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Emergent interactions in the management of multiple threats to the conservation of harbour porpoises



David Lusseau^{a,*}, Lotte Kindt-Larsen^a, Floris M. van Beest^b

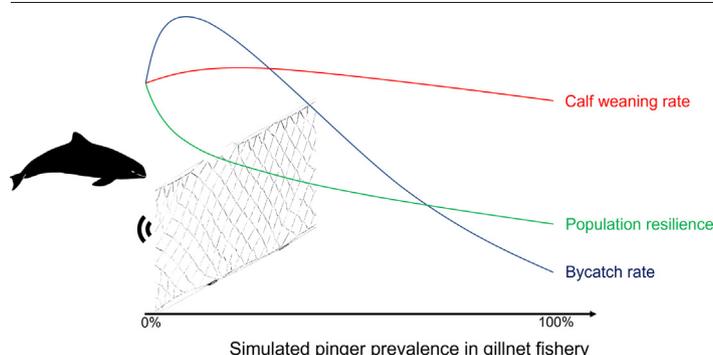
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HIGHLIGHTS

- Pingers are used to ensnify nets to mitigate cetacean bycatch risks.
- They contribute to the anthropogenic noise landscape affecting cetacean conservation.
- We do not know how to plan pinger prevalence to minimise bycatch and acoustic impacts.
- We show that counter-intuitively bycatch rate can increase at lower pinger prevalence.
- Management plans not requiring pingers on all nets could be counterproductive.

GRAPHICAL ABSTRACT



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ABSTRACT

Human activities at sea are intensifying and diversifying. This is leading to more complex interactions of anthropogenic impacts requiring adaptable management interventions to mitigate their cumulative effects on biodiversity conservation and restoration objectives. Bycatch remains the dominant conservation threat for coastal cetaceans. Additionally, the indirect impact of repeated exposure to disturbances, particularly acoustic disturbances, can affect cetacean population growth and therefore conservation objectives. Pingers are used to ensnify nets to provide an effective mitigation of bycatch risk. As those become more prevalent across fisheries at risk to catch for example harbour porpoises, pingers become contributors to the anthropogenic noise landscape which may affect the vital rates of this species as well. Currently, we do not know how to best balance pinger prevalence to minimise both bycatch rate and the population consequences of acoustic disturbance (PCoD). Here we use an agent-based model to determine how pinger prevalence in nets can be adjusted to minimise bycatch rate and noise disturbance propagating to affect population growth for harbour porpoises. We show that counter-intuitively bycatch rate can increase at lower pinger prevalence. When ecological conditions are such that PCoD can emerge, higher prevalence of pingers can lead to indirect effects on population growth. This would result from condition-mediated decreased reproductive potential. Displacing fishing effort, via time-area closure, can be an effective mitigation strategy in these circumstances. These findings have important implications for current management plans which, for practical consideration, may lead to lower overall pinger prevalence at sea. This study also shows that estimating the reproductive potential of the species should be incorporated in bycatch monitoring programmes. We now need to better understand how physiological condition affect reproductive decisions and behavioural responses to noise in cetaceans to better appraise and estimate the cumulative impacts of bycatch and its mitigations.

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1. Introduction

Entanglement and bycatch in fisheries is the predominant threat to the conservation of cetacean species (Avila et al., 2018; United Nations Office of Legal Affairs, 2021) and a challenge for the conservation of a wide array of marine taxa (Lewison et al., 2004). Ensonifying fishing gear to increase their detectability is an effective management intervention to help cetaceans, and other species, to detect and avoid nets and therefore reduce bycatch risk (Senko et al., 2014). Pingers, small devices attached to fishing gear that emit sound in the cetacean hearing range, are commonly used as such management interventions (Cox et al., 2007; Northridge et al., 2013). At the same time, however, ensonification of the oceans is an emerging threat for cetaceans (Pirota et al., 2018; Williams et al., 2020). The extent to which this threat can affect the conservation of those species remains to be determined, with some species and some populations being particularly sensitive (Bernaldo de Quirós et al., 2019). Therefore, we are faced with a wicked problem (Head, 2019): that is mitigating one conservation threat, namely bycatch, can give rise to the increase prevalence of another threat, namely noise-induced habitat deterioration. In order to manage the conservation of the many cetacean populations which face both bycatch and noise conservation threats, we must therefore find a means to inform trade-offs in mitigation interventions (van Beest et al., 2017).

The impact of anthropogenic noise on marine populations is difficult to estimate because this threat typically does not directly kill individuals. Anthropogenic noise can, however, deteriorate cetacean habitat by impairing their ability to carry out essential activities. Biologically-relevant impacts emerge primarily from foraging disruptions, and depending on life history traits and ecological context these disturbances can have population-level consequences (Williams et al., 2006; Lusseau, 2014; Natrass and Lusseau, 2016; Pirota et al., 2018; Keen et al., 2021). Population consequences of disturbances (PCoD), including acoustic disturbances, emerge from a deterioration of the condition of individuals that are repeatedly exposed to foraging disruption in the affected population. In PCoD, condition is taken as an integrative concept of ecological health of individuals (Derosus et al., 2020). This decrease in condition then compromises their ability to contribute demographically, via survival and reproduction, to population growth. There are now multiple models of condition-mediated population dynamics available to estimate when PCoD might occur and its severity (New et al., 2013; King et al., 2015; Pirota et al., 2015, 2018; van Beest et al., 2017; Nabe-Nielsen et al., 2018; Booth et al., 2020; Mortensen et al., 2021). These models can be used to simulate the population consequences of varied noise exposure scenarios and therefore inform management interventions best suited to address conservation objectives (Christiansen and Lusseau, 2015; Pirota et al., 2015; Nabe-Nielsen et al., 2018).

Behavioural responses to underwater noise by individuals are often variable and expected to be influenced by the context in which noise exposure occurs (Ellison et al., 2012). This suggests that there is not one “optimal” dose-response relationship to study the impact of noise exposure on activity disruption. More generally, the elicitation of behavioural responses to risk and fear is context-dependent (Lima and Dill, 1990; Frid and Dill, 2002; Beale and Monaghan, 2004; Lusseau, 2014; Gallagher et al., 2017) because the perception of risk and fear is integrated with other motivations to yield behaviour (McFarland, 1969; Sibly and McFarland, 1976; Lorenz and Kickert, 1981; Pirota et al., 2014). One of the key motivational axes affecting behavioural dynamics and state resulting from fear and risk perception is condition (Sutton and Krashes, 2020). Condition can be defined in many ways, particularly depending on fields of enquiries, but here we focus on ecologically-relevant condition, that is the state of individuals affecting their demographic contributions; via either survival or reproduction (Derosus et al., 2020). Therefore, PCoD estimation is difficult using simple deterministic models.

