing (season) of DFB applications, the percentage of the population affected, future environmental conditions and environmental stochasticity.

1. Introduction

Marine aquaculture production has lately experienced high economic growth, but also concerns related to production and environmental contamination. For the Atlantic salmon aquaculture industry, the ectoparasitic salmon louse (*Lepeophtheirus salmonis*) has become a major problem. The increasing use of antiparasitic drugs against this crustacean parasite has raised concerns regarding potential impacts on non-target crustaceans (Langford et al., 2014; Macken et al., 2015). A commonly used pesticide against salmon lice is diflubenzuron (DFB), which acts as a chitin synthesis inhibitor (CSI) and thereby interferes with the moulting process of crustaceans during their development.

Elevated levels of CSI have been detected in tissues of non-target crustaceans in areas where medicated feed is used (Langford et al., 2014; Samuelsen, 2016). There is concern that CSI from fish feed may also affect non-target crustaceans, such as the Northern shrimp (*Pandalus borealis*), which is an economically and ecologically important species in colder parts of the Atlantic (Bergström, 2000). In Norway, local fishermen question why they catch less shrimp in fjords with salmon aquaculture, and the competent authorities have requested information on the influence of antiparasitic drugs on non-target crustaceans (Gaulin and Skarland, 2015).

Laboratory experiments have demonstrated that shrimp exposed to DFB through fish feed have reduced survival as adults (Bechmann et al., 2017) as well as during the larval life stage (Bechmann et al., 2018). Waste from fish farms provides food for local shrimp populations (Olsen et al., 2012). Shrimp may therefore accumulate DFB through consumption of both medicated feed and salmon faeces, as well as from contaminated fauna (Langford et al., 2014). Grefsrud et al. (2018) provide some information on the spatial distribution and persistence of DFB in fjords: flubenzurones have been found in sediment up to 1 km from farms, and the half time is estimated to be 110–170 days. However, there is little information on the degree of exposure to shrimp habitats. Therefore, the risks associated with DFB to shrimp populations and other non-target species is largely unknown (Grefsrud et al., 2018).

In their natural environment, shrimp populations may also be affected by environmental stressors that can be expected to increase in the future due to CO_2 emission, such as ocean acidification and warming. A downscaling ocean biogeochemical model projected that bottom waters along the Norwegian coast will reach average temperatures of 9.7 °C (from currently 8.0 °C) and pH down to 7.7 (from currently 8.0) during winters in the decade 2090–2099 (Wallhead et al., 2017). These additional stressors should also be accounted for when assessing the population-level effects of DFB on shrimp in the long-term future.

The aim of this study was to assess the potential effects of DFB exposure from salmon aquaculture on local shrimp populations, based on information on effects on individual shrimp. The hypothetical location represents a shrimp field in a fjord in South-Western Norway, where there is a high density of both salmon aquaculture sites and shrimp fields along the coast (Fig. 1). Fjord shrimp populations tend to be genetically different from open sea populations (Knutsen et al., 2015), and even populations from spatially proximate fjords may respond differently to environmental stress (Hall, 2017). Although the fjord populations are of less economic value than open sea populations, local stocks may prove important to uphold genetic variability and biocomplexity in a changing environment (Knutsen et al., 2015).

Most existing population models for shrimp are developed for stock assessment, based on commercial landings and effort data from shrimp populations in open sea. The *Pandalus borealis* stock of Skagerrak and the Norwegian Deep was assessed annually by the International Council for the Exploration of the Sea (ICES), by qualitative non-model-based interpretation of various stock indices until 2012. From 2012 onwards, a Bayesian surplus production model based on yearly estimates of the total biomass formed the basis for the stock assessment and for deriving catch advice (Hvingel and Kingsley, 2006). More recently, a length-based model implemented in Stock Synthesis (SS3) with a fixed natural mortality rate has been applied to better represent the demography of the shrimp population (ICES, 2016). The model has a quarterly (3-month) time step to better capture the rapid growth of the shrimp.

A population model for our purpose needed more detailed specification of processes such as stage- or age-specific survival than the mentioned SS3 stock-assessment model. One reason is that the adult and larval stages have shown different sensitivity to DFB exposure (Bechmann et al., 2017, 2018). An age-structured population model might also show different effects of DFB treatment in different seasons, since the larval stage only lasts for a few months in spring. We constructed an age-structured population model with a seasonal (3-month) time step and age-specific survival and reproductive rates. This model structure could capture stage- and sex-specific sensitivity to the toxicant, to seasonal changes in the environment, and to DFB application in different seasons.

The shrimp population model contains stochastic components in survival rates, representing both environmental and demographic stochasticity. The modelled effects of DFB exposure and environment change are derived from experimental data (Bechmann et al., 2017, 2018). The model was run for scenarios representing different timing of DFB application and different degrees of DFB exposure to the shrimp populations, as well as different levels of environmental fluctuation. The purpose of the model was to investigate (1) how the effects of DFB exposure documented for larval and adult shrimp individuals transfer to the population level, and (2) how the population-level effects of DFB are affected by future environmental conditions. Such a population model can be used to assess the risk of shrimp population decline below a threshold abundance under different scenarios of stressors and environmental conditions.

2. Materials and methods

2.1. Model structure

2.1.1. Life cycle

The structure and parameters of our population model for *Pandalus borealis* are largely based on information from Rasmussen (1953) and Shumway et al. (1985) (their Fig. 6). Northern shrimp are protandric hermaphrodites (i.e. born as males and later develop into females), and breed more than once as females (Shumway et al., 1985). The longevity of shrimp in the North Sea is typically 3–5 years (Bergström, 2000).

The population model (Fig. 2) corresponds to a Leslie matrix with density-dependent functions in the adult survival rates. The time step is 3 months, starting with spring (March - May). The abundance of shrimp in this model is modelled as density: the number of individuals per 100 m². Since very little information is available on the abundance of shrimp populations in Norwegian fjords, our results are best interpreted as relative abundance (e.g. the abundance of populations in a given scenario relative to the control population). For simplicity, all individuals were assumed to have the same developmental rate, so that the stage structure corresponds to the age structure. This means that for each time step, an individual can either move to the next developmental stage or die, but it cannot stay in the same developmental stage. The simplified life cycle assumed for our model is represented in Table 1, together with the age-specific demographic rates. Eggs are fertilised during autumn and carried by females during winter until they hatch and are released as larvae next spring (year 1 of the model). The larval developmental stage is commonly divided into six distinct substages (Shumway et al., 1985). In our model, for simplicity, we let age class 1 correspond to the whole larval stage. The larvae develop into juveniles and settle to the bottom during the summer of year 1. Juveniles develop into mature males (hereafter called "males") during summer of year 2, and further develop into females during spring of year 3. Females can live until they are 5 years old and release new larvae up to 3 times: during spring of year 3, 4 and 5. After the last reproduction, all females are assumed to die.

The model does not consider meta-population dynamics, such as migration between local shrimp populations in nearby fields or from the open sea.
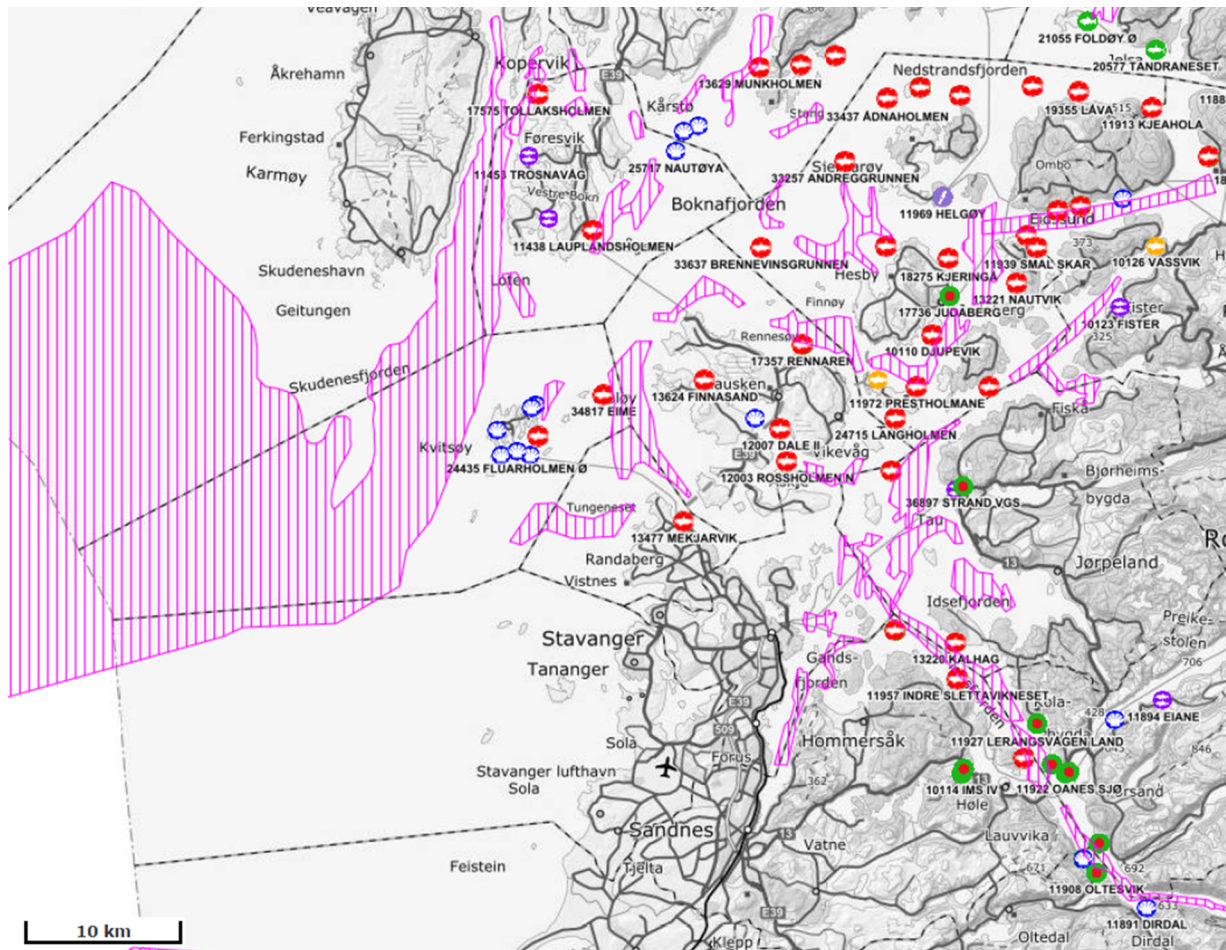
Fig. 1. Map showing the positions of shrimp fields (pink polygons) and salmonid fish farms (red circles with white fish) in fjords along the coast of South-Western Norway (county Rogaland). Source: http://kart.fiskeridir.no.

2.1.2. Demographic rates

The parameter values of the Leslie matrix are given in Table 1. The values given in the column "AmbCon" (ambient environment, control treatment) will be referred to as baseline parameters.

2.1.2.1. Survival. The baseline survival was the proportion of individuals surviving from one 3-month time step to the next, before accounting for density-dependent processes, in the control populations (AmbCon). We have not found precise survival rates for each stage from the literature. Previously published population models are generally based on whole populations without parameters for stage-specific survival (e.g. Hvingel and Kingsley, 2006). The stage-specific survival rates in our model were therefore based on literature information and expert knowledge, and tuned to generate a stable control population. Shrimp larvae in laboratory cultures can obtain high survival, but in nature larvae will be sensitive to environmental conditions such as temperature and food availability (Bergström, 2000). The survival of adult shrimp seems to be regulated by fish predation, particularly by cod (Berenboim et al., 2008; Fu et al., 2001; Wieland et al., 2007).

