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Predicting the population-level impact of mitigating harbor porpoise bycatch with pingers and time-area fishing closures

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Abstract. Unintentional mortality of higher trophic-level species in commercial fisheries (bycatch) represents a major conservation concern as it may influence the long-term persistence of populations. An increasingly common strategy to mitigate bycatch of harbor porpoises (*Phocoena phocoena*), a small and protected marine top predator, involves the use of pingers (acoustic alarms that emit underwater noise) and time-area fishing closures. Although these mitigation measures can reduce harbor porpoise bycatch in gillnet fisheries considerably, inference about the long-term population-level consequences is currently lacking. We developed a spatially explicit individual-based simulation model (IBM) with the aim to evaluate the effectiveness of these two bycatch mitigation measures. We quantified both the direct positive effects (i.e., reduced bycatch) and any indirect negative effects (i.e., reduced foraging efficiency) on the population size using the inner Danish waters as a biological system. The model incorporated empirical data on gillnet fishing effort and noise avoidance behavior by free-ranging harbor porpoises exposed to randomized high-frequency (20- to 160-kHz) pinger signals. The IBM simulations revealed a synergistic relationship between the implementation of time-area fishing closures and pinger deployment. Time-area fishing closures reduced bycatch rates substantially but not completely. In contrast, widespread pinger deployment resulted in total mitigation of bycatch but frequent and recurrent noise avoidance behavior in high-quality foraging habitat negatively affected individual survival and the total population size. When both bycatch mitigation measures were implemented simultaneously, the negative impact of pinger noise-induced sub-lethal behavioral effects on the population was largely eliminated with a positive effect on the population size that was larger than when the mitigation measures were used independently. Our study highlights that conservationists and policy makers need to consider and balance both the direct and indirect effects of harbor porpoise bycatch mitigation measures before enforcing their widespread implementation. Individual-based simulation models, such as the one presented here, offer an efficient and dynamic framework to evaluate the impact of human activities on the long-term survival of marine populations and can serve as a basis to design adaptive management strategies that satisfy both ecological and socioeconomic demands on marine ecosystems.

Key words: acoustic alarms; agent-based model; bycatch; cetaceans; disturbance; gillnet fisheries; marine mammals; *Phocoena phocoena*; population dynamics; time-area fishing closures; underwater noise.

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INTRODUCTION

A major concern in the successful conservation of marine systems is fisheries bycatch (Kappel 2005, Komoroske and Lewison 2015). Fisheries bycatch is the unintentional injury or mortality of marine species, which occurs globally in all commercial fishing operations (Hall et al. 2000, Lewison et al. 2004a, Read et al. 2006). Marine populations that are subject to bycatch can decline over relatively short timescales when unintentional mortality exceeds the population growth rate (Caswell et al. 1998, D'agrosa et al. 2000). Because life-history traits of marine vertebrates (marine mammals, sea birds, sea turtles, sharks) include relatively low reproductive rates and late age at maturity, they are particularly vulnerable to bycatch mortality (Brothers 1991, Baum et al. 2003, Dans et al. 2003, Lewison et al. 2004b).

The harbor porpoise (*Phocoena phocoena*) is a small marine top predator subject to bycatch in commercial gillnet fisheries throughout its distribution, the cold temperate waters of the Northern Hemisphere (Jefferson and Curry 1994, Read et al. 2006). The species is protected in the United States (U.S.) through the Marine Mammal Protection Act of 1972 and in the European Union (EU) through Annex II and IV of the Habitats Directive of 1992. Various mitigation measures exist to mitigate harbor porpoise bycatch in gillnets. For example, designated areas can be closed temporarily for commercial fishing activity (time-area fishing closures) or acoustic alarms (pingers) can be attached to gillnets. Pingers typically emit high-frequency sound pulses intended to spatially deter porpoises and reduce the risk of entanglement (Dawson et al. 2013). Arguably, the best-known experimental and empirical case studies addressing harbor porpoise bycatch in gillnet fisheries have been done in the Gulf of Maine region in the United States (e.g., Kraus et al. 1997, Murray et al. 2000). There, the implementation of time-area fishing closures and thereafter the use of pingers on gillnets coincided with a reduction in bycatch of harbor porpoises from ~2900 individuals/yr in 1990 to 323 individuals/yr in 1999 (Read 2013). This trend is generally considered a conservation success story. However, it remains unclear whether the mitigation measures were the main cause of the reduction in harbor porpoise bycatch or whether the trend was confounded by

effort controls in the fishery industry itself (Geijer and Read 2013). Moreover, data on changes in the harbor porpoise population size during the study period were scant, inhibiting conclusions about the population-level consequences of reduced bycatch rates and employed mitigation measures (General Accountability Office 2008).

Despite great experimental success in reducing marine vertebrate bycatch with a variety of pinger types (see Dawson et al. 2013 for a review), there is growing concern that underwater noise in general can be harmful for marine vertebrate species (Francis and Barber 2013, Nowacek et al. 2015). This concern is especially pertinent for harbor porpoises as it is highly susceptible to anthropogenic disturbances (Wisniewska et al. 2016). For example, underwater noise from seismic surveys and ships can disrupt the natural behavior of harbor porpoises (Pirotta et al. 2014, Dyndo et al. 2015), which may convey energetic costs through reduced foraging efficiency (Pirotta et al. 2014). Because harbor porpoises must feed extensively to support their high metabolic demands (Wisniewska et al. 2016), prolonged declines or recurrent disruptions in energy acquisition rapidly increase the risk of starvation (Kastelein et al. 1997, Lockyer et al. 2003). Thus, it seems plausible that where pingers are widely deployed across seascapes, including high-quality harbor porpoise habitat, foraging success of individuals can be frequently undermined with potential deleterious effects on populations. To our knowledge, no empirical data exist that can test this hypothesis as it requires long-term data over large spatial scales in order to link sub-lethal noise-induced behavioral changes of individuals to population dynamics.

An urgent need exists to develop predictive ecological models that can assess the impact of human activities on the long-term survival of species and to design strategies that can remedy any negative impact (Sutherland et al. 2004, Crain et al. 2008). Particularly suited for this purpose are spatially explicit individual-based simulation models (IBMs) as they can be parameterized to incorporate realistic animal movement patterns (Tang and Bennett 2010), life-history traits, individual variation in energy budget (Sibly et al. 2013), and noise avoidance/disturbance behavior (Nabe-Nielsen et al. 2014). Moreover, IBMs offer a mechanistic framework to evaluate the efficacy of

conservation strategies designed to offset any negative impact of human activities on animal populations (Wood et al. 2015). Our aim was to develop a spatially explicit IBM that can be used to evaluate the long-term, population-level consequences of mitigating harbor porpoise bycatch with pingers and time-area fishing closures. To do so, we extended an existing IBM developed for the harbor porpoise population in the inner Danish waters (IDW; Nabe-Nielsen et al. 2014) by incorporating empirical data on gillnet fishing effort and pinger noise avoidance behavior of free-ranging harbor porpoises. Harbor porpoise bycatch in gillnets occurs regularly within the IDW (International Council for the Exploration of the Sea [ICES] 2015), yet pinger use is infrequent and time-area fishing closures are not yet implemented in the area. As such, we aimed to evaluate the efficacy of pingers and time-area fishing

closures as a harbor porpoise bycatch mitigation strategy in the IDW by quantifying the direct and indirect effects of both bycatch mitigation measures on the population as a whole.

MATERIALS AND METHODS

Study area

The study area (Fig. 1a) covered the IDW including Kattegat (57°50' N, 10°80' E), Great Belt (55°20' N, 10°58' E), Little Belt (55°23' N, 9°43' E), and the western Baltic Sea (54°50' N, 12°50' E). Most of the IDW has water depths of ~10–30 m, with maximum depths of 50 m in Kattegat. Harbor porpoises are present in all parts of the IDW and the area hosts a distinct population (Sveegaard et al. 2015). Porpoise abundance in the area varies spatially between seasons (Edrén et al. 2010). Porpoises in the IDW prey predominantly