Previous studies have used agent-based simulation models to assess changes in harbour porpoise abundance when exposed to bycatch risk (Nabe-Nielsen et al., 2014) and the noise emerging from pingers used for bycatch mitigation (van Beest et al., 2017). The harbour porpoise (*Phocoena phocoena*) exemplifies the challenge of wicked problem

emergence in the management of multiple conservation threats. The species ranges across most coastal waters of the Northern Hemisphere where it is exposed to the threat of bycatch, primarily in gillnets (Northridge et al., 2013; Reeves et al., 2013; Kindt-Larsen et al., 2016). Pingers are used frequently as a management intervention to reduce harbour porpoise bycatch rate in commercial fisheries, therefore leading to an increased anthropogenic soundscape across the range of the species. Harbour porpoises have a unique physiological ecology for a cetacean in that their body condition reacts rapidly to lost opportunities of energy intake (Kastelein et al., 2019b) and at the same time their foraging ecology is plastic, with an ability to have very large energy intakes in one bout (Kastelein et al., 2019a). Therefore, body condition of individuals can fluctuate rapidly with pronounced inter-annual variation in starvation mortalities for the species (Fenton et al., 2017; Murphy et al., 2020). Overall, the population biology of the species is related to this fast physiological pace with higher reproductive rate, younger age at first reproduction and shorter lifespan (Lockyer, 1995, 2007; Lockyer and Kinze, 2003; Murphy et al., 2020; Genu et al., 2021). These adaptations have the scope to increase the sensitivity of harbour porpoises to the physiological impacts of PCoD, but it is unclear whether those may be compensated by a more resilient population biology (Lusseau, 2014; Natrass and Lusseau, 2016; Pirota et al., 2018). While agent-based models can provide some estimate of system state, their full potential to appraise the shape of the basin of attraction around those equilibria has been understudied (Nardini et al., 2021). Here we extend numerical analyses of agent-based model outcomes to estimate the basin of attraction of equilibria (Natrass and Lusseau, 2016) under different anthropogenic conditions to assess not only whether we can find trade-offs in management interventions that can meet conservation objectives, but also appraise whether those trade-off solutions leave the population in a resilient state. Population dynamical resilience, measured as engineering resilience (Caswell, 2000; Natrass and Lusseau, 2016), is crucial to accommodate for stochastic events likely to impact the populations, such as disease outbreaks, which we know will increase in frequency as climate changes (Sanderson and Alexander, 2020).

van Beest et al. (2017) used multi-agent simulations to show that pinger implementation could be associated with increased mortalities leading to potentially a non-trivial relationship between bycatch rate decrease (gains) and PCoD-related mortalities (losses) as fishing gear are instrumented with pingers. In other words, while high pinger prevalence decreased bycatch, it increased noise induced impacts on demographic contributions. We therefore need now to determine whether pinger implementation could be designed in a way that maximises bycatch rate reduction, minimise PCoD emergence and maintains a resilient population. Here we assess whether changes in pinger prevalence in nets could be used to balance trade-offs in excess mortalities that could still achieve the conservation objectives for the species. Moreover, because the previous model of van Beest et al. (2017) did not account for condition mediation in the avoidance response to pinger noise, we integrate here condition mediation to assess whether changes in risk-taking by individuals as their condition deteriorates can ultimately affect population trajectory.

2. Methods

2.1. Multi-agent model to determine the population consequences of fishing gear modification for harbour porpoises in an existing fishery

Here we use the multi-agent model DEPONS (Disturbance Effects on the Harbour Porpoise population in the North Sea) tuned to the gillnet fisheries exploiting the region between Denmark and Sweden (Fig. 1). This model is described in detail in van Beest et al. (2017) as well as in the TRACE document of DEPONS available at <https://github.com/jacobnabe/DEPONS> (Nabe-Nielsen et al., 2018).

The model takes a data-driven, bottom-up mechanistic approach where population dynamics emerge from the individuals' competition for a dynamically changing food resource and from altered movements and reduced foraging when porpoises are disturbed by underwater noise. Each