The baseline survival rate was assumed to be 0.05 for larvae, maximum 0.95 for juveniles and males, and 0.90 for females (Table 1). Survival was assumed to be lower for age classes where individuals either develop into a new stage or reproduce. The assumptions are as follows: Larvae have low survival as newly hatched in spring (age class 1; baseline survival 0.05). Juveniles have lowest survival during settlement at the bottom in summer (age class 2; baseline survival 0.75) and during development to males in spring (age class 5; baseline survival 0.75). Males have lowest survival during development to transitionals in winter (age class 8; baseline survival 0.75), which also have low survival during development to immature females in spring (age class 9; baseline survival 0.75). Females have lowest survival in autumn when they have produced eggs (age classes 11, 15 and 19, baseline survival 0.70) as well as during spring due to moulting (age classes 13 and 17, baseline survival 0.70). The stochastic version of the model had a range of values for survival rates based on these baseline rates to represent variation in fishing and predation pressure (see Section 2.1.4).

2.1.2.2. Reproduction. The mean reproductive output (number of live larvae) per female per season was based on information from previous experiments at IRIS (International Research Institute of Stavanger): 1000–2000 live larvae per female. The numbers were consistent with the range of fecundities reported for similar environments, e.g.: 600–5000 offspring per female (Shumway et al., 1985); 500–3000 eggs per female (Rasmussen, 1953); 1000–3000 eggs per female (Bøhle, 1976). Fecundity of female northern shrimp tends to increase with size and therefor with age (Shumway et al., 1985). We assumed the age-specific average fecundity to increase from age 3 years (1000 offspring per female) to age 4 (1500) and further to age 5 (2000). The total number of larvae (N_1) produced in spring was modelled as the sum of
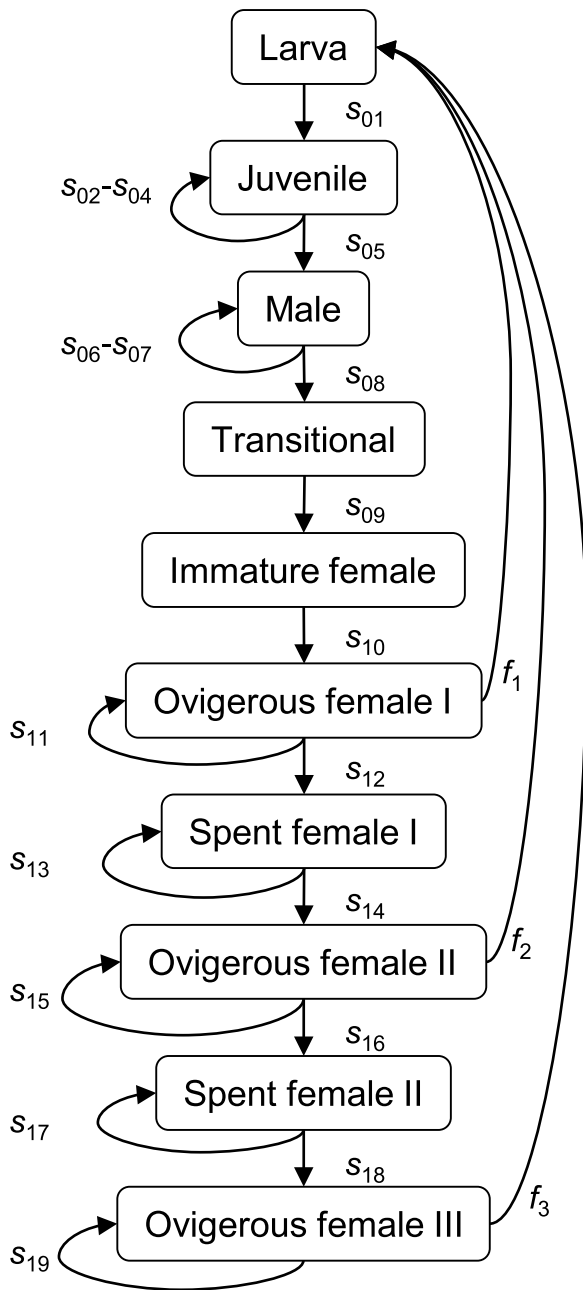
Fig. 2. Conceptual diagram of the population model for the northern shrimp (*Pandalus borealis*), showing the stage structure. For definition of the age classes and parameters *s* (survival) and *f* (fecundity), see Table 1.

larvae produced by the three female age classes (Eq. 1).

$$N_1(t + 1) = f_1 \cdot N_{12}(t) + f_2 \cdot N_{16}(t) + f_3 \cdot N_{20}(t) \tag{1}$$

where f_1 - f_3 are the age-specific fecundities of females in age classes 12, 16 and 20 respectively (Table 1).

2.1.3. Density dependence

A difficult and unsolved question in fisheries biology is: how, and to what extent, can populations of marine fish compensate for additional negative impacts imposed upon them (Nisbet et al., 1996)? For shrimp populations, likewise, it might be expected that density-dependent

processes result in some compensation of negative effects by external stressors, although the importance of such processes for natural shrimp populations are uncertain (Bergström, 2000). In stock assessment models for shrimp, density dependence in yearly recruitment is often modelled by a Beverton-Holt function representing fishing mortality (Fu et al., 2001; ICES, 2016; Oh et al., 1999; Punt et al., 2013). The population dynamics in our model was governed by density-dependent survival of adult shrimp, which does not distinguish between predation and harvest. The process is modelled by a density-dependent function (after Maynard Smith and Slatkin, 1973) (Eq. 2):

$$N_{k+1}(t + 1) = \frac{s_k \cdot N_A(t)}{1 + (a \cdot N_A(t))^b}, \text{ where } k \geq 6. \tag{2}$$

where $N_k(t)$ is the number of individuals in age class k, N_A is the total number of adults, s_k is the survival rate of individuals in age class k, a is the strength of the density dependence, and b is the degree of compensation. This density-dependent function is recommended for populations with undercompensatory density dependence (Bellows, 1981). When $b = 1$, this is identical to the original Beverton-Holt model (Beverton and Holt, 1957), on which many fisheries models are based. In the deterministic version our model (see section 2.1.3), parameter value $a = 0.0003$ corresponds to a carrying capacity of approximately 1000 adult individuals per 100 m² (i.e. 10 individuals per m²). We considered this a realistic maximum density compared to the high-density range (0.5–3 individuals per m²) estimated for Greenland (Wieland, 2004). The parameter value $b = 0.5$ represents partly compensating density dependence. In our case, this type of density dependence can be considered as top-down regulation: a higher density of shrimp will result in a higher number of shrimp removed by predation and/or harvest. We assumed that the adults of all age classes had density-dependent survival, and that the density dependence within each age class k was based on the total adult density. The SS3 model used by ICES has a Beverton-Holt function in the yearly recruitment rate (Methot, 2015), but the parametrization of this function cannot be directly transferred to the adult survival function in our age-structured model. We have not found other similar density-dependent models for shrimp in the literature, and therefore no relevant information for these parameters. The parameters were therefore set to give a reasonable carrying capacity and stable population dynamics for the control population.

2.1.4. Stochasticity

Three main versions of the model can be defined: (1) the deterministic version (as described above), (2) a version with environmental stochasticity (temporal variation in larval survival), and (3) a version with both environmental and demographic stochasticity (variation in survival among replicate populations). The two types of stochasticity are implemented as follows.

2.1.4.1. Environmental stochasticity: temporal variation in larval survival. The year-class strength variability of pandalids is mainly determined during the pelagic larval phase by bottom-up processes and variability in the timing of zooplankton production (Anderson, 2000; Pedersen and Storm, 2002). Therefore, it is likely that a match between the hatching of northern shrimp larvae and the development and timing of the plankton production cycle in spring is important for the success of a cohort (Ouellet et al., 2011). We assumed the survival rate of newly hatched larvae to be affected by temporal fluctuation in environmental conditions, representing the availability of zooplankton as food at the time of hatching (see section 2.3. Model scenarios). Each year of the model run would have a 25% probability of adverse environmental conditions, which reduced the survival of age class 1

Table 1

Parameters for demographic rates in the population model for northern shrimp. Column headers: Amb = ambient environment, Fut = future environment, Con = control, DFB = diflubenzuron. Parameters: s = survival, f = fecundity.

Year	Season	Stage	AgeClass	Parameter	AmbCon	AmbDFB	FutCon	FutDFB
Survival								
1	Spring	Larva	1	s_{01}	0.0500	0.0189	0.0361	0.0045
1	Summer	Juvenile	2	s_{02}	0.750	0.750	0.750	0.750
1	Autumn	Juvenile	3	s_{03}	0.950	0.390	0.950	0.390
1	Winter	Juvenile	4	s_{04}	0.950	0.950	0.950	0.950
2	Spring	Juvenile	5	s_{05}	0.750	0.308	0.750	0.308
2	Summer	Immature male	6	s_{06}	0.950	0.950	0.950	0.950
2	Autumn	Mature male	7	s_{07}	0.950	0.390	0.950	0.390
2	Winter	Mature male	8	s_{08}	0.750	0.750	0.750	0.750
3	Spring	Transitional	9	s_{09}	0.750	0.308	0.632	0.213
3	Summer	Immature female	10	s_{10}	0.950	0.950	0.950	0.950
3	Autumn	Ovigerous female I	11	s_{11}	0.700	0.288	0.700	0.288
3	Winter	Ovigerous female I	12	s_{12}	0.900	0.900	0.900	0.900
4	Spring	Spent female I	13	s_{13}	0.700	0.288	0.700	0.288
4	Summer	Spent female I	14	s_{14}	0.900	0.900	0.900	0.900
4	Autumn	Ovigerous female II	15	s_{15}	0.700	0.288	0.700	0.288
4	Winter	Ovigerous female II	16	s_{16}	0.900	0.900	0.900	0.900
5	Spring	Spent female II	17	s_{17}	0.700	0.288	0.700	0.288
5	Summer	Spent female II	18	s_{18}	0.900	0.900	0.900	0.900
5	Autumn	Ovigerous female III	19	s_{19}	0.700	0.288	0.700	0.288
5	Winter	Ovigerous female III	20	s_{20}	0	0	0	0
Reproduction								
3	Winter	Ovigerous female I	12	f_1	1000	1000	1000	1000
4	Winter	Ovigerous female II	16	f_2	1500	1500	1500	1500
5	Winter	Ovigerous female III	20	f_3	2000	2000	2000	2000

larvae by 50% (i.e. from the baseline survival s_{01} = 0.05 to 0.025). All replicate populations were affected equally by these "adverse years".

2.1.4.2. Demographic stochasticity: among-population variation in survival.

The model was run for 100 replicate populations with different survival rates. A range of survival rates was generated based on the assumed baseline survival rate (Table 1). For each replicate population, the survival rate of all stages (s_k, where k = 1:19) was modified by a stochastic component VS representing an arbitrary amount of variation in survival (Eq. 3). The exponent VS was generated from a normal distribution with mean = 1 and standard deviation = 0.1, and applied to all age classes and all time steps for the given population.

$$N_{k+1}(t + 1) = (s_k)^{VS} \bullet N_k(t) \tag{3}$$

The range of survival rates can represent different levels of predation, harvest and/or other environmental conditions.

2.2. Effects of DFB and environment on demographic rates

Information on the effects of DFB and environment treatments were obtained from experiments performed at IRIS, described in full detail by Bechmann et al. (2017, 2018). Experiments were carried out separately for shrimp larvae (Bechmann et al., 2018, Experiment 1) and for adult females (Bechmann et al., 2017, Experiment 1, treatment DFB$_{high}$). In brief, the experimental set-up was a 2 × 2 treatment with two levels of DFB treatment (control and DFB exposure) and two levels of environmental conditions (representing ambient and future environment). The ambient environment treatment had water temperature 7.0 °C and pH 8.0, while the future environment treatment had water temperature 9.5 °C and pH 7.6. The future environment treatment (called OAW – ocean acidification and warming) represented conditions of higher water temperature due to global warming, and lower pH due to ocean acidification caused by increased atmospheric CO_2 concentration. Both experiments had six replicate aquaria for each treatment combination.

Table 2

Effects of DFB and future environment treatment on survival at the termination of the experiments with (a) larvae (Bechmann et al., 2018) and (b) adult females (Bechmann et al., 2017). The survival ratio for each treatment is calculated by dividing the percentage survival of this group with the percentage survival of the ambient environment control treatment (AmbCon). For abbreviations, see Table 1. For more details on the experiments, see Section 2.2.