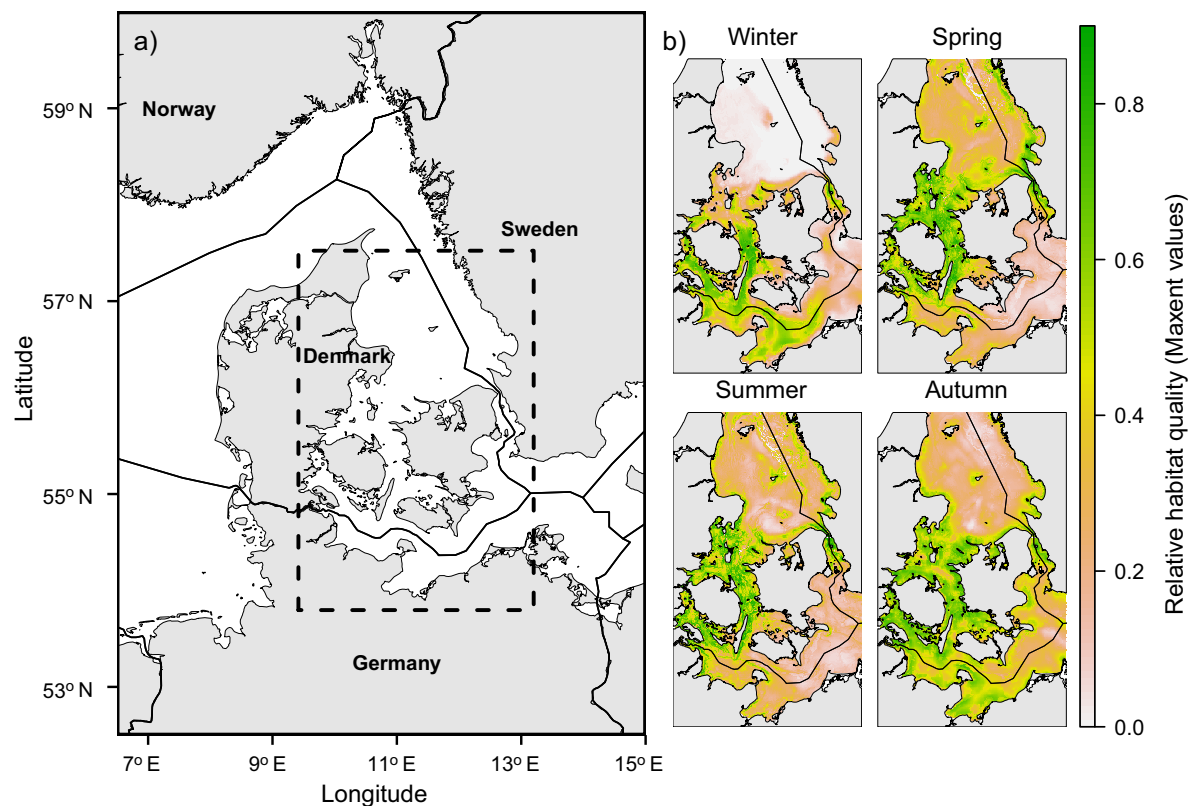


Fig. 1. Map of the study area (a) with the dashed square highlighting the extent of the inner Danish waters (IDW) used in the individual-based simulation model and (b) spatiotemporal variation in harbor porpoise density/habitat quality within the IDW using season-specific maximum entropy (Maxent) maps (modified and reproduced with permission from Edrén et al. 2010).

on small Atlantic herring (*Clupea harengus* L. 1758) and a variety of Gadidae species (Börjesson et al. 2003).

Overview of the individual-based model

Our IBM builds on the general ecological assumption that food availability is a limiting factor of animal population growth (McNab 1980) and on the simple decision rule that individuals attempt to optimize their foraging behavior, and hence to maximize Darwinian fitness (Sibly and McFarland 1976). Most processes, scheduling, and design concepts in our IBM (Fig. 2) are identical to the IBM presented in Nabe-Nielsen et al. (2014). Therefore, we describe only key elements of the IBM below with a focus on the new and updated elements, and refer to Nabe-Nielsen et al. (2013) for a detailed description on the fine-scale movement behavior and spatial memory of the porpoise agents and to Nabe-Nielsen et al. (2014) for more detailed descriptions of the energy models, life-history parameters, and a full overview, design concepts, and details description (Grimm et al. 2010).

Porpoise agents and food availability

Porpoise agents are characterized by their location, speed and direction of movement, age, energy level, and reproductive status. Porpoise agents move and forage in a landscape that is identical to the IDW (Fig. 1a) with home range sizes and dispersal patterns that are equal to those observed for free-ranging individuals in the area (Nabe-Nielsen et al. 2013). The combined movements of all individual porpoise agents produce the same spatiotemporal distribution patterns in the IDW as found by Edrén et al. (2010; Fig. 1b). All porpoise agents spend energy as they move, but gain energy when encountering food. The amount of food consumed by an individual agent decreases as its energy level increases. The food is patchily distributed throughout the landscape. The energy level of a food patch decreases when a porpoise agent consumes food, but afterward it gradually replenishes. As such, the amount of food in patches is dynamically changing (Nabe-Nielsen et al. 2014). Pinger noise in the IBM did not influence the distribution of food patches as catch rates of most commercial target fish species (i.e., prey for porpoises) appear to be largely unaffected by the use of pingers (Trippel et al. 1999,

Gearin et al. 2000, Culik et al. 2001, Carlström et al. 2002). Furthermore and for Atlantic herring specifically, contrasting evidence has been found (Kraus et al. 1997, Culik et al. 2001).

Free-ranging harbor porpoises display extremely high feeding rates, which is due to their high metabolic demand as compared to other cetacean species (Wisniewska et al. 2016). A short period without feeding (>3 d) can already reduce body mass and chances of survival (Kastelein et al. 1997). As such, when the energy level of a porpoise agent decreases for three consecutive days, it disperses to an area with high potential food levels (i.e., porpoise agents have a spatial memory) in an attempt to increase foraging success. Once every day, and depending on age, age of maturity, season, and current energy levels, a porpoise agent may die, mate, give birth, or become pregnant (Fig. 2). Hence, the population size in the IBM emerges from a balance between mortality, through bycatch or natural causes such as starvation (Koopman et al. 2002, Thompson et al. 2007), and reproduction, both of which are influenced by individual energy levels. Values of parameters influencing life-history traits/strategy (e.g., age of maturity, gestation time) and energetics (e.g., energy use in warm and/or cold waters, energy use while lactating) of porpoise agents were derived from published literature or empirical data and are presented in Nabe-Nielsen et al. (2014). Porpoise agents do not learn from experiences of others and interact only indirectly via competition for food. Because the absolute population size of harbor porpoises in the IDW is unknown, each porpoise agent represents several real-world porpoises and the carrying capacity (i.e., baseline population size) in the IBM is lower than in reality. Differences in population sizes between model scenarios (Table 1) are therefore measured on a relative scale (i.e., percentage change in mean population size) instead of on an absolute scale.

Calibration of porpoise agents' response to pinger noise

The IBM of Nabe-Nielsen et al. (2014) includes a generic framework to model underwater noise avoidance behavior of harbor porpoises. The framework consists of four parameters: the impact factor (unitless measure of sound strength at the noise source), deterrence distance (parameter