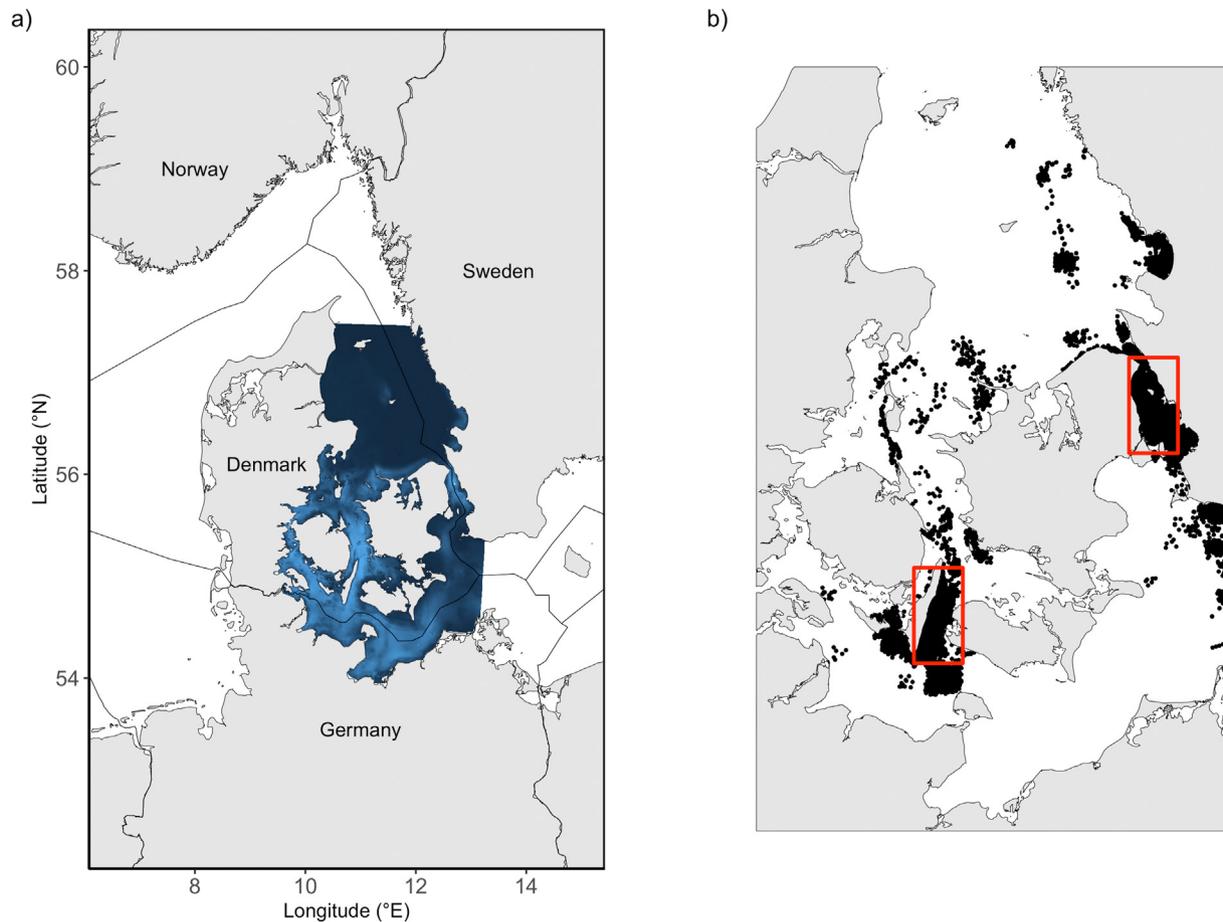


Fig. 1. Study area and design: a. relative density of harbour porpoises assumed in the simulations taken from estimations (Edrén et al., 2010) used in van Beest et al. (2017), b. location of gillnets in simulations and area closed seasonally in the time area closure scenario taken from van Beest et al. (2017).

porpoise in the model (also called agents) is a ‘super individual’ and represent approximately 100 individual porpoises, estimated using population counts in the inner Danish waters (Hammond et al., 2017). Movement of porpoise agents switches between fine-scale foraging movements and large-scale dispersal movements. Both movement modes are parameterized and calibrated based on empirical tracking data to ensure that agents have home range sizes, displacement distances and residence times that match those of real porpoises (Sveegaard et al., 2011; van Beest et al., 2018). Switching between the two movement modes is directly determined by the energetic status of the agent. When a porpoise agent manages to locate food resources in a given area, its energy level is maintained or increases, which allows it to reproduce successfully. When foraging success and thus the energy level of a porpoise agent declines for a predetermined amount of time, the porpoise agent switches to large-scale movement behaviour and starts moving towards another potential feeding area. Porpoise agents have a spatial memory of where in the landscape food resources were found previously, which guides their inter-patch movements. If food is not found in previously visited feeding areas (e.g. due to depletion as a result of competition with other porpoise agents), the porpoise’s energy level steadily declines, which increases the risk that it abandons its lactating calf or dies. As such, foraging success directly influences individual fitness and population dynamics.

Energy expenditure in the model is determined by the animals’ field metabolic rate and movement, which is dependent on season (e.g. water temperature) and by reproductive status, with higher energy use for lactating females. Underwater noise also has a negative effect on the energy level of porpoise agents as any foraging activity is interrupted and deterrence movements away from the sound source lead to increased energy

expenditure. Porpoise agents remain deterred to noise for a maximum of 2.5 h, but the extent to which they are deterred is halved at every time step. If a deterred porpoise agent moves far enough away from a sound source so that the sound level is below a predetermined threshold, it stops being deterred and, depending on its energy level, either resumes fine-scale foraging movements or starts dispersal movements. The impact of underwater noise is thus the combination of lost foraging opportunities and increased energy expenditure due to deterrence movements, which influences the energy level of an agent and its probability of reproducing and surviving successfully.

To estimate the population-level consequences of bycatch and pinger deployment, the DEPONS model used in this study has the option to activate gillnet agents (with or without a pinger present). The number, length, location, and soak time of gillnet agents in the IBM seascape are based on empirical data of Swedish and Danish gillnet fisheries. Each gillnet agent is assigned a bycatch probability value, which was calibrated by van Beest et al. (2017) to get a realistic annual bycatch rate for the inner Danish waters landscape. As such, gillnet agents have a direct negative effect on porpoise agents’ survival probability. In scenarios where pingers are activated on gillnet agents, the probability of bycatch by gillnet agents is drastically reduced, but porpoise agents are impacted by pinger noise through loss of foraging opportunities and deterrence movements away from pinger noise.

In this study, we built on the pinger noise avoidance framework of van Beest et al. (2017) to ensure that porpoise agents responded to pinger noise with deterrence movements that lead to temporary declines in harbour porpoise densities in the vicinity of active pingers as observed in nature. Briefly, this response, described fully in van Beest et al. (2017), was

informed by a previous empirical study estimating the change in porpoise acoustic activity, used as a proxy for presence, at different range of a pinger depending on whether it was enabled or not. The pinger, an Aquamark100 (Kindt-Larsen et al., 2019), was placed in the center of an array of porpoise click detectors (C-PODs, www.chelonia.co.uk) that were placed at 0, 400, 800, and 1600 m from the pinger. An internal clock activated the pinger in cycles of 23 h on (with noise) and 23 h off (without noise). Results of the empirical studies were subsequently used in van Beest et al., 2017 to tune the noise deterrence behaviour of porpoise agents in the model using pattern-oriented modelling (POM) (Grimm et al., 2005). Because in this version of the model the sound level received by porpoise agents, R , was modelled assuming spherical spreading (Urlick, 1967), which differs from the linear decrease used in van Beest et al. (2017), we redid the POM, by varying the level of sound emitted by the pingers (impact, to reflect those used in the fisheries) and the deterrence coefficient (c) of porpoise agents until we identified the combination of values that produced the same decrease in porpoise densities with distance to the pingers in the model as observed during the empirical studies.