Treatment	AmbCon	AmbDFB	FutCon	FutDFB
(a) Larvae				
Survival	90 %	34 %	65 %	8 %
Survival ratio	1	0.378	0.722	0.089
(b) Adult females				
Survival	95 %	39 %	80 %	27 %
Survival ratio	1	0.411	0.842	0.284

The larval experiment had on average 187 larvae per replicate, while the adult experiment had on average 17 ovigerous females per replicate.

Both larvae and adult females were exposed to DFB through medicated feed for two weeks, which is the maximal allowed treatment period with DFB-medicated feed for salmon farms. The concentration of DFB in the food pellets was 0.7 g/kg. In addition, the shrimp were exposed to a low concentration of suspended sediment particles containing medicated fish feed. In the larval experiment, the mean total concentration of DFB in the water (dissolved and bound to particles) was 1.5 µg/L while the tissue concentration of exposed larvae was 180 ng/g. In the adult experiment with DFB treatment, the mean concentration of DFB in the sediment was 568 ng/g dry weight, while the tissue concentration of exposed adults was 77 ng/g.

The effects of the DFB and environment treatments on survival of larvae and adults are displayed in Table 2. In summary, the survival of both stages was strongly reduced by the DFB treatment and to a less degree by the future environment treatment. Larvae were slightly more sensitive to the DFB treatment than adults, and considerably more sensitive to the future environment treatment than adults.

2.3. Model scenarios

A set of 60 scenarios have been defined for the model. The scenarios were a combination of the following five dimensions (explained in more detail below):

1) <u>DFB exposure</u>, 2 levels: Control or DFB, corresponding to the experimental treatments.
2) <u>Environment</u>, 2 levels: Ambient or Future (warming and ocean acidification), corresponding to the experimental treatments.
3) <u>Timing of DFB application</u>, 3 levels: Spring, Autumn or Spring + Autumn.
4) <u>Percentage of the population exposed to DFB</u>, 3 levels: Low, Medium or High, corresponding to respectively 5%, 25% or 50% of individuals of a population being exposed.
5) <u>Environmental stochasticity</u>, 3 levels: Number of years where larval survival was reduced due to adverse environmental conditions (never, once or frequently; see Section 2.1.4.1).

The DFB treatment levels were combined with all levels of the next four scenario dimensions, resulting in $2 \times 3 \times 3 \times 3 = 54$ scenarios. The six remaining scenarios were the ambient and future environment scenarios without DFB treatment (corresponding to AmbCon and FutCon), each with the three levels of environmental stochasticity. The scenario of ambient environment without DFB treatment or stochasticity is referred to as the baseline scenario (no. 28 in Table A1).

2.3.1. DFB exposure

2.3.1.1. Survival.
The effect of the different treatments on survival of larvae and adults was obtained from the percentage survival at the termination of the experiments described in Section 2.2 (see Table 2). In the population model, we modified the larval survival rate s_{01} in scenarios with ambient environment and DFB treatment by multiplying the baseline survival function of the control population $s_{k,AmbCon}$ by the corresponding survival ratio from Table 2 (Eq. 4):

$$s_{01,AmbDFB} = 0.378 \cdot s_{01,\ AmbCon} \tag{4}$$

For all subsequent age classes ($k \geq 2$), likewise, the age-specific survival s_k (see Eq. 2) in ambient DFB scenarios were calculated as (Eq. 5):

$$s_{k,AmbDFB} = 0.411 \cdot s_{k,\ AmbCon} \tag{5}$$

The effect of DFB and environment treatments reported for adult females (Bechmann et al., 2017) was assumed to apply also for the juvenile, male and transitional stages, which had not been tested. The modelled exposure to DFB was assigned to spring and/or autumn, when DFB is most likely to be applied in fish farms. Therefore, only spring and/or autumn survival was assumed to be affected by the DFB treatment. Any additional effects of the DFB treatment on survival in other seasons due to the long half-life of this chemical are ignored by the model. Larvae were assumed to be affected by DFB treatment in spring only, since the larval stage lasts only for the months March - May. The juvenile and adult shrimp could be exposed during both spring and autumn, when they feed on organic matter containing DFB at the bottom. The resulting survival rates for each treatment are listed in Table A2.

2.3.1.2. Fecundity.
The reproductive rates were assumed not to be affected by the toxicant exposure, because we have currently no relevant information from the experiments or from literature. However, DFB concentration of 0.075 ug/L was reported to reduce reproduction in the mysid shrimp (*Mysidopsis bahia*) (Fischer and Hall,

1992). If fecundity of *P. borealis* would actually be reduced by DFB under the conditions represented by our model, then our results will be more conservative in this respect (i.e., predict weaker population-level effects than experienced by real populations).

2.3.1.3. Development.
In the experiment with larvae (Bechmann et al., 2018), future environment treatment resulted in a quicker development: the intermoult period between the larval substages was approximately 9 and 6 days in AmbCon and FutCon treatments, respectively. Conversely, DFB exposure in the experiments resulted in slower development for the surviving larvae, especially in the future environment treatments. For example, at the end of the experiment (19 days post hatching), 70% of the larvae in the FutCon treatment had reached larval stage IV, while 77% of the surviving larvae in the FutDFB treatment were still in stage II (Fig. 3 in Bechmann et al., 2018). The larvae that had not reached stage IV at this time would most likely not develop further and therefore not survive. Although these effects on development rates would be relevant for the population dynamics, it is not possible to include it in the current model where each stage has a fixed duration. This effect might be included later in a more advanced model with variable developmental rates.

2.3.2. Future environment

The effect of future environment (higher water temperature and reduced pH) on survival in the model was based on the experiments, in the same way as the effect of DFB exposure (Table 2). The experimental environment treatment had a strong negative effect on survival for both larvae and adults. For both stages, the effect of the environment treatment was weaker than the effect of DFB exposure. The combined effect of the two treatments was additive, i.e. there was no significant interaction between the two factors (Bechmann et al., 2017, 2018).

It is reasonable to assume that the sensitivity of organisms to future environment can vary within a population, due to variation in tolerance and processes such as acclimatisation and natural selection. Moreover, it is likely that the effects of future environment will vary during the year. The bottom water reaches the highest temperatures during winter and spring (Wallhead et al., 2017). We chose to implement the effect of future environment on survival observed in the experiment for only for two age classes: larvae developing into juveniles (age class 1) and adults in the transition from male to female (age class 9). Our reasoning was that individuals that survived this developmental transition in a future environment would be adapted to those environmental conditions and therefore have normal (baseline) survival in the subsequent stages. The survival rates of age classes 1 and 9 of the future environment population (see Table 1) were based on the effects on survival reported in Table 2 and calculated as follows (Eqs. 6 and 7 respectively):

$$s_{01,FutCon} = 0.722 \cdot s_{01,AmbCon} \tag{6}$$

$$s_{09,FutCon} = 0.842 \cdot s_{09,AmbCon} \tag{7}$$

Likewise, the survival rates of these age classes in the future environment with DFB treatment were calculated as follows (Eqs. 8 and 9):

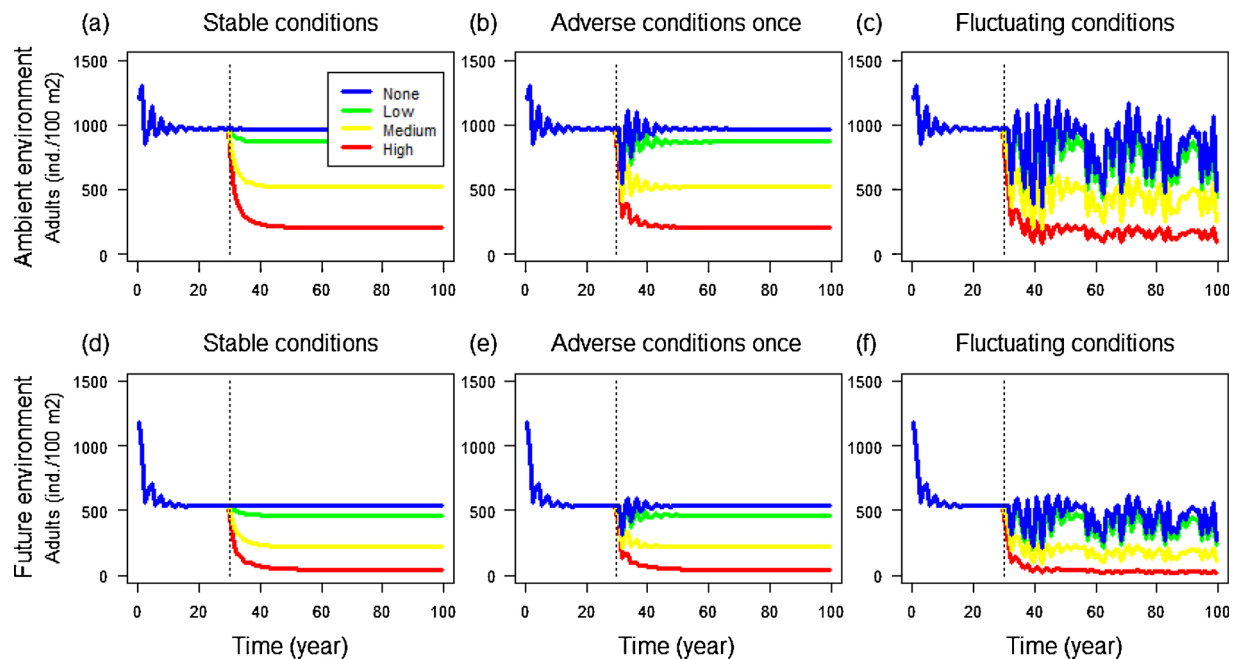$$s_{01,FutDFB} = 0.089 \cdot s_{01,AmbCon} \tag{8}$$

$$s_{09,FutDFB} = 0.284 \cdot s_{09,AmbCon} \tag{9}$$

We did not model any effects of future environment on fecundity, since we had no information on such effects from the experiments.

2.3.3. Timing of DFB application

The recommended frequency of treatment with flubenzurones is maximum every six months (Mattilsynet, 2016). The application of DFB

Fig. 3. Time series of summer abundance of adult shrimp from one realisation of the population model, under scenarios of ambient environment (upper panel) or future environment (lower panel). The colour code represents the proportion of the population affected by DFB exposure in spring: none, low (5%), medium (25%) or high (50%). The vertical line indicates the on-set of DFB treatment, after a stable age structure has been obtained. The central panel (b and e) shows the effect of a single year with adverse environmental conditions (reducing the survival of larvae by 50%), to illustrate the population's capacity for recovery. In the right panel (c and f), such adverse conditions occur in one out of 4 years (randomly distributed in time).

is most common in spring, but can also occur in autumn. We wanted to investigate the effects of DFB exposure in spring and autumn both separately and in combination, since DFB exposure may affect the developmental stages differently, and a population's stage structure vary during the year.

The timing of DFB exposure was implemented by selecting age-specific survival rates from the respective columns in Table 1. For example, for the scenario "ambient environment with DFB application in spring", survival parameters were selected from the column AmbDFB (Table 1) for all age classes in spring (1, 5, 9, 13 and 17) and from column AmbCon for all other age classes.

2.3.4. Degree of DFB exposure: percentage of the population affected

In the experimental DFB treatment populations, 100% of the individuals were exposed to DFB. In a natural shrimp population in a fjord, however, the percentage of individuals exposed to DFB is likely to be lower. Adults and juveniles, which feed on the sea bottom, may be more exposed to DFB through fish feed and debris than the pelagic larvae. In the absence of information on the actual percentage of exposed individuals in a field population, we have used the following hypothetical scenarios: Low, medium and degree of exposure affects respectively 5%, 25% and 50% of the population, by reducing these individuals' probability of survival to the next age class by the same factor as reported in Table 2.