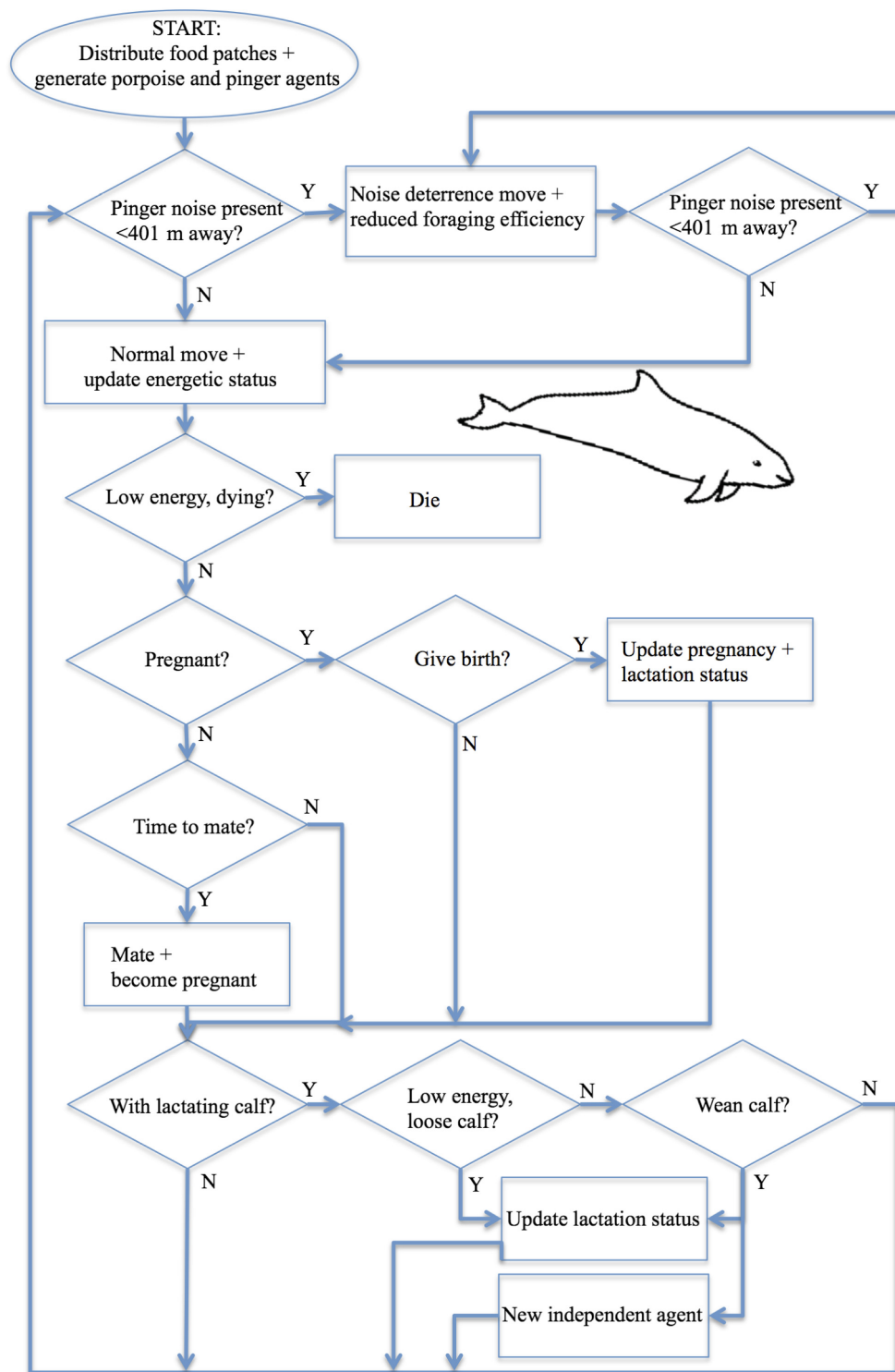


Fig. 2. Simple flow diagram of the individual-based simulation model highlighting the main processes and decisions made by all porpoise agents during each time step in a simulation. Diamond-shaped symbols indicate decisions made by porpoise agents, and rectangles indicate calculations (see Nabe-Nielsen et al. 2014 for details).

controlling the distance [m] at which agents respond to noise), deterrence coefficient (unitless parameter controlling the strength of deterrence at the source), and deterrence time (number of 30-min time steps the deterrence effect lasts after the noise has disappeared). The deterrence behavior (i.e., the porpoise agents' tendency to move away from a noise source; Fig. 2) decreases linearly with the distance from the sound source, and after the noise disappears, the bias in movement away from the sound source gradually disappears (i.e., residual deterrence). In general, noise avoidance behavior has a negative effect on the energy level of porpoise agents as any foraging activity is interrupted and deterrence movements lead to increased energy expenditure.

Here, we updated the generic noise avoidance framework of Nabe-Nielsen et al. (2014) to ensure that porpoise agents responded to pinger noise with deterrence movements that lead to temporary declines in harbor porpoise densities in the vicinity of active pingers as observed in nature. To do so, we conducted a field study in Jammerland Bay, Denmark, using passive acoustic monitoring. We placed a single AQUAmark100 pinger, producing randomized broadband high-frequency (20- to 160-kHz) signals (Aquatec Group Ltd., www.aquatecgroup.com), at the center of an array of porpoise click detectors (C-PODs, www.chelonia.co.uk). The AQUAmark100 pinger was chosen as it is known to reduce harbor porpoise bycatch in the Danish North Sea to 0% (Larsen et al. 2013, Larsen and Eigaard 2014). C-PODs were spaced at 0, 400, 800, and 1600 m from the center (pinger location). An internal clock activated the pinger in cycles of 23 h on (with noise) and 23 h off (without noise). Each cycle was repeated

23 times and porpoise clicks were recorded by the C-PODs during all cycles (total of ~44 data recording days). The field data showed a reduction in the number of porpoise clicks at distances ≤ 400 m when the AQUAmark100 pinger was on (Fig. 3a). The mean decline in number of porpoise clicks recorded was 85.5% (range: 80.4–91.6%) and 52.1% (47.5–57.6%) at 0 and 400 m distances (Tukey's honest significant difference [HSD] test: $P < 0.05$) and 30% (24.8–39.4%) and 11% (9.2–14.4%) at 800 and 1600 m distances, respectively (Tukey's HSD: $P > 0.05$; Fig. 3b).

To ensure that the porpoise densities decreased with distance to the pingers in the same way in the IBM as they did in the field experiment, the observed changes in harbor porpoise clicks during pinger on/off cycles were used directly to calibrate noise avoidance behavior of porpoise agents in the IBM. To do so, we calibrated the impact factor using pattern-oriented modeling (POM; Grimm et al. 1996, Kramer-Schadt et al. 2007). We selected the impact factor for calibration, as this was the pinger noise parameter that had the largest influence on model results (see sensitivity analysis, Appendix S1: Fig. S1). We used deterrence distance = 300 m, deterrence coefficient = 7.6, and deterrence time = 2.5 h, as these values had yielded realistic declines in number of porpoises with distance from the sound source in a different study (Nabe-Nielsen et al. 2014). After calibration of the impact factor, these parameter values proved to be suitable in this study as well. The POM was performed by building the Jammerland Bay seascape (40 × 40 km) within the IBM. We used the same locations for the pinger and C-PODs as in the field study and the same pinger on/off time cycles. All simulations

Table 1. Overview of the simulation scenarios performed in the IBM.

Scenario name	Gillnet agents	Bycatch rate (% per yr)	Pinger noise	Time-area closures
Baseline	Excluded	0	Off	Excluded
Bycatch contemporary	Included	1.19†	Off	Excluded
Bycatch worst-case	Included	5.02†	Off	Excluded
Pinger use only	Included	0‡	On	Excluded
Time-area closures and bycatch contemporary	Included	0.84§	Off	Included
Time-area closures and bycatch worst-case	Included	3.70§	Off	Included
Pinger use and time-area closures	Included	0‡	On	Included

Notes: Each scenario (40 simulation years) was replicated 10 times. IBM, individual-based simulation model.

† Bycatch rate was calibrated (Appendix S4: Fig. S1).

‡ Bycatch rate was set to 0% per yr based on the available literature for the AQUAmark100 pinger (Larsen and Eigaard 2014).

§ Bycatch rate was calculated based on model output.

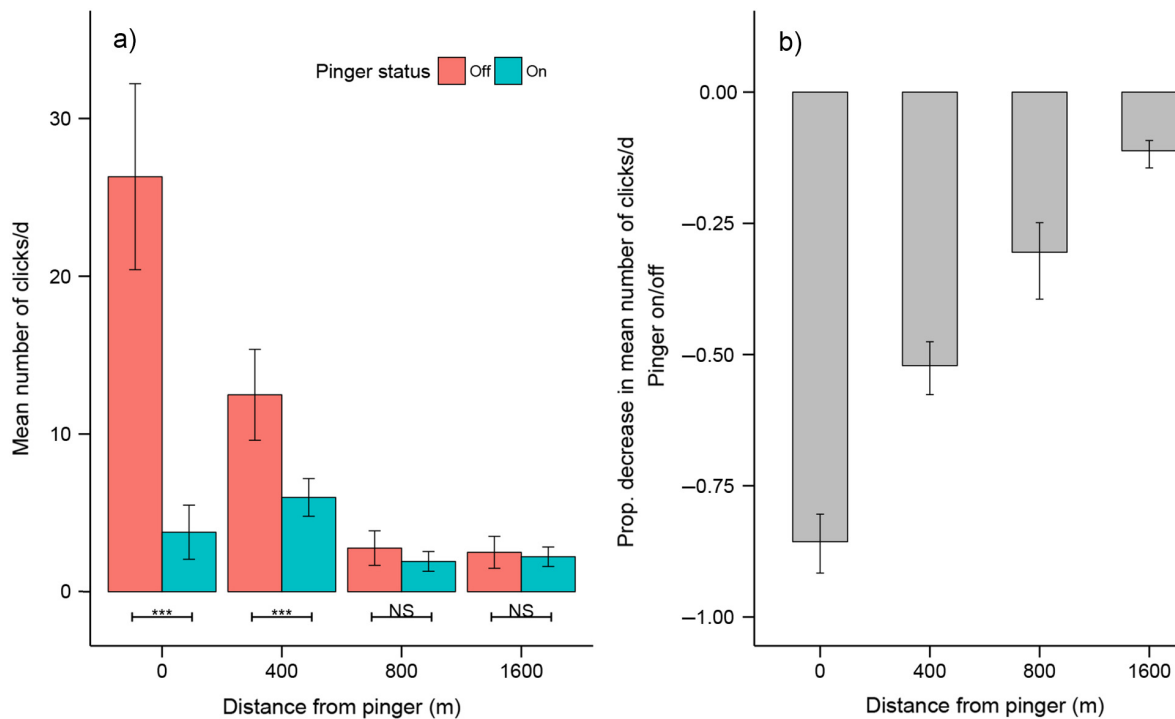


Fig. 3. Results of a field experiment in Jammerland Bay, Denmark, testing the effect of the AQUAmark100 pinger on harbor porpoise echolocation activity. Panels show the absolute (a) and proportional (b) change in mean daily number of porpoise clicks recorded during pinger on/off cycles as a function of distance from the pinger. NS indicates no significant difference in clicks between pingers on and off cycles.