Once the deterrence behaviour of porpoise agents was tuned, we explored two gillnet exposure scenarios: one (*pingers only*) in which all areas are available for fishing and net deployment mimics actual gillnet deployment locations and effort in the study region (van Beest et al., 2017), and a second (*pingers and area closure*) where time area closures are implemented but keeping fishing effort constant across the landscape by redistributing fishing effort outside the area closed (see van Beest et al., 2017 for full details). Area closures were implemented in locations and seasons with higher bycatch risk and the fishing effort redistribution was implemented to mimic the expected compensatory fishing behaviour that would be implemented by fishers in such circumstances (O'Keefe et al., 2014). The stochastic nature of the effort redeployment led to an overall slight drop in fishing effort (by 10 %), which would be expected in reality, as fishers would not always be able to fully replace all fishing effort displaced (Smith et al., 2020).

For each scenario, we run 30 replicate simulations of 40 years for each level ($n = 11$) of pinger prevalence treatment in gillnets (from 0 % to 100 % in 10 % increment). For each level, established gillnets were randomly selected to be equipped with pingers with a probability equal to the prevalence set for the treatment level.

2.2. Integrating condition-mediation of behavioural responses in existing agent-based model

One shortcoming of current DEPONS implementations is a lack of condition-mediated behavioural responses to noise exposure. Thus, all porpoise agents respond to noise with the same deterrence strength and independent on current condition. However, this is an important feature of PCoD which influences system state and dynamics (Natrass and Lusseau, 2016), and, given the life history traits of harbour porpoises, we assume that it could lead to overestimation of condition-mediated mortalities (Dall and Johnstone, 2002). Particularly in our case, harbour porpoises are known to change their behavioural responses to noise exposure over time (Graham et al., 2019; Kindt-Larsen et al., 2019), a functional response that could emerge from changes in body condition (Bejder et al., 2009). It is therefore important to introduce condition-mediation mechanisms in agent's response to noise exposure. Here we introduce three possible functional responses of the movement to noise depending on condition: linear; non-linear; and asymmetrically non-linear, assuming that behavioural response is resilient to condition changes (Fig. S1). This was done by altering the file *Porpoise.java* (function 'deter', lines 1237–1238, <https://github.com/jacobnabe/DEPONS>).

To do so the length of the deterrence vector (V_D) was associated to the condition of the individuals. The deterrence vector determines the response of porpoises to noise exposure (the direction and magnitude of the movement change). Full details of the variables and functions is available in the TRACE document of DEPONS (Nabe-Nielsen et al., 2018):

Without condition-mediation (unaltered DEPONS):

$$|V_D| = c(R - T) \quad (1)$$

Linear condition-mediation:

$$|V_D| = \frac{cE_p}{E_{pmax}}(R - T) \quad (2)$$

Non-linear, symmetric condition-mediation:

$$|V_D| = \frac{c}{1 + e^{-E_p + \frac{E_{pmax}}{2}}}(R - T) \quad (3)$$

Non-linear, asymmetric condition-mediation:

$$|V_D| = \frac{c}{1 + e^{-1.24E_p + \frac{E_{pmax}}{2}}}(R - T) \quad (4)$$

where c is a tuned deterrence coefficient, which we kept with the same value for Eqs. 1–4, R is the sound received level by the porpoise and T the threshold at which sound elicits a deterrence response (if $R < T$, then $V_D = 0$). E_p is the energy level of the individual porpoise, a measure of its condition, and E_{pmax} is the maximum value E_p can take (in DEPONS E_p varies from 0 to 20).

The 330 model runs (40-years each) of '*pingers only*' described in the previous section were simulated for each of these four types of condition mediation. When contrasting the outcome of the different functional responses it became apparent that there was no qualitative difference in outcomes and the responses only varied the effect sizes. For simplicity we contrast the inclusion of the non-linear symmetric condition mediation (Eq. 3, yielding the largest effect of the condition functional responses) and the current DEPONS model lacking condition-mediation (Eq. 1) for the main analyses (660 runs across both scenarios).

We did not fully reparameterise the DEPONS model to integrate condition mediation i) so as to facilitate comparison with previous work (van Beest et al., 2017) and ii) because we currently do not have data to inform the absolute changes in behavioural response with changes in condition. Instead, we applied the functions described above (Eqs. 1–4) to the tuned model described in van Beest et al. (2017). This means that we cannot interpret the absolute change in abundance trajectory between simulations with and without condition mediation. However, we can appraise whether the behaviour of the modelled system changes with the integration of condition mediation (a non-trivial question given the physiological dynamics and population dynamics of the species). Implementation of these changes and simulation outcomes are available at the DEPONS fork: <https://github.com/dlusseau/DEPONS>.

2.3. Estimating changes in population dynamics with changes in pinger prevalence

Here we estimated whether abundance was associated with pinger prevalence, whether the implementation of condition mediation in the model interacted with this association and whether these effects changed depending on the scenarios. We fitted generalised linear mixed effects models (GLMMs) to the abundance time series assuming a Poisson distribution of residuals and accounting for a random effect of run replicates and an autoregressive autocorrelation structure with a lag of 1-year (following preliminary inspection of the autocorrelation of residuals) within run replicates. We fitted models with a categorical fixed effect of prevalence, scenario, and condition mediation function type as well as a potential interaction between those effects. We fitted these models to both the whole 40-year time series and to the last 20 years of the time series. The first set of models account for both long-term behaviour of abundance as well as behaviour as the system moves away from initial conditions (which captures some understanding of reactivity). The latter set accounts for the behaviour of abundance away from initial conditions.

We replicate this modelling process with mortalities, assessing whether the mortality rate changed with prevalence and condition mediation; assuming a Poisson distribution of the residuals of the number of deaths per year and an offset effect of the log of the abundance. We then assessed whether bycatch rate changed with these fixed effects (prevalence, condition mediation and scenario) by fitting similar generalised linear mixed effects models to the proportion of porpoises dying of bycatch out of recorded yearly abundance, assuming a binomial distribution of the residuals.

Finally, as PCoD are most likely to emerge from changes in reproductive rate, we estimated whether the lifetime reproductive success (LRS) of females was associated with the fixed effects. LRS was estimated as the number of weaned calves produced by a female over her lifespan. This count was not offset by the age at death of the female as LRS capture trade-offs between survival and reproductive investment. We complemented this analysis by determining whether the number of calves produced by females by a given age (offset by the age of females when they die) varied across simulation sets and implementing the same models to the proportion of weaned-to-produced calves.