3. Calculation

3.1. Model running

The model was run for 400 time steps of 3 months, which corresponded to the four seasons (spring, summer, autumn, winter) starting with spring. The first 120 time steps were considered as a burn-in period for obtaining a stable population structure, after which the

application of DFB was implemented. The following 80 time steps were considered as a burn-in period for the effect of DFB treatment and discarded from further analysis, so that only the final 200 time steps were used in the data analyses. The model was run for 100 replicate populations, which differed due to the demographic stochasticity components in survival. The initial abundance was 60,000 individuals (per 100 m²), distributed across the respective age classes (1, 5, 9, 13, and 17) in these proportions: 96.667%, 3%, 0.3%, 0.03%, and 0.003%. This corresponds to an initial spring abundance of ca. 200 adults per 100 m², followed by a summer abundance of ca. 1200 adults per 100 m², which is slightly above the carrying capacity of ca. 1000 adults per 100 m². The assumed age class distribution was loosely based on information from age-specific catch data (Shumway et al., 1985, Table 6; Yanez, 2000, Tables 1 and 2). The youngest age classes are usually missing from catch data; instead we assumed a high proportion for the first age class based on the reproductive rates and the final age structure of preliminary model versions.

3.2. Calculation and analysis of population-level endpoints

Three types of population-level endpoints were calculated from the simulated abundances, from the end of the burn-in period to the end of the simulation period.

Long-term abundances for each age class were calculated as the mean abundance over the given period. Only summer abundances were reported as results (Figs. 3 and 4; Table A1).

Realised demographic rates: Realised survival rates were calculated from the abundances of each age class, divided by the abundance of the previous age class in the previous age step, and averaged for the given period. Realised reproductive rate was calculated as the number of newly hatched larvae (N_1) divided by the number of ovigerous females in the previous time step (age classes 12, 16 and 20 combined) (Table A2).

The risk of quasi-extinction (Akçakaya, 2000) was calculated as the percentage of replicate populations with long-term summer abundance of adults falling below a given threshold abundance, within the given period (Fig. 5).

The population-level endpoints were analysed across three dimensions: (1) the timing of the DFB application, (2) the proportion of individuals exposed to DFB, and (3) future vs. ambient environment. All statistical analyses were performed in the programming environment R version 3.5.0 (R Core Team, 2018). Differences in long-term abundances between scenarios were analysed by ANOVA. Firstly, the combined effects of DFB exposure and environment change were analysed within each scenario of DFB application season and exposure level (Table 3). Secondly, the long-term abundance was analysed by one-way ANOVA across all scenarios of DFB application and exposure within the ambient and future environment scenarios, respectively (Fig. 4). Scenarios resulting in significantly different abundance were identified by Tukey's significantly honest difference (R package *multcompView*) (Graves et al., 2015).

3.3. Sensitivity analysis

For density-independent matrix population models, sensitivity or elasticity analysis of the population growth rate is commonly performed e.g. by analysis of eigen values (Caswell, 2009) or by simulated perturbations (Åberg et al., 2009). However, density-independent elasticities of the intrinsic population growth rate are a poor indicator of the effects of changes in demographic parameters on population size (Grant and Benton, 2003). In our study, we analysed the sensitivity of the population dynamics to stage-specific stressor impacts by perturbing four key demographic parameters and inspecting the effects on long-term stage-specific abundances (Figs. A1 and 6).

The deterministic model version (without environmental fluctuation or demographic stochasticity) was used for the sensitivity analysis. The following parameters were perturbed: larval survival (s_{01}), juvenile survival (s_{05}), male survival (s_{08}), female survival (s_{12}) and reproduction ($f_1 + f_2 + f_3$). Each parameter was perturbed by a gradient of 16 values ranging of 35%–115% of the reference value (column AmbCon in Table 1). The lower end of the perturbation (35% of the reference value) was set to exceed the most severe effect imposed by the experimental DFB exposure under ambient environment (Table 2, survival in treatment AmbDFB relative to survival in AmbCon: 37.8% for larvae, 41.1% for adults).

4. Results and discussion

4.1. Behaviour of the population model

The simulated dynamics of the adult stage of one of the populations in the baseline scenario (ambient environment, no DFB, stable environment) is illustrated in Fig. 3a (blue curve). The damped oscillations during the initial years (0–20) result from density-dependent compensations in combination with discrete time steps (four per year).

The average final adult abundance of all replicate populations in the deterministic model with the baseline scenario was 1024 individuals per 100 m^2 (Table A1, scenario no. 28), corresponding to the assumed carrying capacity of approximately 1000 adults, with 58% coefficient of variation. The variation among the replicate populations was due to the stochastic component of the survival rates, which were intended to represent a range in predation and fishing pressures.

Adverse environmental conditions were modelled by reducing the survival of the larvae by 50%. When adverse conditions occurred only once (Fig. 3b, blue curve), the population would recover and obtain approximately the same long-term abundance as for the stable environment (Table A1, scenario 29). The recovery was due to density-dependent compensation: the cohort that experienced high larval mortality obtained lower density when they became adults, and therefore had lower loss of adults due to density-dependent mortality (predation and fishing). The single reduction in larval survival resulted in damped oscillations in abundance lasting for 20–30 years, corresponding to the oscillations in the initial years. These oscillations are not meant to represent the actual population dynamics and are not expected to influence the analysed population-level endpoints.
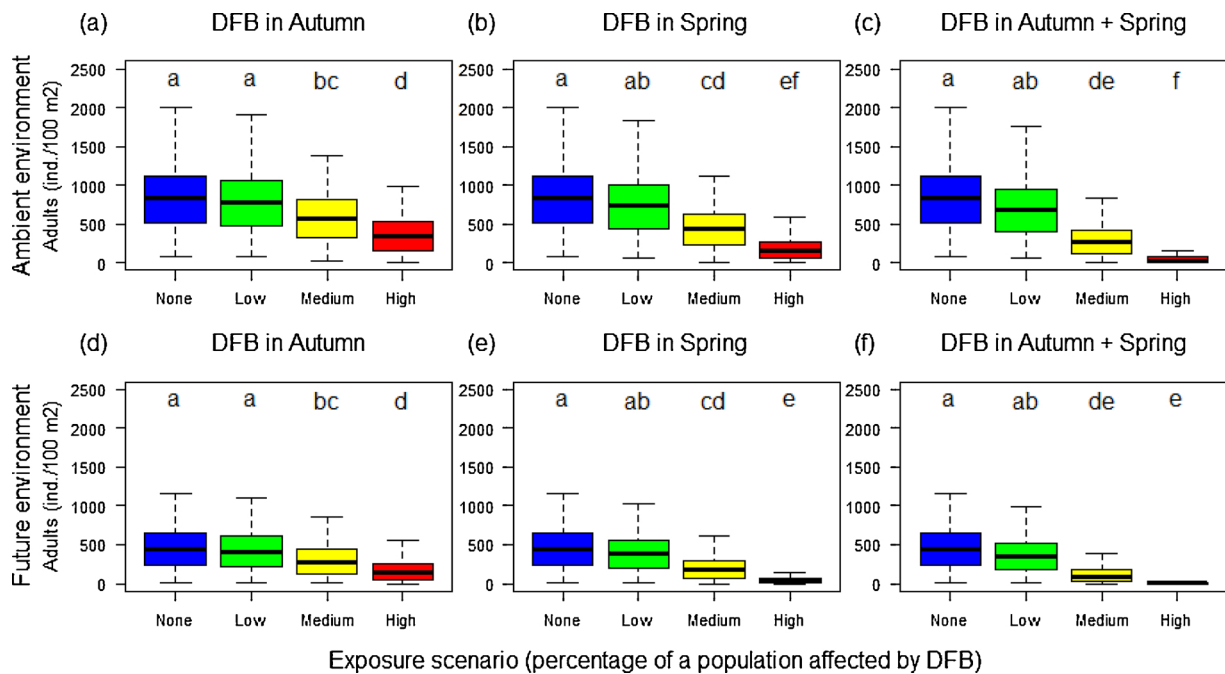
When adverse environmental conditions occurred frequently (Fig. 3c, blue curve), the population was not able to fully recover between each adverse year, and the resulting long-term abundance was reduced by 12.7% compared to the baseline (Table A1, Scenario 28), to 894 adults per 100 m^2 (scenario 30). The long-term average larval survival was decreased e.g. from 0.0506 (Table A2, Scenario 28) to 0.0456 (scenario 30). However, this reduction in larval survival was to some degree compensated by an increase in survival of the subsequent stages (e.g. from 0.143 to 0.155 for males). The slightly lower long-term abundance in scenarios with fluctuating conditions corresponds to lower carrying capacity due to insufficient food for the larvae in some of the years. Thus, the population dynamics of this model were regulated by both bottom-up (food limitation) and top-down processes (predation and fishing). The temporal variation in abundance (coefficient of variation) in the baseline scenario with environmental fluctuation (scenario 30) was 30% for juveniles, 26% for adults and 21% for the total population.

The long-term stage structure (not shown) was consistent across different scenarios. All further results are therefore described for the adult stage only.

4.2. Predicted effects of DFB on shrimp populations under ambient and future environment

The dynamics of the populations subject to DFB treatment stabilised at lower abundances than the baseline population (Fig. 3, blue vs. other curves). This implies that the loss of individuals due to DFB-related mortality was only partly compensated by a reduction in density-dependent mortality. The effect of DFB treatment on the abundance of adult shrimp depended on the degree of exposure as well as the season of application (Table 3). The negative effect of DFB treatments on abundance was statistically significant when the exposure level was

Table 3
Effects of DFB exposure and future environment scenarios on predicted long-term summer adult abundance, under the fluctuating environment scenario (cf. Fig. 3c). The effects are estimated by ANCOVA with DFB exposure scenario as a continuous variable (percentage of the population affected by exposure) and environment scenario as a categorical variable (future ocean warming and acidification vs. ambient environment). For more details on the scenarios, see Section 2.3.

Scenario	DFB exposure effect		Future environment effect		Interaction	
DFB Season	parameter estimate	p value	parameter estimate	p value	parameter estimate	p value
Autumn	−35	< 0.001	−157	0.028	26	< 0.001
Spring	−50	< 0.001	−40	0.536	36	< 0.001
Both	−62	< 0.001	19	0.749	47	< 0.001

Fig. 4. Predicted long-term summer abundance of adult shrimp, under scenarios of ambient environment (upper panel) or future environment (lower panel) with fluctuating conditions (cf. Fig. 3 c and f). The colour code represents the proportion of the population affected by DFB exposure: none, low (5%), medium (25%) or high (50%). Box plots show the variation among the 100 replicate populations. Within each environmental scenario (horizontal panel), groups with no common letters above the boxes have significantly different abundance (cf. Tukey's honestly significant difference test).

medium or high, i.e. affecting 25–50% of the population (Fig. 4).

The future environment scenario, which represent bottom water conditions altered by ocean acidification and warming towards the end of this century, also reduced the population abundances (Figs. 3 and 4, lower vs. upper panel). The long-term adult abundance of populations in all the future scenarios (Table A1, no. 31-60) was on average only 52% of the corresponding ambient environment scenarios. In combination with DFB treatment, however, the future environment effect was statistically significant only in scenarios where DFB had the lowest effect (i.e. treatment in autumn only; Table 3).

The future environment treatment had a positive interaction with the DFB treatments (Table 3). The positive interaction implies the reduction in abundance caused by DFB is lower under future environment than ambient environment; e.g. the slope from the midpoint of the blue box to the yellow box in Fig. 4 f is less steep than the corresponding slope in Fig. 4c. Such a positive interaction mainly reflects the fact that the simulated populations under future environment start at a lower density, and therefore cannot obtain as steep reduction (slope) due to DFB treatment as the ambient environment populations. The interaction between these two factors will therefore not be further discussed. Instead, the combined effects of DFB application season and exposure level were inspected in more detail by one-way ANOVA within each environment scenario, with each group corresponding to one bar in Fig. 4.

The combined effects of DFB application season and exposure level showed the same pattern within both environment scenarios (i.e., the upper and lower panel of Fig. 4 mostly have the same set of letters above the bars). Across all scenarios of season, the medium and high exposure levels resulted in significantly lower adult abundance than the control and the low exposure level. Moreover, the effect of the high exposure was significantly stronger than the medium exposure (except for in Fig. 4f). Effects of DFB treatment with low exposure did not differ from the control.

DFB treatment in spring (Fig. 4b) resulted in lower abundance than autumn treatment (Fig. 4a), when the exposure was high. A likely explanation is that treatment in spring also exposed the larval stage, which was more strongly affected by the DFB treatment than adults (Table 2). The effects of spring treatment with low exposure overlapped with the effects of autumn treatment with medium exposure. Similarly, the effects of spring treatment with medium exposure overlapped with the effects of autumn treatment with high exposure. DFB treatment in both seasons (Fig. 4c) resulted in lower abundance than DFB treatment in autumn only, when the exposure was medium or high. However, the effects of DFB treatment in both seasons were not significantly different from the treatment in spring only.

