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Effects of noise and by-catch on a Danish harbour porpoise population☆

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ABSTRACT

Ships and wind turbines generate noise, which can have a negative impact on marine mammal populations by scaring animals away. Effective modelling of how this affects the populations has to take account of the location and timing of disturbances. Here we construct an individual-based model of harbour porpoises in the Inner Danish Waters. Individuals have their own energy budgets constructed using established principles of physiological ecology. Data are lacking on the spatial distribution of food which is instead inferred from knowledge of time-varying porpoise distributions. The model produces plausible patterns of population dynamics and matches well the age distribution of porpoises caught in by-catch. It estimates the effect of existing wind farms as a 10% reduction in population size when food recovers fast (after two days). Proposed new wind farms and ships do not result in further population declines. The population is however sensitive to variations in mortality resulting from by-catch and to the speed at which food recovers after being depleted. If food recovers slowly the effect of wind turbines becomes negligible, whereas ships are estimated to have a significant negative impact on the population. Annual by-catch rates $\geq$10% lead to monotonously decreasing populations and to extinction, and even the estimated by-catch rate from the adjacent area (approximately 4.1%) has a strong impact on the population. This suggests that conservation efforts should be more focused on reducing by-catch in commercial gillnet fisheries than on limiting the amount of anthropogenic noise. Individual-based models are unique in their ability to take account of the location and timing of disturbances and to show their likely effects on populations. The models also identify deficiencies in the existing database and can be used to set priorities for future field research.

1. Introduction

Disturbances can affect animal foraging and dispersal with large effects on individual fitness and population survival (Kerley et al., 2002; Tuomainen and Candolin, 2011). Their effects on fitness are partly caused by the exclusion of animals from high-quality foraging areas (Baveco et al., 2011; Gill et al., 1996) and partly by the net energy losses associated with fleeing from disturbances (Rodríguez-Prieto and Fernández-Juricic, 2005). Disturbances contribute to the fragmentation of landscapes and can have particularly large effects on population dynamics in fragmented landscapes where local subpopulations recover more slowly (Altermatt et al., 2011; Nabe-Nielsen et al., 2010). As the impacts of anthropogenic disturbances to a large extent arise from their effect on animal movements, effective conservation of species in disturbed habitats must be built on a better understanding of the link between animal movement and population dynamics. Although this it is widely recognised (Buchholz, 2007; Caro, 2007; Gonzalez-Suarez and Gerber, 2008) the effects of disturbances on animal behaviour are rarely taken into account when managing populations.

Animals in natural environments are exposed to a wide range of factors that influence their fitness, including multiple types of disturbance, predation, competition and variations in food availability. These factors may influence fitness directly, e.g. by increasing the animals' probability of dying, or indirectly by influencing their energy balance. As the influence of the different factors varies in both space and time, their cumulative impact on the fate of the population is most appropriately studied using spatially explicit models such as behaviour-based individual-based models (IBMs;

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sometimes referred to as agent-based models) (Bennett et al., 2009; Davidson et al., 2012). One advantage of IBMs is that they make it possible to study the population-level consequences of altered animal movements, for example changed foraging behaviour in disturbed areas, while at the same time allowing the incorporation of direct mortality events.

The study of cumulative effects is particularly challenging in marine environments where it is often difficult to quantify the spatial and temporal distribution of resources, disturbances and other factors that affect the organisms living there. Nevertheless there is an increasing demand for such studies in order to evaluate the potential effects of different management options (Crain et al., 2008; Korpinen et al., 2012). When multiple stressors interact synergistically, as would be the case if additional sources of noise prevent animals from moving through the last remaining corridor to important foraging areas, it may have large effects on the population. Perhaps the largest challenge is to quantify the distribution of resources. For many marine organisms, including most marine mammals, little is known about the distribution of the prey they depend on. For species with low energy storage capacities the spatial distribution of food may instead be assessed indirectly by assuming that the habitat types where animals spend most time are also the ones where their food is abundant. In this study we demonstrate how this approach can be used for modelling the prey distribution in an IBM for the harbour porpoise (*Phocoena phocoena*) population in the Inner Danish Waters (IDW).

The potential carrying capacity for the modelled porpoise population, that is, the equilibrium population size in the absence of human activities, would presumably be determined by the amount of available food as is generally the case for mammals (Sinclair, 1989). The size of the population has, however, most likely been reduced by by-catch in commercial fisheries (Berggren et al., 2002; Fock, 2011) as well as by anthropogenic disturbances. Noise from large ships and operational noise from wind turbines may, for example, affect porpoises in large parts of their range. The relative importance of different kinds of disturbances and by-catch for the population is, however, not known. In this paper we investigate the cumulative effects of noise and by-catch on the harbour porpoise population in the IDW. We examine their relative impacts on equilibrium population size and population resilience and consider whether effects are additive, synergistic or antagonistic (Crain et al., 2008).