in the POM procedure covered two simulation years and were replicated 100 times. The data collected in the first simulation year were discarded to allow for a stable population size to emerge (burn-in period). We recorded and used the number of porpoise agents present in the different distance classes from the pinger for each simulation as a proxy for porpoise clicks given that porpoise click frequency is strongly correlated with porpoise density (Kyhn et al. 2012). We ran a series of simulations with a range of values for the impact factor with the aim to find the value that correctly reproduced the results of the field study with the AQUAmark100 pinger. The results of the POM procedure (Appendix S2: Fig. S1) revealed that an impact factor of 3 resulted in the same relative reduction in porpoise density at different distances from active pingers as observed in the field (Fig. 3). Habituation to pinger noise is currently not included in the IBM as field studies thus far (including our own experiment at Jammerland Bay as described above) have not provided evidence that

porpoises habituate to the broadband randomized signals emitted by the AQUAmark100 (Kindt-Larsen 2015), although habituation may occur with signals emitted by other pinger types (Cox et al. 2004, Kyhn et al. 2015).

Gillnet agents

Gillnet agents are characterized by their location (Universal Transverse Mercator coordinates), soak time (start/end time in hours), bycatch probability value, and pinger noise level (i.e., impact factor of 3 as calibrated in the previous section). When a porpoise agent enters a cell (400×400 m; the resolution of the IBM seascape) occupied by a gillnet agent and without pinger noise, it has a certain probability of dying as a result of bycatch (details on how this was calibrated are described below). If n gillnet agents are present in a cell, the bycatch probability calculation is repeated n times. As such, gillnet agents have a negative effect on the population size through direct mortality. When a gillnet agent is

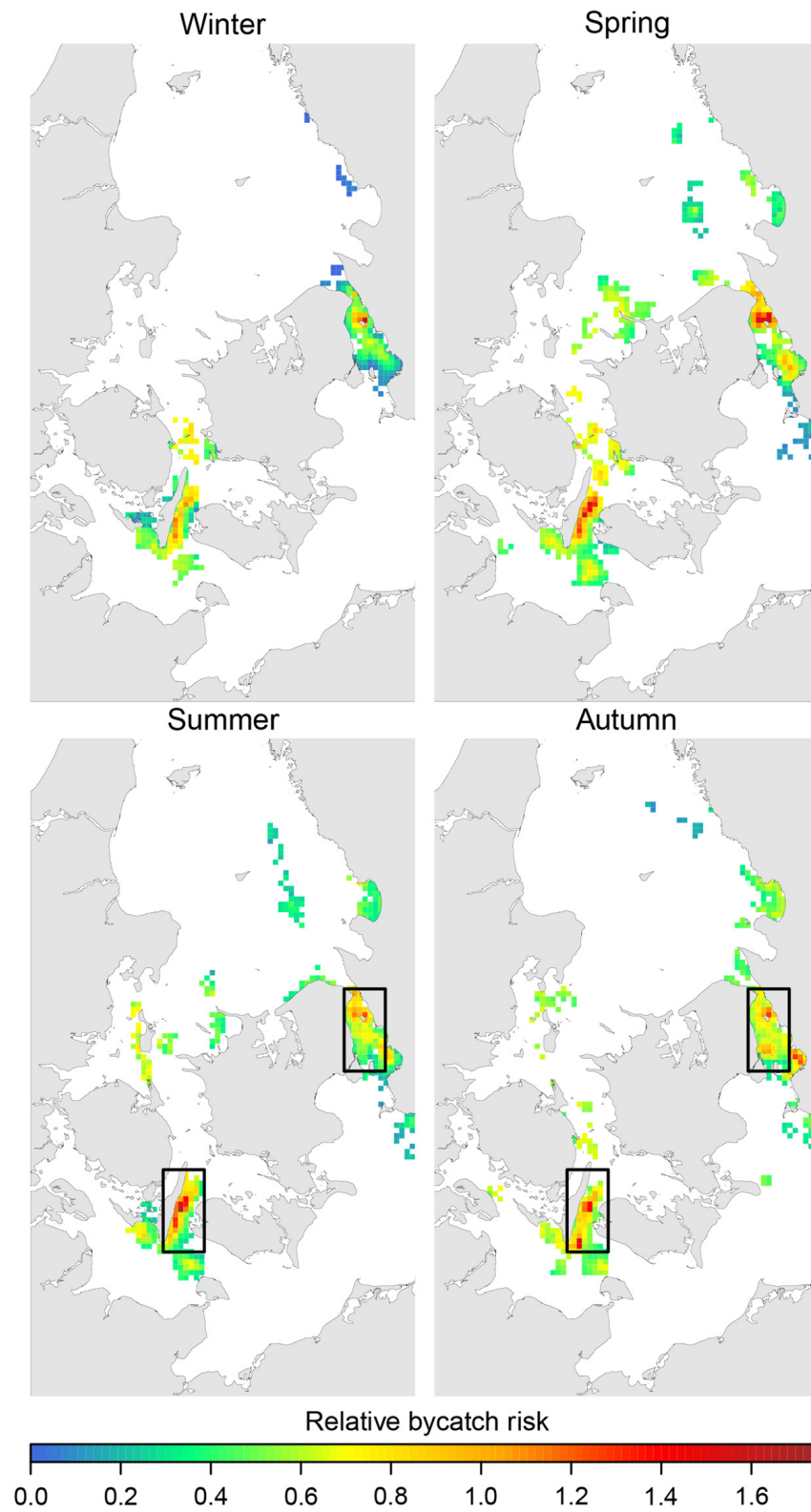


Fig. 4. Spatiotemporal variation in relative bycatch risk of harbor porpoises in the inner Danish Waters

(Fig. 4. Continued)

calculated by taking the sum of the mean harbor porpoise density value (Fig. 1b) and the scaled fishing effort value (see Appendix S3: Fig. S1 and text for details) in each 3×3 km cell. The black outlines in the summer and autumn panels indicate the two time-area fishing closures used in the individual-based simulation model simulations (Table 1).

fitted with a pinger, it emits noise and the probability of bycatch is 0% as the available empirical evidence for the AQUAmark100 pinger suggests (sensu; Larsen et al. 2013, Larsen and Eigaard 2014). The spacing between pingers on gillnet agents is 400 m, which is slightly below the maximum pinger spacing distance of 455 m set by the Danish Fisheries Directorate in 2007 (see Larsen et al. 2013). In few cases (<1%), multiple pingers occurred in the same 400×400 m cell, as two or more vessels deployed gillnets in the same area at the same time.

To determine the number, length, location, and soak time of gillnet agents in the IBM seascape as realistically as possible, we collated data on gillnet fishing activity within the IDW by Danish and Swedish vessels (based on Vessel Monitoring System [VMS] data, Global Positioning System data, and logbook information; see Appendix S3). German vessels were not considered due to confidentiality concerns with the German VMS data. We included all fishing locations of large (≥ 12 m) gillnet vessels (six Danish vessels and three Swedish vessels) and small (<12 m) Swedish gillnet vessels ($n = 16$) known to operate in the IDW during 2014 (Appendix S3: Fig. S1). Data on fishing activity of small Danish gillnet vessels are not systematically recorded so we relied on fishing activity data provided by 10 small Danish gillnet vessels as part of a marine mammal bycatch monitoring project in the IDW (Olesen et al. 2015). These 10 vessels comprise approximately 21% of the total cod quota landed by small Danish gillnet vessels in the IDW (The Danish AgriFish Agency and Ministry of Environment and Food 2015). A more detailed description of the processing of gillnet fishing activity data is provided in Appendix S3.

The current annual bycatch rate of harbor porpoises in the IDW is estimated to be within 0.61–1.22% (ICES 2015). To reproduce this level of bycatch in IBM simulations, we assigned a bycatch probability value of 0.0011 to each gillnet agent (Video S1). This value was selected based on a calibration process in which we tested a range of

bycatch probability values using 25 simulation runs of 10 yr for each tested value. The selected value of 0.0011 produced a mean population-level bycatch rate of 1.19% per yr (Appendix S4: Fig. S1). Besides the upper ICES bycatch rate estimate, we also considered a bycatch probability value of 0.0046 for each gillnet agent. This value produced a mean annual population-level bycatch rate of 5.02% per yr (Appendix S4: Fig. S1). We considered this bycatch level a worst-case scenario as higher bycatch rates lead to unstable population sizes or extirpation (sensu: Nabe-Nielsen et al. 2014).