The risk of population decline below a given threshold (quasi-extinction cf. Akçakaya, 2000) is illustrated in Fig. 5. The risk curves are extracted from the long-term average abundances of all replicate populations (cf. Moe et al., 2008). This way, the variation in survival among the replicates (representing unknown harvest and predation rates) is summarised as percentages which can be interpreted as probability. For example, in the ambient control scenario (blue curves), the probability that abundance drops from ca. 1000 to below 500 adult shrimp per $100\,m^2$ (x-axis) is only 18%. Considering DFB treatment with medium exposure level under ambient environment (arrows in Fig. 5), there is a 58% probability of decline below 500 adults if DFB is applied in spring only (Fig. 5b), and 78% probability if DFB is applied in both seasons (Fig. 5c). For the same DFB treatment in future environment conditions, the corresponding probabilities of population decline are 89% if DFB is applied in spring (Fig. 5e) and 96% if DFB is applied in both seasons (Fig. 5f).

4.3. Model assessment

The purpose of this population model was to investigate the long-term population-level responses under different scenarios of DFB
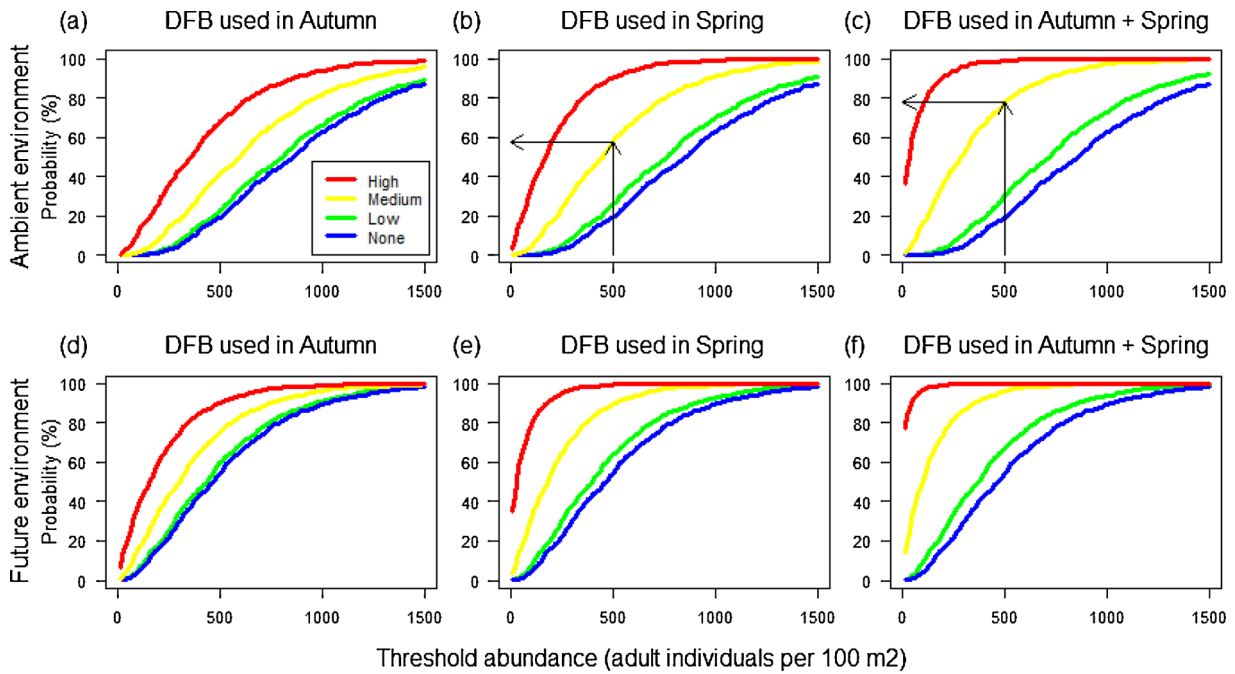
Fig. 5. Risk of population decline: Probability (y-axis) of adult summer abundance declining below the given threshold (x-axis), under scenarios of ambient environment (upper panel) or future environment (lower panel) with fluctuating conditions. The colour code represents the proportion of the population affected by DFB exposure: none, low (5%), medium (25%) or high (50%). For example, in the scenario of ambient environment and medium exposure, the probability of decline below 500 adults per 100 m² is 58% when DFB is used in spring, and 78% when DFB is used in both seasons.
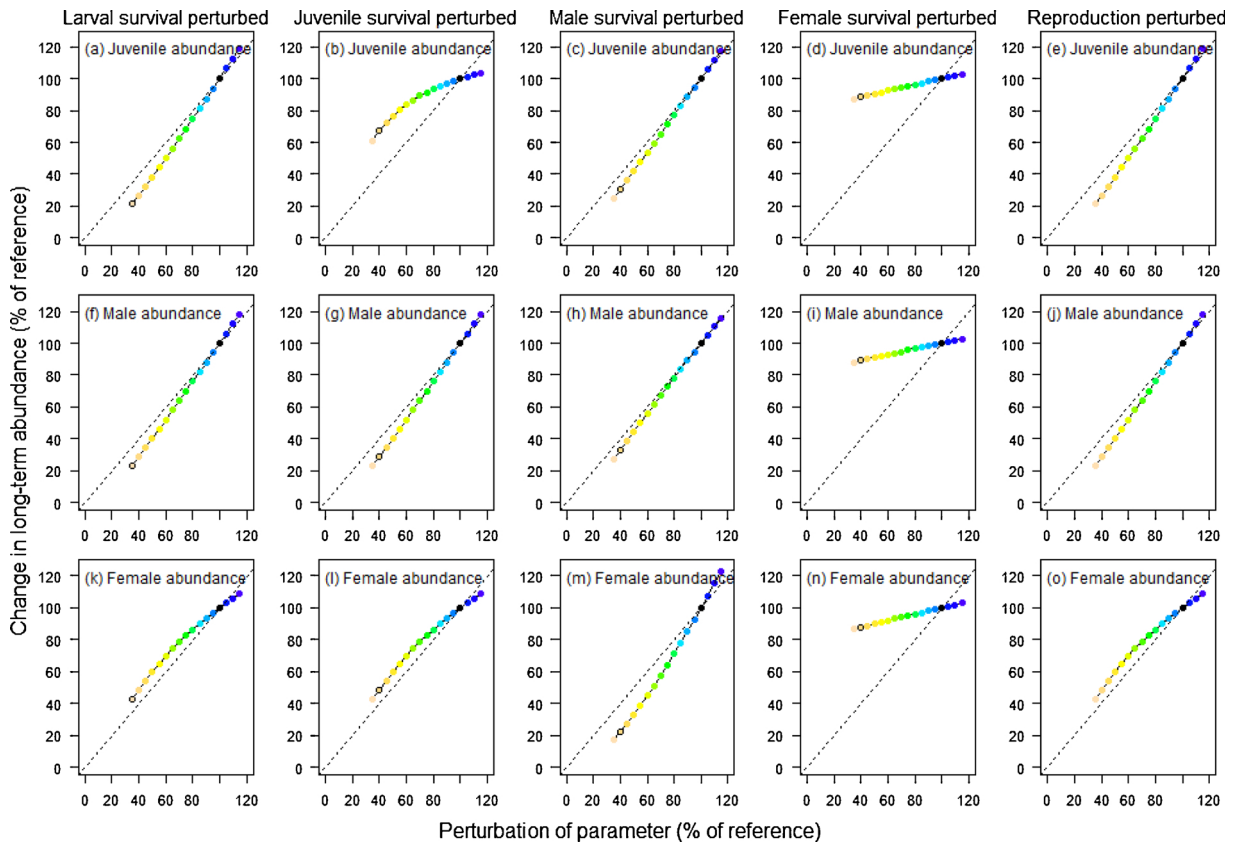
Fig. 6. Sensitivity analysis of the shrimp population model. Each vertical panel represents a demographic rate perturbed in the sensitivity analysis (see Section 3.3), while each horizontal pane represents the resulting stage-specific long-term summer abundance. The amount of perturbation (x-axis) ranges from 35% to 115% of the reference value for the given parameter (Table 1, column AmbCon). The diagonal lines indicate the 1:1 line, where the effect on population abundance (as percentage of the reference value) is equal to the amount of perturbation at the individual level. The reference value for stage-specific abundances are given in Table A2, scenario no. 28 (deterministic model). The black open circles indicate the amount of perturbation corresponding to the effects of the DFB treatment in ambient environment (Table 2, column AmbDFB).

treatment and environmental conditions. Since most parameters were unknown, we also accounted for variation in environmental conditions and ecological processes. Larval survival rates were unknown, but can be expected to be variable over time; this was accounted for by environmental fluctuation (adverse conditions) with irregular intervals. Adult survival is likely to be affected by predation and fishing, but the extent is unknown and probably variable. This was accounted for by among-population variation in survival rates (Eq. 3; Table A2). Our model assumes an intrinsic yearly survival rate of 0.397 for females (e.g. $s_{13} \cdot s_{14} \cdot s_{15} \cdot s_{16}$, Table 1) for the baseline scenario (no. 28). The realised survival rate for these age classes are lower in all scenarios (0.118 - 0.215, Table A2), due to the assumed density-dependent processes of fishing and predation. The realised survival rates are comparable to the estimated yearly survival rates of 0.225 - 0.350 for spawning females of *P. borealis* in Skagerrak and the Norwegian Deep for the period 1998-2014. These estimates are based on fishing mortality assessments found in Table 5.2.3 (column "F (1–3 years)") of ICES (2016) and include both yearly natural mortality (M = 0.75) and yearly fishing mortality (F = 0.483), calculated as exp(-(F + M)).

For reproduction, reliable and relevant estimates for egg production by individual females (Eq. 1) were available from the authors (R. K. Bechmann, unpublished), and corresponded well with fecundities reported previously (e.g. Shumway et al., 1985). There are no monitoring data on abundance of shrimp populations in Norwegian fjords available for comparison with our model predictions. However, the temporal variation in abundances predicted by our model with environmental fluctuation (coefficient of variation 26% for adults, 22% for the whole population) corresponds well with the temporal variation in estimated biomass for shrimp in Skagerrak and the Norwegian Deep for the period 1988–2014 (ICES, 2016, Table 5.2.3): 31% for spawning stock biomass, 26% for total biomass. This correspondence indicates that a reasonable amount of environmental fluctuation has been assumed for our population model.

Potential effects of DFB on fecundity were not accounted for in our model, since it was not tested in the experiment with adult shrimp (Bechmann et al., 2017). In this respect, our model can be considered conservative, i.e. it predicts a lower population-level risk of DFB than what real populations might experience.

The developmental rate was reported to increase under future environment but decrease with DFB treatment (Bechmann et al., 2018); neither of these changes was not accounted for in our model with fixed stage structure. The larvae that developed more slowly after DFB exposure were likely not able to complete their development at all, and therefore contributed to higher mortality than reported by the end of the experiments (Table 2). This implies that the cumulative (including delayed) effects of DFB on survival may be higher than those assumed in the population model (Table 1). Faster development of shrimp embryos in warmer water has also been reported by others (Brillon et al., 2005) and might in principle benefit the population growth. However, changes in the development time may also imply a higher risk of temporal mismatch with the food sources, corresponding to more frequent or stronger adverse conditions in our model. Since climate change is associated with many indirect effects and high uncertainty, we did not investigate this possibility further.

Density dependence is normally required in population models to obtain stable abundances in the long run. A density-independent model was developed for projecting population-level effects of toxicants on the shrimp *Americamysis bahia*; this model predicted exponential population growth and would become more realistic with density dependence (Kuhn et al., 2001, 2000). In other shrimp population models without density dependence, parameters have been adjusted to avoid population extinction or explosion (Labat, 1991; Raimondo and McKenney, 2006). In our model, the assumed density dependence in adult survival (Eq. 2) strongly affected the simulated population dynamics and thus the modelled effects of DFB on long-term abundance. If a natural shrimp population has weaker density dependence than assumed in our model, it would have lower capacity of compensation for DFB-related mortality; this implies that population-level effects of DFB would be stronger. Therefore, our model with relatively strong density dependence can be considered conservative also in this respect. Further development of this model can include scenarios with alternative types and strengths of density dependence, following the example of a modelling study of consequences for adult fish stocks of human-induced mortality on immatures (Nisbet et al., 1996).