2. Methods

2.1. Study species

The harbour porpoise is a small cetacean that is wide spread along the coasts of Europe and North America. The porpoises in the IDW constitute a distinct population (Andersen et al., 1997; Wiemann et al., 2010) that predominately preys on cod (*Gadus morhua*) and pelagic herring (*Clupea harengus*), but also on gobies (Gobiidae) and a number of other benthic species (Aarefjord et al., 1995; Börjesson et al., 2003). Many of these species have a patchy distribution, either because they occur in schools or because they are associated with particular microhabitats. The porpoise population is particularly dense in the areas around Funen and north of Sealand (Edrén et al., 2010; Sveegaard et al., 2011) where food is presumably abundant. The animals often stay within a limited area for weeks, although they are capable of dispersing between different parts of their range at speeds of up to at least 30–40 km per day for several days (J. Teilmann unpubl. data). Porpoises only occasionally collaborate in catching prey, although they sometimes occur in small groups (SCANS II, 2008).

Reproduction is a major determinant of the porpoises' population dynamics. Female porpoises on the average become sexually mature when 3.4 years old (Read, 1990). After the mating season, which peaks in August (Lockyer, 2003), 68% of the adult females are pregnant (Read and Hohn, 1995). After ten months they give birth to a single calf that stays together with them for approximately eight months while lactating (Lockyer, 2003; Lockyer and Kinze, 2003). Adult females are able to mate even when they are lactating.

The natural mortality of porpoises is presumably related to their energy levels, as is the case for a wide range of animal species (Sibly et al., 2013). Data from captive animals suggest that they spend energy at a constant rate, which increases up to about 30% when the water temperature drops during winter (Lockyer et al., 2003) and up to 40% when animals lactate (Magnus Wahlberg, pers. comm.). In addition to the natural mortality porpoises are frequently bycaught in gillnet fisheries. In the North Sea an estimated 5900 animals were bycaught annually in 1987–2001 just by the Danish gillnet fleet (Vinter and Larsen, 2004). No estimate of the bycatch rate exists for the IDW. This incidental bycatch in gillnet fisheries is considered a significant threat to harbour porpoises in European waters (Carlström et al., 2009; Kock and Benke, 1996).

There is evidence that porpoises react to disturbances by being scared away. During the construction of offshore wind farms harbour porpoise densities are reduced up to 20 km away from the construction site (Brandt et al., 2011; Carstensen et al., 2006), and in at least one case (the Nysted Offshore Wind Farm) the porpoise densities remained low after several years of normal wind farm operation (Teilmann and Carstensen, 2012). In two studies from the North Sea porpoise densities were not reduced near the wind farm during normal operation (Scheidat et al., 2011; Tougaard et al., 2006). Little is known about how porpoises react to other kinds of disturbances, although they have been reported to avoid boats (Polacheck and Thorpe, 1990).

2.2. Model description

The model description follows the updated ODD (Overview, Design concepts, Details) protocol suggested by Grimm et al., 2006, 2010.

2.2.1. Purpose

The model simulates how harbour porpoise population dynamics are affected by by-catch and noise emitted from wind turbines and large ships. The animals' survival is related to their energy levels, and the population dynamics are affected by noise through its effect on the animals' foraging behaviour.

2.2.2. Entities, state variables, and scales

The model includes three kinds of agents: porpoises, wind turbines and ships. The porpoise agents are characterised by their location, speed, movement direction, age, age of maturity, energy level, pregnancy status and lactation status. Their energy levels are scaled to lie in the range 0–20. Each porpoise agent is a 'super individual' (Scheffer et al., 1995) representing several real-world female porpoises. The wind turbines are characterised by their location and noise level. Ships are characterised by location, speed, movement direction and noise level. Simulations are based on a 240 km × 400 km landscape covering the IDW around the islands Funen and Sealand (Fig. 1). The landscape is divided into 600 × 1000 grid cells, each covering 400 m × 400 m. The grid cells are characterised by their location, average water depth, distance to land, food level and maximum food level. The landscape includes land (52.1%), 4572 randomly distributed food patches with a size of 1 cell (0.76%) and water without food (47.1%). The distribution of the patches is the same as used by Nabe-Nielsen et al. (2013), i.e. it included on the average 1000 food patches per 100 km × 100 km. The