Time-area fishing closures

Time-area fishing closures are most effective when implemented in areas and periods with the highest bycatch risk (Murray et al. 2000). Harbor porpoise bycatch risk in the Danish part of the North Sea is known to increase with harbor porpoise density and gillnet fishing effort (Kindt-Larsen et al. 2016). As such, we calculated bycatch risk in the IDW based on the seasonal harbor porpoise density maps (Fig. 1b) and the fishing effort data used to create gillnet agents (see *Gillnet agents* and Appendix S3: Fig. S1). To do so, we placed a grid consisting of 3×3 km cells over the study area and calculated for each season and cell the mean porpoise density value (value between 0 and 1, see Fig. 1b). Fishing effort was also calculated for each season and cell by aggregating the number of fishing locations weighted by their soak time. We scaled fishing effort to lie within 0 and 1 as for the density values. Bycatch risk was then estimated seasonally by taking the sum of both the fishing effort and harbor porpoise density in each cell (value between 0 and 2; Fig. 4).

Based on the harbor porpoise bycatch risk maps (Fig. 4), we selected two distinct areas (both 1500 km^2) in which we banned all gillnet fishing activity during both summer (June–August) and autumn (September–November). The time period of the closures was based on energy intake of lactating females, which is

highest during summer and autumn (Lockyer et al. 2003). Although the size of the time-area closures was arbitrary, they were sufficiently large to include most sites (cells) with the highest bycatch risk, which is necessary to ensure fishing closures are effective (Murray et al. 2000). All known fishing locations within the time-area closures were relocated to the nearest known fishing ground in the vicinity of the closures. As such, time-area fishing closures did not lead to a reduction in fishing effort but instead fishing effort was redistributed over space and time, with the greatest increase in effort in the surroundings of the time-area closures.

Simulation scenarios

Once all parameter values were calibrated, gillnet agents were created, and time-area fishing closures were selected, we were able to run a variety of scenarios in the IBM to evaluate the population-level consequences of mitigating harbor porpoise bycatch with pingers and time-area fishing closures (Table 1). We ran a total of seven IBM scenarios (10 simulation repetitions of 40 yr for each scenario) with different bycatch rates (contemporary or worst-case), pinger use (on or off), and time-area fishing closures (included or excluded). The baseline scenario did not include gillnet agents and pinger noise, thus providing simulation data on the porpoise agent population size in the absence of any human disturbance (Table 1).

The population size and dynamics in the baseline scenario stabilized within the first 10 simulation years. We therefore computed the mean (\pm standard deviation: SD) annual population size over simulation years 11–40 for each scenario. Because the population size in the IBM is on a relative scale, we calculated the percentage change in mean annual population size among simulation scenarios. Spatiotemporal variation in bycatch of porpoise agents was calculated and visualized with the same grid of 3×3 km cells used to identify the time-area fishing closures. For each cell, we calculated the sum of the number of porpoise agents bycaught over simulation years 11–40.

RESULTS

The baseline scenario without bycatch, pingers, and time-area fishing closures (Table 1) had

a simulated population size of 246 ± 11.9 (mean \pm SD) individuals/yr (Fig. 5a). The contemporary bycatch scenario, with an annual bycatch rate of $1.19\% \pm 0.18\%$ (Table 1, Fig. 5b), had a population size of 230 ± 11.1 individuals/yr (Fig. 5a), corresponding to a 6.5% decline in population size compared to the baseline scenario. When considering an annual bycatch rate of $5.02\% \pm 0.55\%$ (our worst-case bycatch scenario; Table 1, Fig. 5b), the mean annual population size was 178 ± 7.83 individuals/yr (Fig. 5a), corresponding to a 28% decline in population size compared to the baseline scenario. Bycatch of porpoise agents varied spatially and between seasons and was consistently highest in areas with the highest bycatch risk (Fig. 4 and Appendix S5: Figs. S1, S2 for the contemporary and worst-case bycatch scenarios, respectively).

The pinger use-only scenario with an annual bycatch rate of 0% had a mean population size of 195 ± 9.53 individuals/yr (Fig. 5a). This was 15.2% lower than in the contemporary bycatch scenario but 8.7% higher than in the worst-case bycatch scenario.

When implementing time-area fishing closures into the contemporary bycatch scenario, the mean population size was 237 ± 10.85 individuals/yr (Fig. 5a), which was 2.9% higher than in the contemporary bycatch scenario and 3.6% lower than in the baseline scenario. Even though fishing effort in the landscape remained constant, implementing time-area fishing closures in this scenario reduced the mean annual bycatch rate from $1.19\% \pm 0.18\%$ to $0.84\% \pm 0.18\%$ (Table 1, Fig. 5b). However, the redistribution of fishing effort over space during summer and autumn (when time-area closures were implemented) led to an increase in the absolute number of porpoise agents' bycaught in the vicinity of the time-area closures (Appendix S5: Fig. S3). Implementing time-area fishing closures into the worst-case bycatch scenario reduced the annual bycatch rate from $5.02\% \pm 0.55\%$ to $3.7\% \pm 0.36\%$ (Table 1, Fig. 5b) and increased the absolute number of porpoise agents' bycaught in the vicinity of the time-area closures (Fig. 6). This scenario had a mean population size of 200 ± 8.83 individuals/yr (Fig. 5a), which was 11.0% higher than in the worst-case bycatch scenario without time-area closures and 18.6% lower than in the baseline scenario.

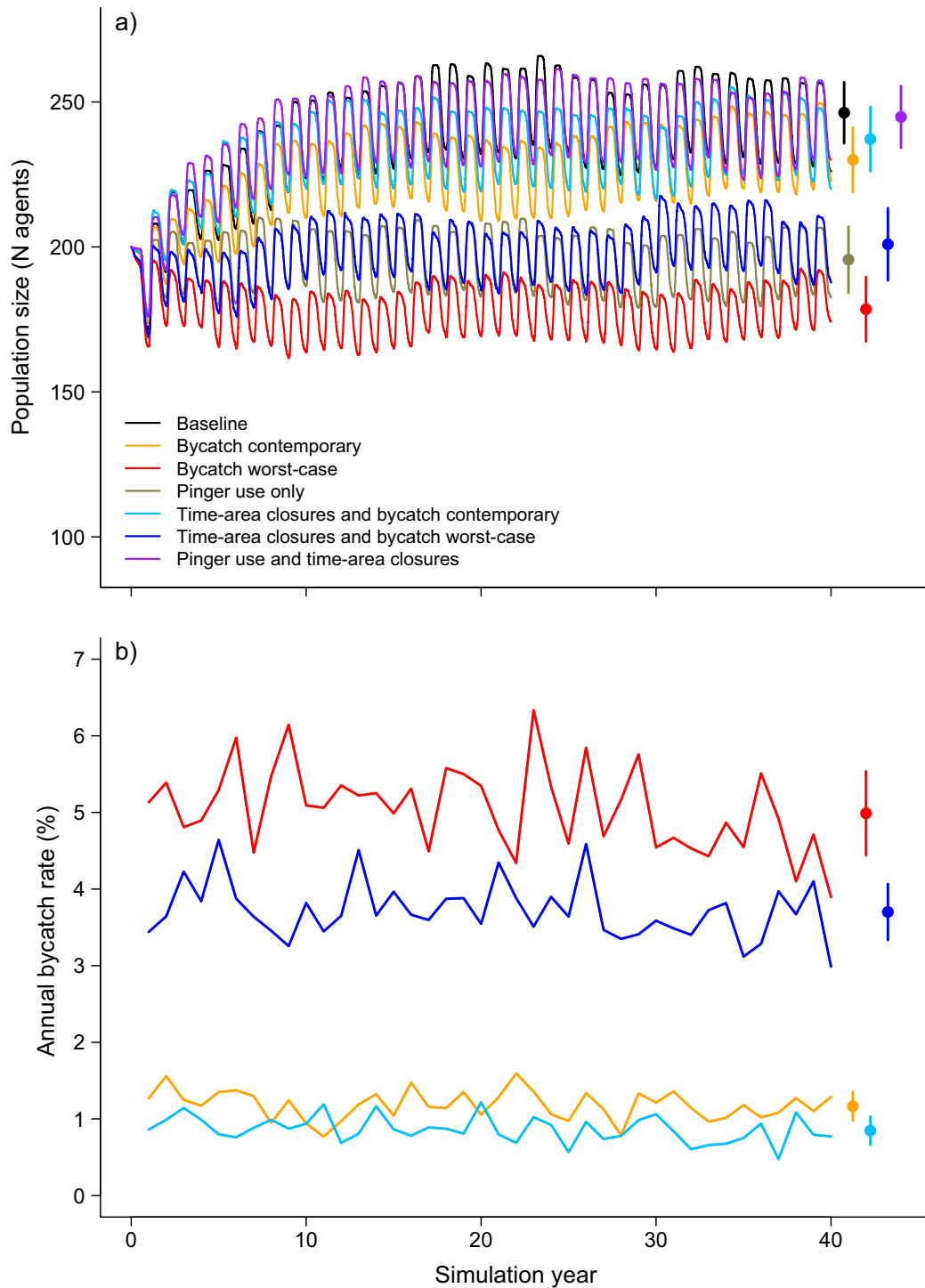


Fig. 5. Output of the individual-based simulation model simulations (Table 1) showing (a) the daily population size (N porpoise agents) for all seven simulation scenarios and (b) the annual bycatch rate for the four simulation scenarios with bycatch and time-area fishing closures included. The mean ± 1 standard deviation population size provided at the end of each line was calculated based on daily population sizes in simulation years 11–40 to exclude a 10-yr burn-in period in which the size of the population stabilized.