It should be noted that complete extinction of a population is prevented by the density dependence in our model, even when abundance falls below one individual. It would be possible to modify the model to allow for extinction in such cases. On the other hand, we have not taken into account processes preventing local extinction, such as migration among shrimp fields. Therefore, the probability of extinction is not the most relevant population-level endpoint for our study.

The sensitivity analysis illustrates how each of the stage-specific abundances responded to a range of perturbation in different demographic rates, in the deterministic version of the model (Figs. A1 and 6). The population was most sensitive to the survival of males in transition to females (Fig. 6c, h, m). This perturbation reduced the recruitment to the first female age group, which had the highest density of females and therefore the highest contribution to the total offspring production. The population was least sensitive to reduced female survival, i.e. survival of 3-year old females after their first reproduction (Fig. 6d, i, n). The likely explanation is that the older females contributed relatively little to the total abundance of females and therefore also to the total offspring production. Reduced larval survival strongly reduced the abundance of juveniles and males (Fig. 6a, f). The subsequent reduction in abundance of females was lower (Fig. 6k), since this loss was partly compensated by density dependence in the adult stage (corresponding to reduced competition or predation rate). Reduced reproduction had a very similar effect as reduced larval survival (Fig. 6e, j, o). Reduced juvenile survival strongly reduced the abundance of the next stage (males, Fig. 6g), while the subsequent reduction in abundance of females (Fig. 6h) was partly compensated by density dependence.

The larval stage was more sensitive to DFB than the adult stage in the laboratory experiments (Table 2), which is in accordance with studies of DFB impacts on other shrimp species (Wilson and Costlow, 1987). In contrast, the modelled shrimp populations were more sensitive to reduction in adult (male) survival than to reduction in larval survival. The sensitivity analysis demonstrates that a population-level risk assessment needs to account for stage-specific impacts on the population as well as stage-specific sensitivity to the stressor.

4.4. Implications for ecological risk assessment of DFB to fjord shrimp populations

The harmful effects of DFB to survival of both adult and larval shrimp have been clearly demonstrated by recent laboratory experiments (Bechmann et al., 2017, 2018). Extrapolation of these results to the population level and to the natural environment by population modelling will make these findings more applicable for ecological risk assessment. However, the many assumptions underlying the population model must be considered when interpreting the predicted risks to shrimp populations. Our population model may be considered conservative (i.e., predicting weaker effects than in reality) in some respects: (i) the density dependence in adult survival provided some capacity for compensation to external mortality factors; (ii) DFB exposure

affected only a proportion of the population; (iii) future environmental conditions affected the population for only a part of the year; and (iv) adverse conditions for larval survival may happen more frequently than one out of four years (NAFO/ICES, 2017). On the other hand, the high levels of stochasticity, affecting survival of both larvae and adults, increased the risk of quasi-extinction by chance. Given these uncertainties, the most reasonable use of our results is by focusing on the comparison of effects of the different scenarios, rather than on the predicted values of abundances.

Our results demonstrate that the number of DFB treatments per year affect the risk to shrimp populations: DFB application in both seasons with high degree of exposure resulted in significantly lower abundance than application in either autumn or spring (Table 3, Fig. 4). A stronger population-level effect might be expected by DFB application in spring than in autumn; the spring treatment affected also larval survival, which was more strongly reduced than adult survival (Table 2). Our results indicated a stronger effect of DFB application in spring (Table 3), when a medium or high proportion of the population was affected (Fig. 4). This finding suggests that shifting the timing of DFB application from spring to autumn might be beneficial for shrimp populations. Since our results are not conclusive, the effects of such a change should be further investigated.

The degree of DFB exposure to the population (i.e., the proportion of the population experiencing the same effect as in the experiments) strongly affected the population-level risk of DFB. Having fish farms in a certain distance from shrimp fields, as recommended by Mattilsynet (2016), can limit the proportion of the shrimp population exposed. For a specific shrimp field, local conditions such as bathymetry, mud thickness, currents and resuspension will be important to predict the exposure to the shrimp populations. An investigation of the dispersal of particulate organic matter from salmon farms in Central Norway (Broch et al., 2017) showed that the distribution of organic matter in the bottom layer was non-homogeneous, with significant temporal variation and transport and settling of matter up to 0.5 km away from a farm. Dispersal model simulations indicated that transport as far as 2 km from the fish farms may be significant (Broch et al., 2017). Moreover, a real fjord population can be exposed to DFB from several fish farms located in the same fjord (see Fig. 1), each of which can apply DFB twice per year. Shrimp may also move towards fish farms too feed on residual feed and faeces. Obtaining realistic estimates of DFB exposure for real shrimp will therefore be a challenge.

The assumed future environment conditions in this study (temperature 9.5 °C, pH 7.6) resulted in significantly lower population abundance than the ambient environment (Table 3), although the effects on survival observed in experiments were implemented only for limited periods in the model (age classes 1 and 9). This level of ocean warming can be expected in bottom waters in South-Western Norway by the end of this century (simulated average winter temperature for 2090–2099: 9.70 °C), while the level of acidification can be expected in the following decades (simulated average winter pH for 2090–2099: 7.69) (Wallhead et al., 2017). It can be argued that shrimp populations will adapt to changed environmental conditions such as warming and ocean acidification in the long term, so that long-term effects of environmental change should be weaker than observed in lab experiments. On the other hand, climate change will also have several indirect effects on shrimp populations via ecological interactions. For example, earlier development of zooplankton (Durant et al., 2007) might result in adverse conditions (less food availability) for shrimp larvae occurring more often. The timing of larval food availability is crucial for the survival of the shrimp recruits (NAFO/ICES, 2017). Moreover, higher temperature will cause higher metabolism of the shrimp larvae, which will increase their energy requirement (Arnberg et al., 2013) and potentially reduce their growth rate (Franco et al., 2006). Either way, to

give accurate predictions on responses to future climate and environmental change is beyond the scope of our study. Instead, we have demonstrated how individual-level effects of a plausible environment scenario in combination with a toxicant stressor can be manifested on the population level.

According to our model, the interaction between the DFB and environmental stressors at the population level was antagonistic (Table 3), meaning that the combined negative effect of the two stressor types was less than additive. The compensatory capacity of the population due to density-dependent adult survival is again a likely explanation. In real populations, individual variation in sensitivity (which was not modelled here) could also contribute to a less-than-additive combined effect (Moe et al., 2013): if the most DFB-sensitive individuals are also the most sensitive to environmental stress, then the individuals surviving the DFB exposure will be more resistant to environmental stress than the population average. Regardless of the strength and direction of the stressor interaction, we can conclude that in a future environment with warmer and more acidic water, shrimp populations are likely to be more sensitive to chemical stressors such as DFB.

Our calculation of risk of the adult population decline below given threshold values (Fig. 5) corresponds to ICES' estimated risk of shrimp spawning stock biomass (SSB) below reference points such as B_{lim} (the lowest observed SSB) and MSY $B_{trigger}$ (the 5th percentile of the expected range of variation in SSB when fishing at maximum sustainable yield) (ICES, 2016). The overarching principle of ICES is that fishing pressure should result in no more than 5% probability of SSB being below B_{lim}. In our model, the calculation of probability of population decline below a threshold was based on the inter-population difference in abundance, which resulted from the modelled variation in survival rate (Eq. 3). In the current version of the population model, the range in survival rate for replicate populations mainly represents our uncertainty. If more information becomes available on adult survival rates in real shrimp populations in our study area, then this range can be adjusted to better represent real inter-population variation. For now, the risk curves (Fig. 5) can serve as a demonstration of how population model predictions can be applied in risk assessment for shrimp under scenarios of stressor combinations.

More reliable ecological risk estimates for northern shrimp populations in fjords will require data on abundances as well as more knowledge on ecological factors affecting the population dynamics of these populations. Shrimp populations in Northern-Norwegian fjords have been monitored since 2017, but the data are not yet available (pers. comm. G. Søvik, IMR); such data can later be used to assess and adjust our population model. Further development of this population model would particularly benefit from more information on: (i) effects of environmental fluctuations on larval survival, (ii) effects of predation and fishing on adult abundance, and (iii) the strength of density-dependent mechanisms that compensate the losses due to toxicant exposures and other environmental stressors.

Furthermore, more realistic scenarios on DFB exposure to shrimp populations in fjords could be obtained from more field data and modelling of the spread and fate of waste from aquaculture sites (Olsen et al., 2012). Exposure modelling for another commonly used salmon lice treatment, hydrogen peroxide (Refseth et al., 2016), has demonstrated the importance of several environmental factors for the risk of chemical to different non-target species. A combination of exposure, effect and population modelling would more strongly support the risk assessment of such stressors.

4.5. Conclusions

The population model developed for northern shrimp populations in fjords with salmon farms can be used to assess how the risk from

exposure to salmon lice medicine (diflubenzuron) is affected by factors such as the frequency and timing of DFB applications, the proportion of the population affected by exposure, future environmental conditions (ocean warming and acidification) and environmental fluctuations in food availability for larvae. More reliable estimates of risks to shrimp populations in fjords could be obtained with monitoring data on shrimp population abundances in such fjords and more knowledge on the fate and distribution of DFB in these environments.
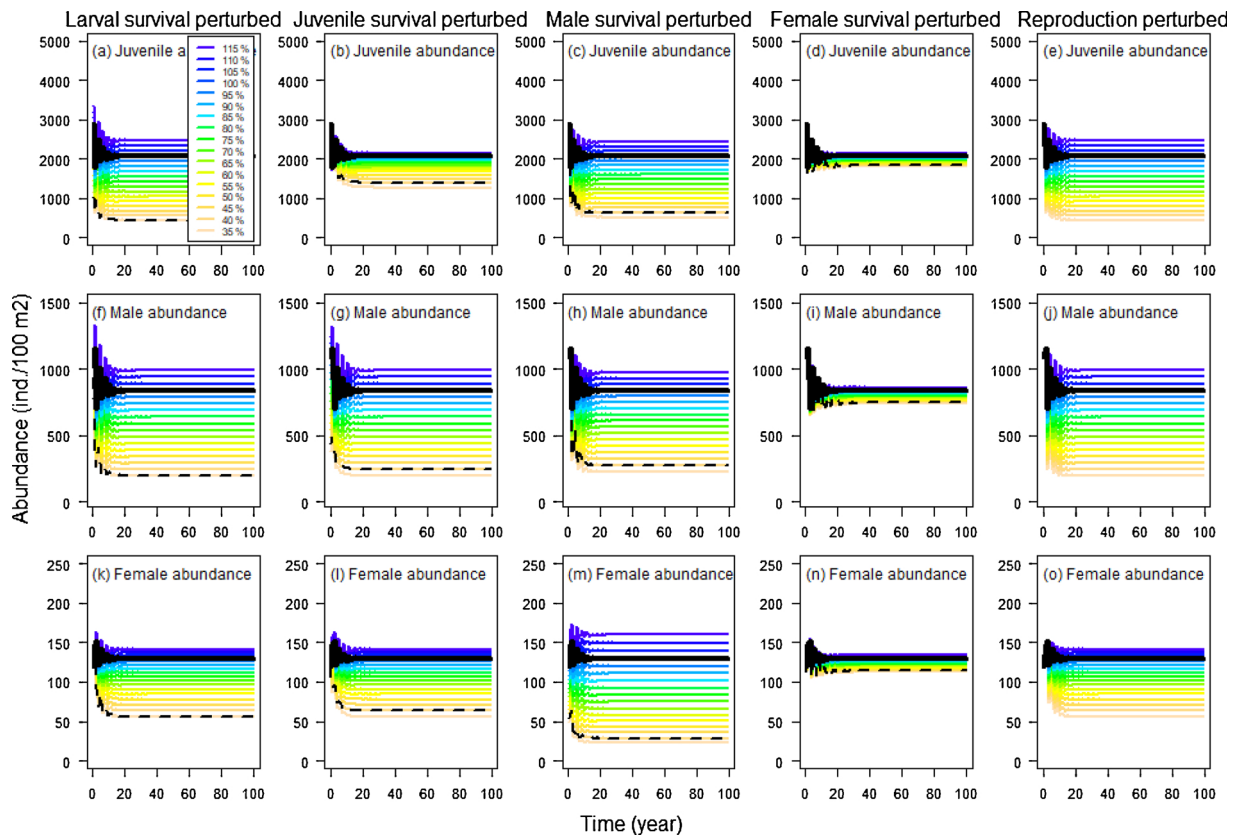
CRediT authorship contribution statement

S. Jannicke Moe: Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Software, Visualization, Writing - original draft, Writing - review & editing. **Dag Ø. Hjermann:** Formal analysis, Investigation, Methodology, Software, Writing - review & editing. **Elisa Ravagnan:** Investigation, Methodology, Validation, Writing - review & editing. **Renée K.**

Bechmann: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Project administration, Resources, Supervision, Validation, Writing - review & editing.