2.4. System transient dynamics — basin of attraction of attractors, the resilience of porpoise populations exposed to different scenarios

We can explore the temporal dynamics of the way the population moves away from initial conditions (year 0) towards the levels at which it settles under the different scenarios to understand its resilience in the state in which it settles. This state can be defined by two dimensions which are in the model the primary drivers of population dynamics: abundance and the condition (energy) of porpoises in the population. To do so, we approximated the flow trajectory of the system's phase portrait in the {abundance, porpoise energy} plane using a general additive model (GAM) relating the change in a bivariate response variable $(\frac{dabundance}{dt}, \frac{denergy}{dt})$ to a spline relationship of the interaction between abundance and average energy level of individual porpoises at time t . As the models are not parameterised in a way that food availability will vary the relationship between porpoise abundance and porpoise condition ("energy level"), we focussed on the abundance/porpoise energy plane dimension of the phase portrait. Fitted values of this GAM provide insights about the system's behaviour by approximating the partial derivatives of the coupled abundance and energy time series (Natrass and Lusseau, 2016). Hence, this approximates the

Poincaré map of the system, providing a similar information to what a Jacobian matrix would for coupled differential equations (Nardini et al., 2021). We then estimated whether the type of basin of attraction changed with prevalence and condition mediation and whether the attractor changed with prevalence and condition mediation by predicting abundance and average porpoise energy from the GAM for $(\frac{dabundance}{dt}, \frac{denergy}{dt}) = 0$. We finally estimated the engineering resilience of the system state (Natrass and Lusseau, 2016) by estimating the speed of travel of the system (s) in the (abundance, porpoise energy) plane depending on its distance from the estimate equilibrium:

$$s_t = \sqrt{\left(\frac{d\widetilde{abundance}}{dt}\right)^2 + \left(\frac{d\widetilde{energy}}{dt}\right)^2} \tag{5}$$

where \widetilde{x} is the variable centered and scaled by its standard deviation so that rate of movement on both axes (that have different magnitudes) are comparable. We then estimated changes in speed with distance from the equilibria depending on pinger prevalence, condition mediation and scenario using a GLMM, with a random effect of run replicates and assuming a quadratic effect of 'distance from equilibria' on speed and a Gaussian distribution of residuals. All GLMM were implemented in R using glmmTMB (Brooks et al., 2017) and GAM using mgcv (Wood, 2017).

3. Results

3.1. Changes in population dynamics

Condition-mediation functions significantly altered population trajectory with pinger prevalence with the symmetric non-linear function (Eq. 3) being most distinguishable from simulations without condition mediation (Fig. S2). Whether we considered the whole simulated times series (Fig. S3) or the latter halves (Fig. 2), abundance varied with prevalence and, moreover, the effect of prevalence depended on whether condition mediation was implemented or not. The effects remained in both scenarios but the effect size of these interactions differed (Tables S1–3, Fig. 2).

As expected, implementing condition mediation increased the realised abundance, particularly for higher pinger prevalence (Figs. 2 & S2). These

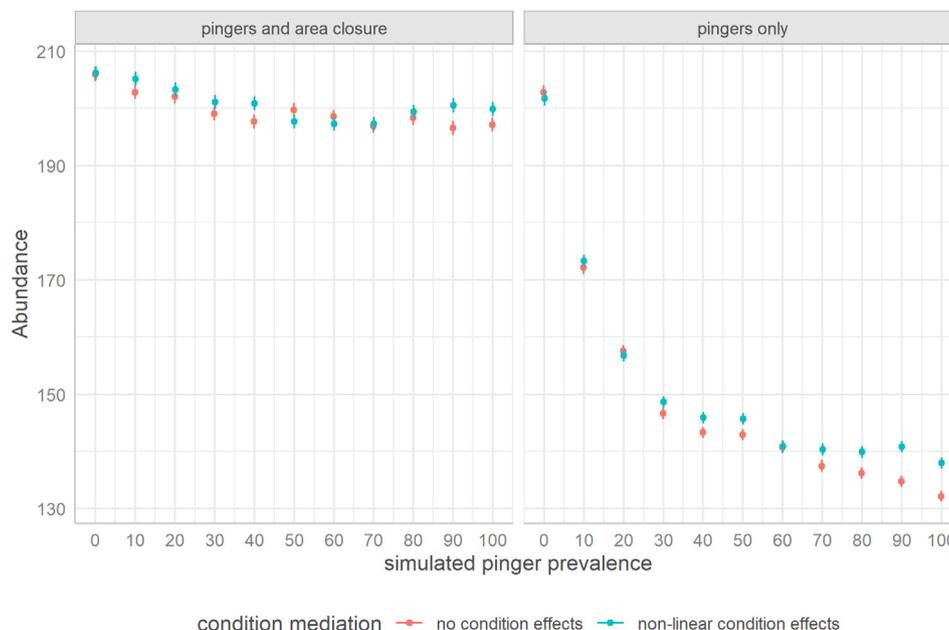


Fig. 2. Predicted effect of prevalence, condition mediation and scenario on harbour porpoise abundance when considering the last 20 years of simulations. Error bars are 95 % confidence intervals around the mean.

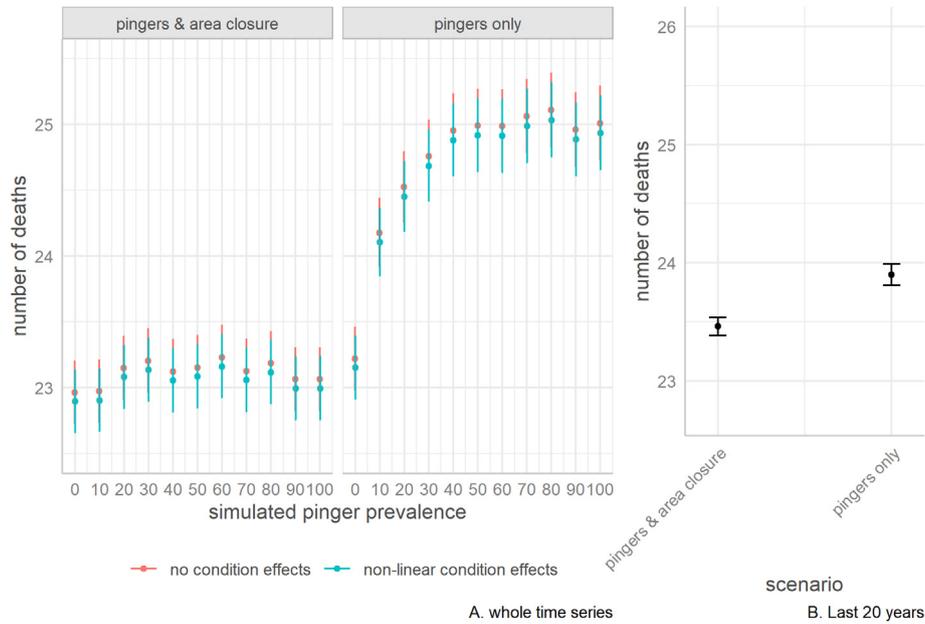


Fig. 3. Predicted average annual mortalities (all causes of death included) for the average annual abundance of each simulation set (offset model) depending on condition mediation, pinger prevalence and scenario when (A) estimated over the whole time series or (B) the last 20 years. The final model retained differed between these two time series conditions. Error bars are 95 % confidence intervals around the mean.