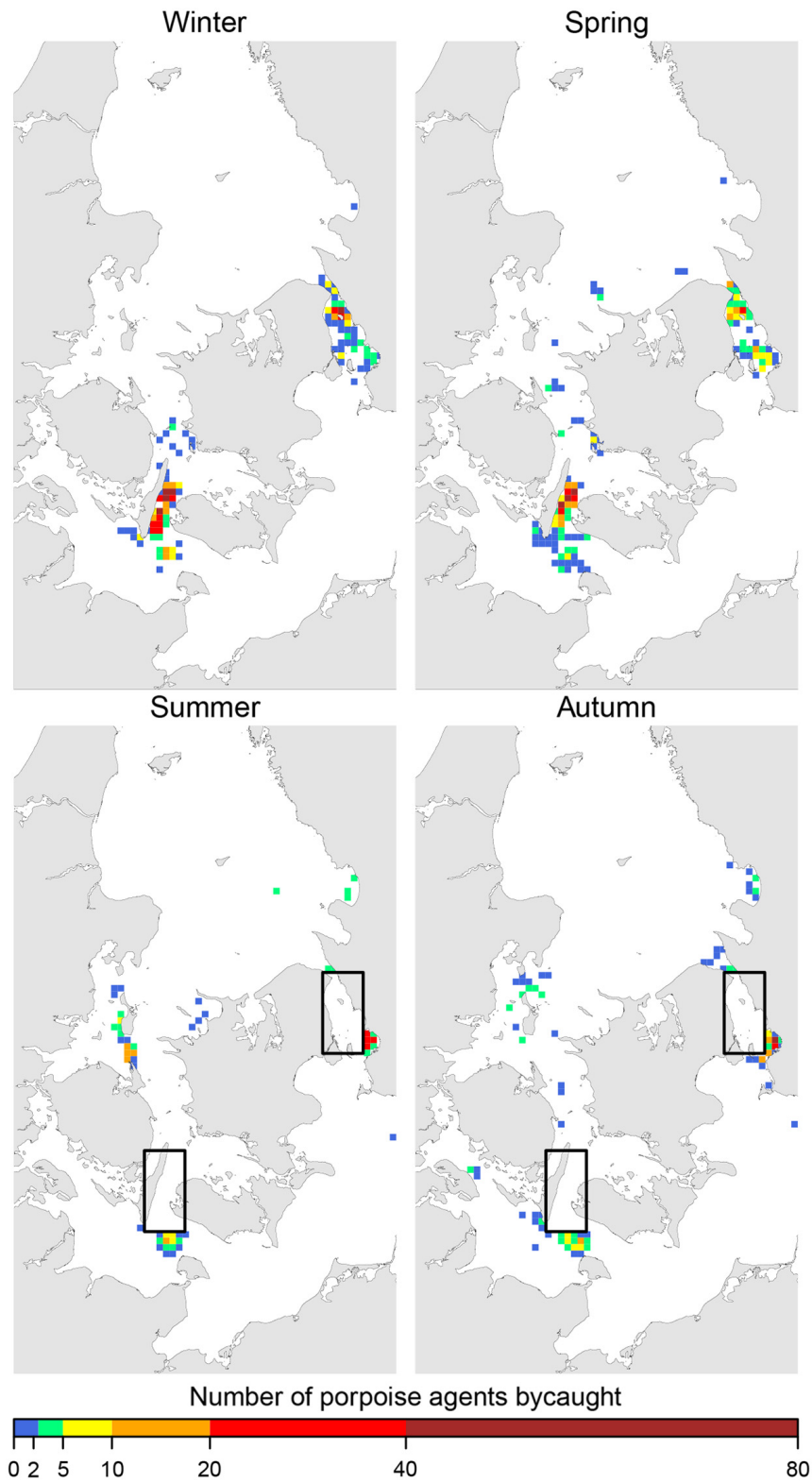


Fig. 6. Spatiotemporal variation in bycatch of porpoise agents in the simulation scenario: "time-area closures"

(Fig. 6. Continued)

and bycatch worst-case.” Each 3×3 km cell shows the sum of the number of porpoise agents bycaught over simulation years 11–40. The black outlines in the summer and autumn panels indicate the two time-area fishing closures.

The scenario with pingers and time-area fishing closures implemented in parallel had a mean population size of 244 ± 11.46 individuals/yr (Fig. 5a). This was 0.8% lower than in the baseline scenario and always higher than the population size in scenarios that considered pingers or time-area closures independently (Fig. 5a).

DISCUSSION

Reducing bycatch mortality of higher trophic-level species is an important goal in marine conservation as their abundance can impact entire food webs (Estes et al. 2011). We developed a predictive modeling tool that can assess the population-level consequences of harbor porpoise bycatch mitigation using time-area fishing closures and pingers that emit randomized high-frequency signals. Our study showed that the joint implementation of time-area fishing closures and pingers produced a population size that exceeded those in model scenarios where bycatch mitigation measures were used independently. Empirical studies from the Gulf of Maine have also shown that bycatch of harbor porpoises was most effectively reduced once time-area closures and pingers were both enforced (Read 2013). Our simulation study, however, builds on this knowledge by quantifying both the direct and indirect effects on the population as a whole, which revealed a strong synergistic relationship between these bycatch mitigation measures.

A novel insight derived from our study is that widespread deployment of pingers can have important indirect population-level consequences that challenge its usefulness as an independent bycatch mitigation measure. Even though pinger deployment eliminated bycatch completely in our simulations, the annual population size was substantially lower when pingers were used as the sole mitigation measure than in the contemporary bycatch scenario without pinger noise present (present-day situation). We only observed a net benefit of pinger deployment in terms of increased annual population size when implementing

pingers under a hypothetical bycatch rate of ~5% per yr (our worst-case scenario). These findings support our hypothesis that when pingers are widely deployed in high-quality porpoise habitat, frequent and recurrent deterrence behavior can negatively impact foraging success with adverse effects on individual survival and ultimately population size. To offset the negative impact of pinger noise-induced sub-lethal behavioral effects on the population and mitigate bycatch successfully, it seems critical to implement pingers and time-area fishing closures concomitantly. Key to this process is that time-area fishing closures are placed in high-quality porpoise habitat with the greatest bycatch risk (Murray et al. 2000, Kindt-Larsen et al. 2016), and fishing activity is excluded during periods of increased energetic demand/stress (e.g., when females are lactating as in this study). Doing so will create pinger- and bycatch-free refuge areas in which foraging behavior of individuals is uninterrupted and indirect negative effects of pinger noise on the population are largely compensated.

Our results have important implications for the development of bycatch mitigation policy and more broadly for marine conservation strategies. Because of the protected status of several marine mammals, including the harbor porpoise, in both EU and U.S. waters, eliminating bycatch is often the ultimate goal. Most bycatch mitigation policies operate on the assumption that reducing bycatch through pinger deployment and/or time-area fishing closures must have a positive effect on the population. Our simulations demonstrate that this holds true for time-area fishing closures but not for pingers and that the overall success of harbor porpoise bycatch mitigation hinges on the combined implementation of both measures. Past experiences from the Gulf of Maine, however, show that these mitigation measures are expensive to implement and often unpopular with fishermen, which can reduce compliance with regulations (Orphanides and Palka 2013, Bisack and Das 2015). Reduced compliance and enforcement of bycatch regulations, especially with pinger

deployment, is likely to revive bycatch levels over time. Moreover, the potential for a double-edged sword effect of pinger noise on the population as shown here suggests that widespread pinger deployment may interfere with (inter)national conservation strategies. For example, the EU Habitats Directive (1992) prohibits deliberate disturbance of individuals. As such, the use of underwater noise through pingers as a large-scale conservation strategy seems inappropriate as it will contribute to a further increase in underwater noise levels (Slabbekoorn et al. 2010) and disturbance of marine populations (Francis and Barber 2013, Nowacek et al. 2015).