Appendix A

Fig. A1. Sensitivity analysis of the shrimp population model. Each vertical panel represents a demographic rate perturbed in the sensitivity analysis (see Section 3.3), while each horizontal pane represents the resulting stage-specific summer abundance over time. The amount of perturbation ranges from 35% to 115% of the reference value for the given parameter (Table 1, column AmbCon). The black solid curve represents the reference scenario: ambient environment without DFB exposure or environment (scenario no. 28 in Table A2). The black stippled curve indicates the amount of perturbation corresponding to the effects of DFB treatment in ambient environmental conditions (Table 2, column AmbDFB).

Table A1

Long-term average summer abundances for all scenarios, for each of the stages: juveniles, males, females, adults (males + females) and total. Numbers in parentheses are the age classes. The scenario code has the following abbreviations. Environment: Amb = ambient, Fut = future; Exposure (i.e., percentage of the population affected by DFB): Hig = high (50%), Med = medium (25%), Low = 5%, Con = control (0%); Season of DFB treatment: Spri = spring, Autu = autumn; Frequency of adverse environmental conditions: Non = never; one = once; Man = many (1 out of 4 years).

Scenario no.	Scenario code	Juveniles (2)	Males (6)	Females (10 + 14 + 18)	Adults	Total
1	AmbHigSpriNon	680	220	37	258	938
2	AmbHigSpriOne	680	220	37	257	938
3	AmbHigSpriMan	561	181	32	213	774
4	AmbHigAutuNon	946	419	61	480	1426
5	AmbHigAutuOne	946	419	61	480	1426
6	AmbHigAutuMan	799	351	53	405	1204
7	AmbHigBothNon	209	74	12	86	295
8	AmbHigBothOne	209	74	12	86	295
9	AmbHigBothMan	162	57	10	67	229
10	AmbMedSpriNon	1352	495	77	573	1925
11	AmbMedSpriOne	1353	495	77	573	1925
12	AmbMedSpriMan	1156	421	69	490	1646
13	AmbMedAutuNon	1521	646	94	740	2261
14	AmbMedAutuOne	1521	646	94	740	2261
15	AmbMedAutuMan	1311	553	84	637	1948
16	AmbMedBothNon	892	339	53	392	1284
17	AmbMedBothOne	892	339	53	392	1284
18	AmbMedBothMan	748	283	46	329	1077
19	AmbLowSpriNon	2006	805	118	923	2929
20	AmbLowSpriOne	2006	805	118	923	2929
21	AmbLowSpriMan	1746	696	107	803	2549
22	AmbLowAutuNon	2044	844	122	966	3010
23	AmbLowAutuOne	2044	844	122	965	3010
24	AmbLowAutuMan	1781	730	111	841	2623
25	AmbLowBothNon	1876	758	111	869	2745
26	AmbLowBothOne	1876	758	111	869	2745
27	AmbLowBothMan	1629	653	101	754	2383
28	AmbConNoneNon	2183	895	129	1024	3206
29	AmbConNoneOne	2183	895	129	1024	3206
30	AmbConNoneMan	1906	776	118	894	2800
31	FutHigSpriNon	189	66	12	78	267
32	FutHigSpriOne	189	66	12	78	267
33	FutHigSpriMan	147	51	10	61	209
34	FutHigAutuNon	463	213	33	246	709
35	FutHigAutuOne	463	213	33	246	708
36	FutHigAutuMan	380	174	28	202	582
37	FutHigBothNon	44	17	3	20	63
38	FutHigBothOne	44	17	3	20	63
39	FutHigBothMan	32	12	2	14	47
40	FutMedSpriNon	591	228	39	267	859
41	FutMedSpriOne	591	228	39	267	858
42	FutMedSpriMan	491	188	34	222	713
43	FutMedAutuNon	798	352	55	407	1206
44	FutMedAutuOne	798	352	55	407	1205
45	FutMedAutuMan	673	295	48	343	1017
46	FutMedBothNon	359	144	24	168	527
47	FutMedBothOne	359	144	24	168	527
48	FutMedBothMan	290	115	21	136	426
49	FutLowSpriNon	1067	445	71	516	1583
50	FutLowSpriOne	1067	445	71	516	1583
51	FutLowSpriMan	911	378	63	441	1352
52	FutLowAutuNon	1117	479	75	553	1671
53	FutLowAutuOne	1117	479	75	553	1670
54	FutLowAutuMan	956	407	67	474	1431
55	FutLowBothNon	988	415	66	481	1470
56	FutLowBothOne	988	415	66	481	1470
57	FutLowBothMan	841	351	59	410	1252
58	FutConNoneNon	1203	512	80	592	1795
59	FutConNoneOne	1203	512	80	592	1794
60	FutConNoneMan	1033	437	72	509	1542

Table A2

Long-term average demographic rates calculated from the simulated abundances for all scenarios. Numbers in parentheses are the age classes (survival from - to). For more explanations, see Table A1.

Scenario no.	Scenario code	Larval survival	Juvenile survival	Male survival	Female (first time spawner) survival	Female (second time spawner) survival	Reproduction per female
		(1 – 2)	(2 – 6)	(6 – 10)	(10 – 14)	(14 – 18)	(12 + 16 + 20)
1	AmbHigSpriNon	0.0351	0.3104	0.1789	0.1467	0.1388	1077
2	AmbHigSpriOne	0.0351	0.3104	0.1789	0.1468	0.1388	1077
3	AmbHigSpriMan	0.0316	0.3141	0.1916	0.1572	0.1487	1086
4	AmbHigFallNon	0.0506	0.4342	0.1499	0.1230	0.1163	1064
5	AmbHigFallOne	0.0506	0.4342	0.1499	0.1230	0.1163	1064
6	AmbHigFallMan	0.0456	0.4388	0.1612	0.1323	0.1251	1071
7	AmbHigBothNon	0.0351	0.3328	0.1773	0.1457	0.1378	1079
8	AmbHigBothOne	0.0351	0.3328	0.1774	0.1457	0.1379	1079
9	AmbHigBothMan	0.0316	0.3359	0.1866	0.1533	0.1451	1088
10	AmbMedSpriNon	0.0429	0.3571	0.1587	0.1302	0.1231	1067
11	AmbMedSpriOne	0.0429	0.3571	0.1587	0.1302	0.1231	1067
12	AmbMedSpriMan	0.0386	0.3612	0.1710	0.1402	0.1327	1076
13	AmbMedFallNon	0.0506	0.4172	0.1464	0.1201	0.1136	1062
14	AmbMedFallOne	0.0506	0.4172	0.1464	0.1201	0.1136	1062
15	AmbMedFallMan	0.0456	0.4217	0.1579	0.1295	0.1225	1069
16	AmbMedBothNon	0.0429	0.3698	0.1619	0.1328	0.1256	1069
17	AmbMedBothOne	0.0429	0.3698	0.1619	0.1328	0.1256	1069
18	AmbMedBothMan	0.0386	0.3740	0.1740	0.1427	0.1350	1077
19	AmbLowSpriNon	0.0491	0.3939	0.1460	0.1197	0.1133	1062
20	AmbLowSpriOne	0.0491	0.3939	0.1460	0.1197	0.1133	1062
21	AmbLowSpriMan	0.0442	0.3982	0.1576	0.1293	0.1223	1069
22	AmbLowFallNon	0.0506	0.4057	0.1438	0.1180	0.1116	1061
23	AmbLowFallOne	0.0506	0.4057	0.1438	0.1180	0.1116	1061
24	AmbLowFallMan	0.0456	0.4101	0.1553	0.1274	0.1205	1068
25	AmbLowBothNon	0.0491	0.3965	0.1466	0.1203	0.1137	1062
26	AmbLowBothOne	0.0491	0.3965	0.1466	0.1203	0.1137	1062
27	AmbLowBothMan	0.0442	0.4008	0.1582	0.1298	0.1228	1069
28	AmbConNoneNon	0.0506	0.4031	0.1432	0.1175	0.1111	1061
29	AmbConNoneOne	0.0506	0.4031	0.1432	0.1175	0.1111	1060
30	AmbConNoneMan	0.0456	0.4074	0.1547	0.1269	0.1201	1068
31	FutHigSpriNon	0.0209	0.3298	0.1978	0.2045	0.1934	1112
32	FutHigSpriOne	0.0209	0.3298	0.1979	0.2045	0.1935	1112
33	FutHigSpriMan	0.0188	0.3331	0.2080	0.2150	0.2034	1123
34	FutHigFallNon	0.0368	0.4507	0.1605	0.1572	0.1487	1083
35	FutHigFallOne	0.0368	0.4507	0.1605	0.1573	0.1487	1083
36	FutHigFallMan	0.0331	0.4555	0.1714	0.1679	0.1588	1092
37	FutHigBothNon	0.0209	0.3467	0.1753	0.1813	0.1716	1110
38	FutHigBothOne	0.0209	0.3467	0.1754	0.1813	0.1717	1110
39	FutHigBothMan	0.0188	0.3485	0.1801	0.1862	0.1763	1120
40	FutMedSpriNon	0.0288	0.3746	0.1752	0.1754	0.1659	1093
41	FutMedSpriOne	0.0288	0.3746	0.1752	0.1754	0.1659	1093
42	FutMedSpriMan	0.0260	0.3789	0.1874	0.1876	0.1774	1103
43	FutMedFallNon	0.0368	0.4332	0.1579	0.1547	0.1463	1081
44	FutMedFallOne	0.0368	0.4332	0.1579	0.1547	0.1463	1081
45	FutMedFallMan	0.0331	0.4380	0.1694	0.1659	0.1569	1090
46	FutMedBothNon	0.0288	0.3876	0.1769	0.1771	0.1675	1094
47	FutMedBothOne	0.0288	0.3877	0.1770	0.1772	0.1676	1094
48	FutMedBothMan	0.0260	0.3919	0.1882	0.1884	0.1782	1105
49	FutLowSpriNon	0.0352	0.4095	0.1584	0.1558	0.1473	1082
50	FutLowSpriOne	0.0352	0.4095	0.1584	0.1558	0.1473	1082
51	FutLowSpriMan	0.0317	0.4142	0.1702	0.1674	0.1583	1091
52	FutLowFallNon	0.0368	0.4211	0.1554	0.1522	0.1440	1080
53	FutLowFallOne	0.0368	0.4211	0.1554	0.1522	0.1440	1080
54	FutLowFallMan	0.0331	0.4258	0.1671	0.1636	0.1548	1089
55	FutLowBothNon	0.0352	0.4123	0.1590	0.1564	0.1479	1082
56	FutLowBothOne	0.0352	0.4123	0.1591	0.1564	0.1479	1082
57	FutLowBothMan	0.0317	0.4169	0.1708	0.1680	0.1589	1091
58	FutConNoneNon	0.0368	0.4183	0.1548	0.1516	0.1434	1079
59	FutConNoneOne	0.0368	0.4183	0.1548	0.1516	0.1434	1079
60	FutConNoneMan	0.0331	0.4230	0.1665	0.1631	0.1542	1088

References

Akçakaya, H.R., 2000. Population viability analyses with demographically and spatially structured models. Ecol. Bull. 23–38.