effects were more pronounced in the last 20 years of simulations (Fig. 2). Indeed, when we considered the death rate (Fig. 3, Tables S4–6), the model best describing annual mortalities differed substantially whether we considered the whole time series (Fig. 3a) or the last 20 years (Fig. 3b) which only detected a difference in annual mortalities between the two scenarios.

Bycatch rate changed non-linearly with pinger prevalence in both scenarios (Fig. 4, Tables S7–8). This non-linearity in bycatch rate is more pronounced in the “pingers only” scenario, in other words when bycatch risk is homogeneous across the landscape (Fig. 4). The effect of including condition mediation changes through the levels of pinger prevalence being more pronounced at lower levels.

Females produced calves at a constant rate throughout all simulation sets with predicted average of 3.13 calves (95 % CI: 3.126; 3.135, Table S9) born to a female by the time she reaches 8 years. Females’ lifetime reproductive success was also constant with a predicted 2.06 weaned calves produced on average by female porpoises in their lifetime (95%CI: 2.058; 2.072, Table S10). The rate at which these calves were successfully weaned depended on pinger prevalence and scenario (Fig. 5, Tables S11–S12). Overall, this rate is higher in the pinger only scenario. The weaning rate is also significantly lower when ≥ 90 % of nets have pingers and significantly higher when 10–30 % of nets have pingers.

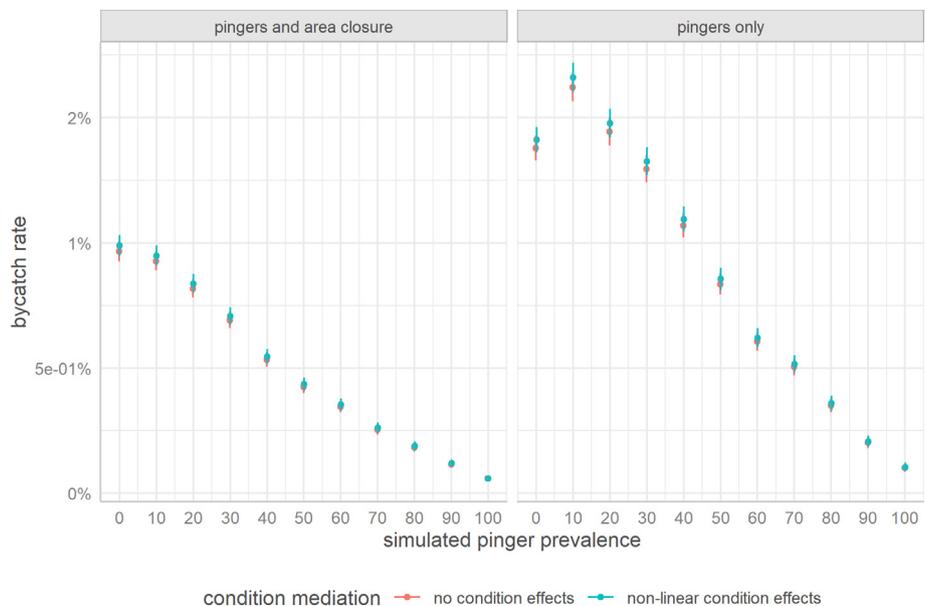


Fig. 4. Predicted annual bycatch rate, estimated as the proportion of individuals dying from bycatch annually out of the annual abundance, depending on condition mediation, pinger prevalence and scenario. Error bars are 95 % confidence intervals around the mean.

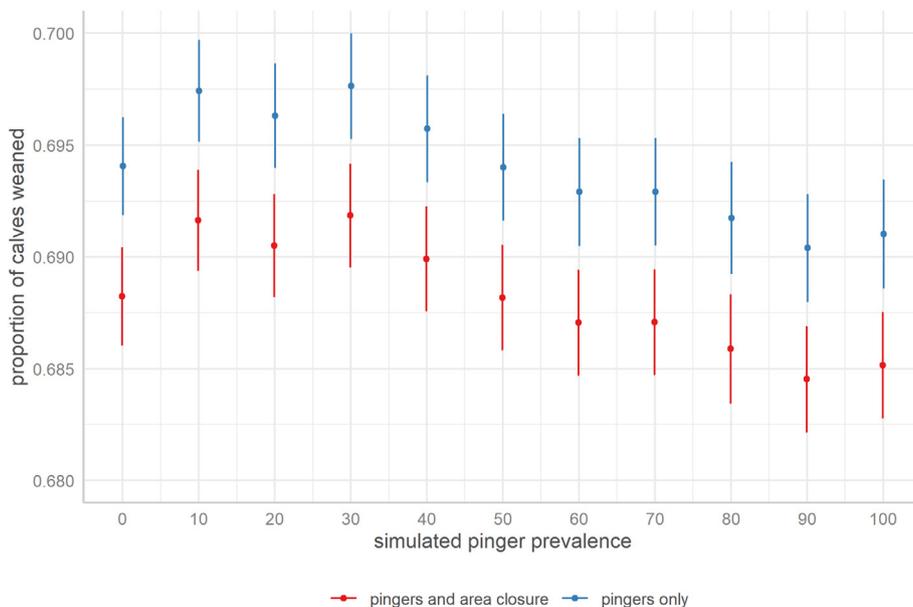


Fig. 5. Predicted proportion of calves born that are successfully weaned in the last 20 years of simulations depending on pinger prevalence and the scenario considered. Error bars are 95 % confidence intervals around the mean.