Our spatially explicit, behavior-based simulation model represents natural processes and is constructed based on empirical data. Such IBMs are considered key support tools for conservation and environmental decision-making (Wood et al. 2015). Nevertheless, they remain simplifications of reality and assumptions are frequently made when empirical data are lacking. In our IBM, for example, deterrence behavior of porpoise agents to pinger noise was calibrated based on passive acoustic monitoring data collected in one small-scale field experiment using one type of pinger (Fig. 3). We focused our efforts on one pinger type (AQUA-mark100) as it is already enforced in the Danish part of the North Sea (Larsen and Eigaard 2014) and thus a likely candidate to be used in other Danish waters in the future. Nonetheless, one field experiment may not capture the full range of deterrence behavior of harbor porpoises to pinger noise. Moreover, increasing evidence suggests that the behavioral response of marine vertebrates to underwater noise is influenced by multiple environmental (e.g., bathymetry, conspecific and prey density, season) and intrinsic (e.g., age, energetic and reproductive status) conditions (Ellison et al. 2012). Thus, developing and incorporating a spatially dynamic noise avoidance mechanism, where individual agents respond to various types of pinger noise as a function of their internal state and the conditions at a site, would be a valuable improvement of the simulation model.

The number of gillnet fishing locations used in the IBM was incomplete and, moreover, fishing effort (i.e., the location, number, and soak time of gillnets) was assumed to be constant across years. Using a calibration process, we accounted for missed fishing locations to produce the correct

contemporary annual bycatch rate within the study area. However, incomplete data on fishing effort do bias the calculation of spatiotemporal variation in bycatch risk (Fig. 4) and subsequently the identification of time-area fishing closures. As such, the fishing closures selected in our study should not be considered a quantitative management suggestion. Instead, we argue that data collection on gillnet fishing effort needs to be intensified and streamlined internationally. For example, all Swedish gillnet vessels are obliged to report data on fishing locations, soak time, and the number of nets deployed. The same holds true for Danish and German vessels, but only for those >12 m in size. A more complete overview of spatiotemporal variation in gillnet fishing effort is essential for the identification of time-area fishing closures with the greatest positive impact on bycatch mitigation and the conservation of the harbor porpoise population. Moreover, continuous monitoring of gillnet fishing effort over space and time would facilitate the process of adaptive management through, for example, the implementation of smart pinger designs or mobile closures. Selecting temporary spatial closures based on expected bycatch risk have been shown an effective strategy to reduce marine vertebrate bycatch in longline fisheries while at the same time minimizing the economic impact on the fishery industry (Grantham et al. 2008). An important extension of our IBM would be to incorporate the economic implications (cost-effectiveness) of various bycatch mitigation measures. This requires close collaboration and consensus among stakeholders involved (e.g., scientist, the gillnet fishing industry, conservationist, policy makers/enforcers), which is essential to minimize the ecological and economic risks of implementing inadequate bycatch mitigation strategies (Kirby and Ward 2014).

Successful mitigation of marine vertebrate bycatch and management of marine systems as a whole require clear conservation goals, engagement of stakeholders, sound policy, and enforcement. Individual-based simulation models, such as the one presented here, offer a mechanistic modeling approach that can be used to evaluate the impact of human activities at sea on the long-term survival of marine populations that is not always possible using short-term empirical studies. Importantly, scientist and stakeholders can continuously extend IBMs as new data become

available, enabling the development of adaptive management practices and conservation strategies that balance ecological as well as socioeconomic demands on marine ecosystems successfully.

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LITERATURE CITED

- Baum, J. K., R. A. Myers, D. G. Kehler, B. Worm, S. J. Harley, and P. A. Doherty. 2003. Collapse and conservation of shark populations in the northwest Atlantic. *Science* 299:389–392.
- Bisack, K. D., and C. Das. 2015. Understanding non-compliance with protected species regulations in the northeast USA gillnet fishery. *Frontiers in Marine Science* 2:91.
- Börjesson, P., P. Berggren, and B. Ganning. 2003. Diet of harbor porpoises in the Kattegat and Skagerrak Seas: accounting for individual variation and sample size. *Marine Mammal Science* 19:38–058.
- Brothers, N. 1991. Albatross mortality and associated bait loss in the Japanese longline fishery in the Southern Ocean. *Biological Conservation* 55:255–268.
- Carlström, J., P. Berggren, F. Dinnétz, and P. Börjesson. 2002. A field experiment using acoustic alarms (pingers) to reduce harbour porpoise by-catch in bottom-set gillnets. *ICES Journal of Marine Science: Journal du Conseil* 59:816–824.
- Caswell, H., S. Brault, A. J. Read, and T. D. Smith. 1998. Harbor porpoise and fisheries: an uncertainty analysis of incidental mortality. *Ecological Applications* 8:1226–1238.
- Cox, T. M., A. J. Read, D. Swanner, K. Urian, and D. Waples. 2004. Behavioral responses of bottlenose dolphins, *Tursiops truncatus*, to gillnets and acoustic alarms. *Biological Conservation* 115:203–212.
- Crain, C. M., K. Kroeker, and B. S. Halpern. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters* 11:1304–1315.
- Culik, B. M., S. Koschinski, N. Tregenza, and G. M. Ellis. 2001. Reactions of harbor porpoises *Phocoena phocoena* and herring *Clupea harengus* to acoustic alarms. *Marine Ecology Progress Series* 211:255–260.
- D'agrosa, C., C. E. Lennert-Cody, and O. Vidal. 2000. Vaquita bycatch in Mexico's artisanal gillnet fisheries: driving a small population to extinction. *Conservation Biology* 14:1110–1119.
- Dans, S. L., M. Koen Alonso, S. N. Pedraza, and E. A. Crespo. 2003. Incidental catch of dolphins in trawling fisheries off Patagonia, Argentina: Can populations persist? *Ecological Applications* 13:754–762.
- Dawson, S., S. Northridge, D. Waples, and A. Read. 2013. To ping or not to ping: the use of active acoustic devices in mitigating interactions between small cetaceans and gillnet fisheries. *Endangered Species Research* 19:201–221.
- Dyndo, M., D. M. Wiśniewska, L. Rojano-Doñate, and P. T. Madsen. 2015. Harbour porpoises react to low levels of high frequency vessel noise. *Scientific Reports* 5:11083.
- Edrén, S. M. C., M. S. Wisz, J. Teilmann, R. Dietz, and J. Söderkvist. 2010. Modelling spatial patterns in harbour porpoise satellite telemetry data using maximum entropy. *Ecography* 33:698–708.
- Ellison, W. T., B. L. Southall, C. W. Clark, and A. S. Franke. 2012. A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds. *Conservation Biology* 26:21–28.
- Estes, J. A., et al. 2011. Trophic downgrading of planet earth. *Science* 333:301.
- Francis, C. D., and J. R. Barber. 2013. A framework for understanding noise impacts on wildlife: an urgent conservation priority. *Frontiers in Ecology and the Environment* 11:305–313.
- Gearin, P. J., M. E. Gosho, J. L. Laake, L. Cooke, R. L. DeLong, and K. M. Hughes. 2000. Experimental testing of acoustic alarms (pingers) to reduce bycatch of harbour porpoise, *Phocoena phocoena*, in the state of Washington. *Journal of Cetacean Research and Management* 2:1–9.
- Geijer, C. K. A., and A. J. Read. 2013. Mitigation of marine mammal bycatch in U.S. fisheries since 1994. *Biological Conservation* 159:54–60.
- General Accountability Office. 2008. Improvements are needed in the federal process used to protect marine mammals from commercial fishing. Page 60. General Accountability Office, Washington, D.C., USA.
- Grantham, H., S. Petersen, and H. Possingham. 2008. Reducing bycatch in the South African pelagic longline fishery: the utility of different approaches to fisheries closures. *Endangered Species Research* 5:291–299.
- Grimm, V., U. Berger, D. L. DeAngelis, J. G. Polhill, J. Giske, and S. F. Railsback. 2010. The ODD protocol: a review and first update. *Ecological Modelling* 221:2760–2768.