Anderson, P.J., 2000. Pandalid shrimp as indicators of ecosystem regime shift. J. Northwest Atl. Fish. Sci. 27, 1–10.

Arnberg, M., Calosi, P., Spicer, J.I., Tandberg, A.H.S., Nilsen, M., Westerlund, S., Bechmann, R.K., 2013. Elevated temperature elicits greater effects than decreased pH on the development, feeding and metabolism of northern shrimp (*Pandalus borealis*) larvae. Mar. Biol. 160, 2037–2048.

Bechmann, R.K., Lyng, E., Berry, M., Kringstad, A., Westerlund, S., 2017. Exposing Northern shrimp (*Pandalus borealis*) to fish feed containing the antiparasitic drug diflubenzuron caused high mortality during molting. J. Toxicol. Environ. Health A

80, 941–953.

Bechmann, R.K., Lyng, E., Westerlund, S., Bamber, S., Berry, M., Arnberg, M., Kringstad, A., Calosi, P., Seear, P.J., 2018. Early life stages of Northern shrimp (*Pandalus borealis*) are sensitive to fish feed containing the anti-parasitic drug diflubenzuron. Aquat. Toxicol. 198, 82–91.

Bellows, T.S., 1981. The descriptive properties of some models for density dependence. J. Anim. Ecol. 50, 139–156.

Berenboim, B.I., Dolgov, A.V., Korzhev, V.A., Yaragina, N.A., 2008. The impact of cod on the dynamics of barents sea shrimp (*Pandalus borealis*) as determined by multispecies models. J. Northwest Atl. Fish. Sci. 27, 69–75.

Bergström, B.I., 2000. The biology of *Pandalus*. Advances in Marine Biology, vol. 38. Academic Press, pp. 55–245.

Beverton, R.J.H., Holt, S.J., 1957. On the dynamics of exploited fish populations. Fishery Investigations Series II Volume XIX. Ministry of Agriculture, Fisheries and Food.

Brillon, S., Lambert, Y., Dodson, J., 2005. Egg survival, embryonic development, and larval characteristics of northern shrimp (*Pandalus borealis*) females subject to different temperature and feeding conditions. Mar. Biol. 147, 895–911.

Broch, O.J., Daae, R.L., Ellingsen, I.H., Nepstad, R., Bendiksen, E.Å., Reed, J.L., Senneset, G., 2017. Spatiotemporal dispersal and deposition of fish farm wastes: a model study from central Norway. Front. Mar. Sci. 4.

Bøhle, B., 1976. Temperatureffekt på embryonalutvikling og klekking av egg hos dypvannsreke (*Pandalus borealis* Krøyer).

Caswell, H., 2009. Sensitivity and elasticity of density-dependent population models. J. Differ. Equ. Appl. 15, 349–369.

Durant, J.M., Hjermann, D.Ø., Ottersen, G., Stenseth, N.C., 2007. Climate and the match or mismatch between predator requirements and resource availability. Clim. Res. 33, 271–283.

Fischer, S.A., Hall, L.W., 1992. Environmental concentrations and aquatic toxicity data on diflubenzuron (Dimilin). Crit. Rev. Toxicol. 22, 45–79.

Franco, A.R., Ferreira, J.G., Nobre, A.M., 2006. Development of a growth model for penaeid shrimp. Aquaculture 259, 268–277.

Fu, C., Quinn, T.J., Shirley, T.C., 2001. The role of sex change, growth and mortality in Pandalus population dynamics and management. ICES J. Mar. Sci 58, 607–621.

Gaulin, G., Skarland, T., 2015. Oppdrettsnæringen «reddet» av vannspeilet, Aftenposten Innsikt.

Grant, A., Benton, T.G., 2003. Density-dependent populations require density-dependent elasticity analysis: an illustration using the LPA model of Tribolium. J. Anim. Ecol. 72, 94–105.

Graves, S., Piepho, H.-P., Selzer, L., Dorai-Raj, S., 2015. multcompView: Visualizations of Paired Comparisons. R package version 0.1-7. https://CRAN.R-project.org/package=multcompView.

Grefsrud, E.S., Glover, K., Grøsvik, B.E., Husa, V., Karlsen, Ø., Kristiansen, T., Kvamme, B.O., Mortensen, S., Samuelsen, O.B., Stien, L.H., Svåsand, Tr., 2018. Risikorapport norsk fiskeoppdrett 2018. (Risk report Norwegian fish farming 2018). Fisken og havet, særnr. 1-2018.

Hall, E.F., 2017. The Vulnerability of Different Populations of the Commercially-important Shrimp *Pandalus borealis* to Environmental Stress. PhD thesis. University of Plymoth.

Hvingel, C., Kingsley, M.C.S., 2006. A framework to model shrimp (Pandalus borealis) stock dynamics and to quantify the risk associated with alternative management options, using Bayesian methods. ICES J. Mar. Sci. 63, 68–82.

ICES, 2016. In: Report of the Benchmark Workshop on *Pandalus borealis* in Skagerrak and Norwegian Deep Sea (WKPAND). 20–22 January 2016, Bergen, Norway. ICES CM 2016/ACOM:39. 72 pp.

Knutsen, H., Jorde, P.E., Blanco Gonzalez, E., Eigaard, O.R., Pereyra, R.T., Sannæs, H., Dahl, M., André, C., Søvik, G., 2015. Does population genetic structure support present management regulations of the northern shrimp (Pandalus borealis) in Skagerrak and the North Sea? ICES J. Mar. Sci. 72, 863–871.

Kuhn, A., Munns Jr., W.R., Champlin, D., McKinney, R., Tagliabue, M., Serbst, J., Gleason, T., 2001. Evaluation of the efficacy of extrapolation population modeling to predict the dynamics of *Americamysis bahia* populations in the laboratory. Environ. Toxicol. Chem. 20, 213–221.

Kuhn, A., Munns Jr., W.R., Poucher, S., Champlin, D., Lussier, S., 2000. Prediction of population-level response from mysid toxicity test data using population modeling techniques. Environ. Toxicol. Chem. 19, 2364–2371.

Labat, J.-P., 1991. Model of a shrimp population (*Philocheras trispinosus*) I. Simulation of the size structure. Ecol. Modell. 53, 75–93.

Langford, K.H., Øxnevad, S., Schøyen, M., Thomas, K.V., 2014. Do antiparasitic medicines used in aquaculture pose a risk to the Norwegian aquatic environment? Environ. Sci. Technol. 48, 7774–7780.

Macken, A., Lillicrap, A., Langford, K., 2015. Benzoylurea pesticides used as veterinary medicines in aquaculture: risks and developmental effects on nontarget crustaceans. Environ. Toxicol. Chem. 34, 1533–1542.

Mattilsynet (Norwegian Food Safety Authority), 2016. Veileder. Legemiddelbruk i oppdrettsnæringen, fiskehelsepersonell. p. 19. .

Maynard Smith, J., Slatkin, M., 1973. The stability of predator-prey systems. Ecology 54, 384–391.

Methot Jr., R.D., 2015. User Manual for Stock Synthesis. Model Version 3.24s. .

Moe, S.J., De Schamphelaere, K., Clements, W.H., Sorensen, M.T., Van den Brink, P.J., Liess, M., 2013. Combined and interactive effects of global climate change and toxicants on populations and communities. Environ. Toxicol. Chem. 32, 49–61.

Moe, S.J., Kristoffersen, A.B., Stenseth, N.C., 2008. Lucilia sericate laboratory populations: toxicant effects modified by stage-specific density dependence and stochasticity. In: Akçakaya, H.R., Stark, J.D., Bridges, T.S. (Eds.), Demographic Toxicity: Methods in Ecological Risk Assessment. Oxford University Press.

NAFO/ICES, 2017. In: NAFO/ICES Pandalus Assessment Group Meeting. 27 September to 3 October 2017. NAFO SCS Doc. 17/17 Serial No.N6762. ICES CM 2017/ACOM:09.

Nisbet, R.M., Murdoch, W.W., Stewart-Oaten, A., 1996. Chapter 13 - consequences for adult fish stocks of human-induced mortality on immatures A2 - Schmitt, Russell J. In: Osenberg, C.W. (Ed.), Detecting Ecological Impacts. Academic Press, San Diego, pp. 257–277.

Oh, C.W., Hartnoll, R.G., Nash, R.D.M., 1999. Population dynamics of the common shrimp, *Crangon crangon* (L.), in Port Erin Bay, Isle of Man, Irish Sea. ICES J. Mar. Sci. 56, 718–733.

Olsen, S.A., Ervik, A., Grahl-Nielsen, O., 2012. Tracing fish farm waste in the northern shrimp *Pandalus borealis* (Krøyer, 1838) using lipid biomarkers. Aquac. Environ. Interact. 2, 133–144.

Ouellet, P., Fuentes-Yaco, C., Savard, L., Platt, T., Sathyendranath, S., Koeller, P., Orr, D., Siegstad, H., 2011. Ocean surface characteristics influence recruitment variability of populations of northern shrimp (*Pandalus borealis*) in the Northwest Atlantic. ICES J. Mar. Sci. 68, 737–744.

Pedersen, S.A., Storm, L., 2002. Northern shrimp (*Pandalus borealis*) recruitment in West Greenland waters part II. Lipid classes and fatty acids in *Pandalus* shrimp larvae: implications for survival expectations and trophic relationships. J. Northwest Atl. Fish. Sci. 30, 47–60.

Punt, A.E., Huang, T., Maunder, M.N., 2013. Review of integrated size-structured models for stock assessment of hard-to-age crustacean and mollusc species. ICES J. Mar. Sci. 70, 16–33.

R Core Team, 2018. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Raimondo, S., McKenney Jr., C.L., 2006. From organisms to populations: modeling aquatic toxicity data across two levels of biological organization. Environ. Toxicol. Chem. 25, 589–596.

Rasmussen, B., 1953. On the Geographical Variation in Growth and Sexual Development of the Deep Sea Prawn (*Pandalus Borealis* Kr.).

Refseth, G.H., Sæther, K., Drivdal, M., Nøst, O.A., Augustine, S., Camus, L., Tassara, L., Agnalt, A.-L., Samuelsen, O.B., 2016. Miljørisiko ved bruk av hydrogenperoksid. Økotoksikologisk vurdering og grenseverdi for effekt. Akvaplan-niva report no. 8200. 56 pp.. .

Samuelsen, O.B., 2016. Persistence and stability of teflubenzuron and diflubenzuron when associated to organic particles in marine sediment. Bull. Environ. Contam. Toxicol. 96, 224–228.

Shumway, S.W., Perkins, H.C., Schick, D.F., Stickney, A.P., 1985. Synopsis of Biological Data on the Pink Shrimp, *Pandalus borealis* Krøyer, 1838. NMFS/S144. .

Wallhead, P.J., Bellerby, R.G.J., Silyakova, A., Slagstad, D., Polukhin, A.A., 2017. Bottom water acidification and warming on the western eurasian arctic shelves: dynamical downscaling projections. J. Geophys. Res. Oceans 122, 8126–8144.

Wieland, K., 2004. Length at sex transition in northern shrimp (Pandalus borealis) off West Greenland in relation to changes in temperature and stock size. Fish. Res. 69, 49–56.

Wieland, K., Storr-Paulsen, M., Sünksen, K., 2007. Response in stock size and recruitment of northern shrimp (*Pandalus borealis*) to changes in predator biomass and distribution in West Greenland waters. J. Northwest Atl. Fish. Sci. 39, 21–33.

Wilson, J.E.H., Costlow, J.D., 1987. Acute toxicity of diflubenzuron (DFB) to various life stages of the grass shrimp, Palaemonetes pugio. Water Air Soil Pollut. 33, 411–417.

Yanez, A.A.G., 2000. A comparison of different assessment models for northern shrimp, *Pandalus borealis*, in Icelandic waters. United Nations University Fisheries Training Programme, Final project. University of Iceland.

Åberg, P., Svensson, C.J., Caswell, H., Pavia, H., 2009. Environment-specific elasticity and sensitivity analysis of the stochastic growth rate. Ecol. Modell. 220, 605–610.