3.2. System transient dynamics

With an observed effect on abundance, it is important to know whether any of the simulation sets may lead to extirpation of the simulated populations. Here we find, given the simulated 40 years, that all simulation sets stabilise around non-zero attractive focus equilibria in the (abundance, porpoise energy) plane along the same isocline (Fig. S4). However, the engineering resilience of the system states varies with pinger prevalence, condition mediation implementation, and scenario (Fig. 6, Tables S13–14). The estimated basin of attraction is more resilient at zero pinger prevalence but we need to be careful that the absolute magnitude of engineering resilience may be caused by the tuning process rather than being an emergent property of the ecological system as the parameters relating energy to abundance are

tuned. When overall bycatch risk is not spatially segregated (“pingers and area closure” scenario) the system resilience does not change with pinger prevalence. In the other scenario, we may be observing critical slowdown (van Nes and Scheffer, 2007) at high pinger prevalence (the speed of the system becomes slower and more varied as we move away from the equilibria, 0 on the x-axis, with decreasing abundance). This indicates that in this tuned system, with the assumption of a given function relationship between condition and response to noise (Eq. 3), a pinger prevalence of 100 % may place the system in danger of a state shift, with alternative equilibria moving away from the current isocline (Fig. 6). However, we can see the difference in behaviour at 100 % prevalence between scenarios that did not have a condition effect and those that include one. When condition-mediation was considered, the resilience increases again at 100 %.

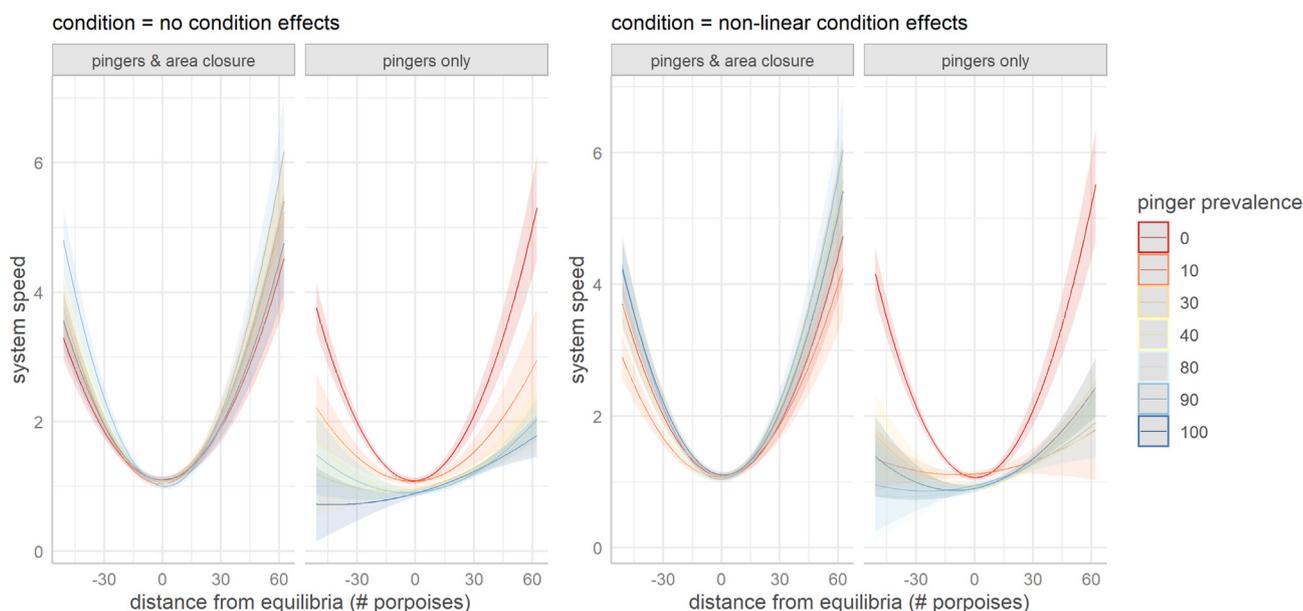


Fig. 6. Predicted speed of travel of the system, a proxy for engineering resilience and the shape of the equilibria’s basins of attraction along the abundance axis, given pinger prevalence, condition-mediation, and scenario. The ‘flatter’ the curve, the less resilient the system is. Error bars are 95 % confidence intervals around the mean.

4. Discussion

As George Box famously said, “all models are wrong, but some are useful”. So, what useful insights can we derive from this modelling study? Firstly, simulation outcomes depended on the inclusion of condition mediation, hence it would be important to retain this feature in future PCoD simulation platforms. To fully understand this mechanism, more experimental studies are needed to estimate dose response relationships for behavioural responses to noise exposure depending on an ecologically-relevant measure of body condition (Derous et al., 2020). Here we introduced condition mediation in a pre-tuned model limiting our capacity to assess the absolute magnitude of change in abundance and mortalities associated with condition mediation implementation. Our results are related to the system state, and its associated resilience, to which the model was tuned. We show how condition mediation influences the effect of pinger prevalence on population dynamics. In contrast, condition mediation did not affect mortality rate once the population was near equilibria, only pinger prevalence did. This indicates that, as also expected from theoretical and empirical studies, PCoD are more likely to emerge from condition-mediated effects on offspring production (Pirota et al., 2018; Allen et al., 2022). Here we assume a risk aversion effect of condition, as expected from theoretical and empirical work with species with the same life history traits as harbour porpoises. It is worth noting that recent meta-analyses do point to the possibility to have risk-taking responses to condition deterioration when we consider species across a broader taxonomic range (Moran et al., 2020). However, those meta-analyses did not fully explore the effect of life history strategies. Overall, this further points to the crucial need to empirically estimate how harbour porpoises respond to noise exposure depending on their condition. This is particularly salient as within cetaceans, harbour porpoises have a faster pace of life.