- Grimm, V., K. Frank, F. Jeltsch, R. Brandl, J. Uchmański, and C. Wissel. 1996. Pattern-oriented modelling in population ecology. *Science of The Total Environment* 183:151–166.
- Hall, M. A., D. L. Alverson, and K. I. Metuzals. 2000. By-catch: problems and solutions. *Marine Pollution Bulletin* 41:204–219.
- International Council for the Exploration of the Sea (ICES). 2015. Report of the Working Group on Bycatch of Protected Species (WGBYC). Page 82. ICES Headquarters, Copenhagen, Denmark.
- Jefferson, T. A., and B. E. Curry. 1994. A global review of porpoise (*Cetacea: Phocoenidae*) mortality in gill-nets. *Biological Conservation* 67:167–183.
- Kappel, C. V. 2005. Losing pieces of the puzzle: threats to marine, estuarine, and diadromous species. *Frontiers in Ecology and the Environment* 3:275–282.
- Kastelein, R. A., J. Hardeman, H. Boer. 1997. Food consumption and body weight of harbour porpoises (*Phocoena phocoena*). Pages 217–233 in A. J. Read, et al., editors. *The biology of the harbour porpoise*. De Spil Publishers, Woerden, The Netherlands.
- Kindt-Larsen, L. 2015. Management of fisheries in harbour porpoise (*Phocoena phocoena*) marine protected areas. Page 52. Dissertation. Technical University of Denmark, Charlottenlund, Denmark.
- Kindt-Larsen, C., J. Berg, T. Tougaard, K. Sørensen, S. Geitner, S. Northridge, S. Sveegaard, and F. Larsen. 2016. Identification of high-risk areas for harbour porpoise *Phocoena phocoena* bycatch using remote electronic monitoring and satellite telemetry data. *Marine Ecology Progress Series* 555:261–271.
- Kirby, D. S., and P. Ward. 2014. Standards for the effective management of fisheries bycatch. *Marine Policy* 44:419–426.
- Komoroske, L. M., and R. L. Lewison. 2015. Addressing fisheries bycatch in a changing world. *Frontiers in Marine Science* 2:83.
- Koopman, H. N., D. A. Pabst, W. A. McLellan, R. M. Dillaman, and A. J. Read. 2002. Changes in blubber distribution and morphology associated with starvation in the harbor porpoise (*Phocoena phocoena*): evidence for regional differences in blubber structure and function. *Physiological and Biochemical Zoology* 75:498–512.
- Kramer-Schadt, S., E. Revilla, T. Wiegand, and V. Grimm. 2007. Patterns for parameters in simulation models. *Ecological Modelling* 204:553–556.
- Kraus, S. D., A. J. Read, A. Solow, K. Baldwin, T. Spradlin, E. Anderson, and J. Williamson. 1997. Acoustic alarms reduce porpoise mortality. *Nature* 388:525.
- Kyhn, L., P. Jørgensen, J. Carstensen, N. Bech, J. Tougaard, T. Dabelsteen, and J. Teilmann. 2015. Pingers cause temporary habitat displacement in the harbour porpoise *Phocoena phocoena*. *Marine Ecology Progress Series* 526:253–265.
- Kyhn, L. A., J. Tougaard, L. Thomas, L. R. Duve, J. Stenback, M. Amundin, G. Desportes, and J. Teilmann. 2012. From echolocation clicks to animal density—Acoustic sampling of harbor porpoises with static dataloggers. *Journal of the Acoustical Society of America* 131:550–560.
- Larsen, F., and O. R. Eigaard. 2014. Acoustic alarms reduce bycatch of harbour porpoises in Danish North Sea gillnet fisheries. *Fisheries Research* 153: 108–112.
- Larsen, F., C. Krog, and O. R. Eigaard. 2013. Determining optimal pinger spacing for harbour porpoise bycatch mitigation. *Endangered Species Research* 20:147–152.
- Lewison, R. L., L. B. Crowder, A. J. Read, and S. A. Freeman. 2004a. Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology & Evolution* 19:598–604.
- Lewison, R. L., S. A. Freeman, and L. B. Crowder. 2004b. Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. *Ecology Letters* 7:221–231.
- Lockyer, C., G. Desportes, K. Hansen, S. Labberté, and U. Siebert. 2003. Monitoring growth and energy utilisation of the harbour porpoise (*Phocoena phocoena*) in human care. *NAMMCO Scientific Publications* 5:107–120.
- McNab, B. K. 1980. Food habits, energetics, and the population biology of mammals. *American Naturalist* 116:106–124.
- Murray, K. T., A. J. Read, and A. R. Solow. 2000. The use of time/area closures to reduce bycatches of harbour porpoises: lessons from the Gulf of Maine sink gillnet fishery. *Journal of Cetacean Research and Management* 2:135–141.
- Nabe-Nielsen, J., R. M. Sibly, J. Tougaard, J. Teilmann, and S. Sveegaard. 2014. Effects of noise and by-catch on a Danish harbour porpoise population. *Ecological Modelling* 272:242–251.
- Nabe-Nielsen, J., J. Tougaard, J. Teilmann, K. Lucke, and M. C. Forchhammer. 2013. How a simple adaptive foraging strategy can lead to emergent home ranges and increased food intake. *Oikos* 122:1307–1316.
- Nowacek, D. P., C. W. Clark, D. Mann, P. J. Miller, H. C. Rosenbaum, J. S. Golden, M. Jasny, J. Kraska, and B. L. Southall. 2015. Marine seismic surveys and ocean noise: time for coordinated and prudent planning. *Frontiers in Ecology and the Environment* 13:378–386.

- Olesen, H. J., F. Larsen, L. Kindt-Larsen, and J. B. Jacobsen. 2015. Pilot project for the preparation of MSC certification of the gillnet fishery in the Baltic Sea. Page 27. National Institute of Aquatic Resources, Technical University of Denmark, Charlottenlund, Denmark.
- Orphanides, C., and D. Palka. 2013. Analysis of harbor porpoise gillnet bycatch, compliance, and enforcement trends in the US northwestern Atlantic, January 1999 to May 2010. *Endangered Species Research* 20:251–269.
- Pirotta, E., K. L. Brookes, I. M. Graham, and P. M. Thompson. 2014. Variation in harbour porpoise activity in response to seismic survey noise. *Biology Letters* 10:20131090.
- Read, A. J. 2013. Development of conservation strategies to mitigate the bycatch of harbor porpoises in the Gulf of Maine. *Endangered Species Research* 20:235–250.
- Read, A. J., P. Drinker, and S. P. Northridge. 2006. Bycatch of marine mammals in U.S. and global fisheries. *Conservation Biology* 20:163–169.
- Sibly, R. M., V. Grimm, B. T. Martin, A. S. A. Johnston, K. Kułakowska, C. J. Topping, P. Calow, J. Nabe-Nielsen, P. Thorbek, and D. L. DeAngelis. 2013. Representing the acquisition and use of energy by individuals in agent-based models of animal populations. *Methods in Ecology and Evolution* 4: 151–161.
- Sibly, R., and D. McFarland. 1976. On the fitness of behavior sequences. *American Naturalist* 110: 601–617.
- Slabbekoorn, H., N. Bouton, I. van Opzeeland, A. Coers, C. ten Cate, and A. N. Popper. 2010. A noisy spring: the impact of globally rising underwater sound levels on fish. *Trends in Ecology & Evolution* 25:419–427.
- Sutherland, W. J., A. S. Pullin, P. M. Dolman, and T. M. Knight. 2004. The need for evidence-based conservation. *Trends in Ecology & Evolution* 19:305–308.
- Sveegaard, S., A. Galatius, R. Dietz, L. Kyhn, J. C. Koblitz, M. Amundin, J. Nabe-Nielsen, M.-H. S. Sinding, L. W. Andersen, and J. Teilmann. 2015. Defining management units for cetaceans by combining genetics, morphology, acoustics and satellite tracking. *Global Ecology and Conservation* 3:839–850.
- Tang, W., and D. A. Bennett. 2010. Agent-based modeling of animal movement: a review. *Geography Compass* 4:682–700.
- The Danish AgriFish Agency, and Ministry of Environment and Food. 2015. Annual Report on the Implementation of Council Regulation (EC). Page 12. The Danish AgriFish Agency, Ministry of Environment and Food, Copenhagen, Denmark.
- Thompson, P., S. Ingram, M. Lonergan, S. Northridge, A. Hall, and B. Wilson. 2007. Climate change causing starvation in harbour porpoises? *Biology Letters* 3:533.
- Trippel, E. A., M. B. Strong, J. M. Terhune, and J. D. Conway. 1999. Mitigation of harbour porpoise (*Phocoena phocoena*) by-catch in the gillnet fishery in the lower Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences* 56:113–123.
- Wisniewska, D. M., M. Johnson, J. Teilmann, L. Rojano-Doñate, J. Shearer, S. Sveegaard, L. A. Miller, U. Siebert, and P. T. Madsen. 2016. Ultra-high foraging rates of harbor porpoises make them vulnerable to anthropogenic disturbance. *Current Biology* 26:1441–1446.
- Wood, K. A., R. A. Stillman, and J. D. Goss-Custard. 2015. Co-creation of individual-based models by practitioners and modellers to inform environmental decision-making. *Journal of Applied Ecology* 52:810–815.

DATA ACCESSIBILITY

The IBM was originally built in the software package NetLogo 4.1 and is available from <https://doi.org/10.5281/zenodo.53097>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1785/full>