van Beest et al. (2017) did not explore the effect of pinger prevalence on population outcomes. Here we showed that bycatch rate increased at non-zero low pinger prevalence in contrast to the simulation of fisheries operating without pingers. This non-linear effect remained in the “*pingers and area closure*” scenario. It is anticipated that pingers at lower prevalence simply increase the movement, via displacement, of harbour porpoises leading them to increase their encounter probability with gillnet unequipped with pingers, and therefore increasing the overall bycatch risk. In the currently tuned model, it takes a prevalence of 30 % and above for the bycatch rate to start falling below conditions where there was no management interventions (20 % with time area closure implementation). We can therefore conclude that if pingers are implemented in a region they need to be consistently implemented over a significant proportion of the fleet in order to not be counter-productive. We anticipate this outcome to be consistent across a range of tuneable parameters, with varying effect size. It also means that the decision to implement pinger interventions needs to be warranted and implemented with a robust monitoring programme as poor compliance may result in increased bycatch. Current European legislation does not account for this indirect effect and in some cases limits pinger intervention only on part of the fleet (EU, 2019). This could have the unintended consequence to increase bycatch depending on the fishing effort covered by pinger deployment. The probability that pinger implementation in fisheries will yield reduced survival probability and reproductive outputs in the population depends on the functional relationship between individual harbour porpoise condition and their demographic contributions. This function is currently approximated, not informed by physiological studies, in a manner that may be useful when applying the precautionary principle to a single impact assessment (Nabe-Nielsen et al., 2018; Pirota et al., 2018) but which needs to be known more precisely if it is to impact management decisions on trade-offs between multiple or cumulative impacts (Pirota et al., 2022).

In our simulations the gillnet density, that is the fishing effort, leads to a decreased porpoise abundance as the pinger prevalence in gillnets increases, but a decrease that does not lead to extirpation of the population. Instead, simulated populations reach non-zero equilibria along the same (abundance, porpoise energy) isocline. This effect is lessened when we

allow individuals to have a condition-mediated response to pingers. Decreasing gillnet density in high porpoise density area, by introducing time-area closures, simply moves the intercept upwards on this relationship. Hence, while area closure can be a useful tool to decrease pinger density if PCoD elicited by pingers are likely to occur, they do not provide additional functional interventions on the porpoise-fishery system. That is, they do not affect the bycatch probability when a net is encountered but affect bycatch rate by decreasing net encounters. In our model, we assume that this decreased encounter does occur by designing the shift of fishing effort so that displaced effort is placed in low harbour porpoise density locations. Here, we assumed fisher behaviour's response to the area closure to have the maximum effect on net encounter probability in the model. Before area closure are implemented it is crucial to better understand fisher behaviour and the socioecological propensity to spatially and temporally shift fishing effort given that the main contribution of area closures to conservation objectives is through the displacement of fishing effort towards areas that are less used by porpoises. We therefore need to better understand the drivers of fisher behaviour in response to area closure. Fisheries microeconomics factors will influence whether fishers are likely to displace all their effort to nearby low bycatch risk areas. It is possible that costs would prevent them to do so or might jeopardise the sustainability of their activities (O'Keefe et al., 2014, 2021). These socioeconomic functions can be complex, with environmentally-associated inter-annual variation (Smith et al., 2020).

Noise-mediated pinger effects (van Beest et al., 2017) are impacting population abundance by decreasing the reproductive potential of individuals. While pinger prevalence influences mortality as the simulated populations move away from initial conditions, once the populations are closer to equilibria, mortality is only influenced by whether locations with high bycatch risk are not fished once we account for the cost of responding to pingers. However, when close to equilibria the proportion of weaned calves depends on pinger prevalence. In our tuned simulations, the proportion of weaned calves is higher at lower prevalence and significantly lower when pinger prevalence exceeds 80 %. As LRS and calf production is estimated to be constant, it is likely that the variation in the proportion of weaned calves can be explained by a selection towards females in better condition. That is, the increased mortality observed is biased towards females in poorer condition, and hence the population average weaning rate is increased by the removal of these females. Such indirect effects could act as selection pressure on the population, changing its phenotypic characteristics. It could also change its vital rates (e.g., age-at-first-reproduction); compensatory measures that are not functionally implemented in our models. Also, this may be the factor affecting the resilience of the simulated population, and hence its ability to cope with added stressors (Natrass and Lusseau, 2016).

In conclusion, we show here that pinger implementation can be an effective management intervention to reduce bycatch rate. However, we also show that when designing such a management intervention it is important to consider that this effectiveness depends on the deployment schedule. If compliance issues are anticipated, and difficult to address and redress, then a low pinger prevalence in nets has the potential to increase bycatch rate. At the same time, at high fishing effort, a high pinger prevalence could lead to PCoD elicitation if the affected population is in a physiological and an ecological context in which we can expect PCoD to emerge (Lusseau, 2014; Natrass and Lusseau, 2016), counteracting against the gains made from reduced bycatch rate. This latter effect is likely to be mediated by an influence on reproductive rate. Therefore, to detect this effect, it will be necessary to ensure that monitoring programmes include observations allowing to estimate this demographic parameter in addition to bycatch rate estimation. Moreover, as others have also concluded on multiple occasions (Booth et al., 2020), such a monitoring programme would aid in estimating PCoD more widely and help attribute the impact of multiple human marine activities on harbour porpoise conservation objectives. Such a framework would ensure that fisheries are not the sole bearer on management interventions to help achieve conservation objectives for these species.

Finally, this study informs more widely issues emerging with cumulative impacts of multiple stressors on coastal species. For marine species that react to noise and are at risk of bycatch, we need to consider the consequences of the interaction of these two stressors more fully. Coastal urbanisation and ambitious plans to develop offshore renewable energy plants is leading these species to change their habitat use in response to noise (Pirota et al., 2015). At the same time, these human activities can displace fisheries and therefore concentrate fishing effort and bycatch-sensitive species in smaller areas with the scope to increase bycatch rates without affecting bycatch probability. Also, pingers are not the sole mitigation techniques aiming to reduce bycatch by eliciting avoidance behaviour. Across bycatch-sensitive species, we now need to ensure that the deployment of deterrent devices does not lead to increased encounters with unmitigated fishing gear which would yield unintended increased total bycatch levels.

CRedit authorship contribution statement

David Lusseau: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Validation; Visualization; Writing - original draft; Writing - review & editing.

Lotte Kindt-Larsen: Conceptualization; Funding acquisition; Investigation; Methodology; Project administration; Resources; Supervision; Validation; Writing - review & editing.

Floris M. van Beest: Conceptualization; Investigation; Methodology; Resources; Software; Validation; Visualization; Roles/Writing - original draft; Writing - review & editing.

Data availability

Code is available at <https://github.com/dlusseau/DEPONS> and the simulation outcomes used in these analyses is available at doi:10.11583/DTU.19455554.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.158936>.

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