Using individual-based bioenergetic models to predict the aggregate effects of disturbance on populations: a case study with beaked whales and Navy sonar

# Introduction

Population dynamics of long-lived organisms are primarily determined by stochastic and seasonal environmental variability that result in variation in reproductive success and juvenile survival (Bonenfant et al., 2009; Gaillard et al., 2000, 1998). To cope with such variability, long-lived animals have evolved a suite of physiological, behavioral and life history adaptations that prioritize survival and optimize reproductive success over the course of their lifetime (Eberhardt, 2002; Roff, 2002; Stearns, 1992). Because of their capacity to cope with variable environments, non-lethal effects of anthropogenic disturbances to populations of long-lived animals are more likely to occur before any lethal effects become apparent. Therefore, disturbances shown to have lethal effect on individuals will likely also have sublethal effects, but for many wildlife populations these might go unnoticed and are often harder to quantify.

Both natural and anthropogenic sources can lead to nonlethal disturbance of individuals. Natural predators cause nonlethal disturbance by inducing antipredator behaviour of their prey, which reduces the risk of predation at the cost of reduced energy intake (*e.g.* vigilance) or increased metabolic costs (*e.g.* avoidance behaviour) (Ferrari et al., 2009). For example, predators can affect the distribution and resource intake of their prey by creating a ‘landscape of fear’ (Laundre et al., 2010; Willems and Hill, 2009). Similar antipredator behaviours are also displayed in response to human-induced disturbances (Frid and Dill, 2002). Both anthropogenic and natural disturbances can therefore be regarded as non-consumptive effects or trait-mediated indirect effects (Schmitz et al., 2004; Werner and Peacor, 2003), which are known to have substantial impacts on animal populations and predator-prey interactions that may cascade down to affect entire communities (Lima, 1998; Peckarsky et al., 2008; Suraci et al., 2016).

Beaked whales (family *Ziphiidae*) are a group of deep-diving odontocete whales that have become a conservation priority because of their sensitivity to military Mid-Frequency Active Sonar (MFAS) (Cox et al., 2006; Dolman et al., 2011b, 2011a; Parsons, 2017). The use of MFAS has been implicated in several mass stranding events involving various beaked whale species, but particularly Cuvier’s beaked whale (*Ziphius cavirostris*, hereafter *Zc*) (D’Amico et al., 2009; Filadelfo et al., 2009; Hildebrand, 2005; Simonis et al., 2020). Although the precise mechanism by which exposure to naval sonar leads to stranding of whales remains unclear, the occurrence of fat and gas emboli in stranded whales indicates that these whales have suffered from decompression sickness (DCS) (Fahlman et al., 2014; Fernández et al., 2005; Hooker et al., 2012; Jepson et al., 2003). The ability of beaked whales to undertake extremely deep dives (up to 3,000 m for *Zc;* (Schorr et al., 2014; Shearer et al., 2019) likely makes them vulnerable to DCS when sonar induces changes in diving behavior (Rommel et al., 2006; Tyack et al., 2006).

Besides these lethal effects, sonar-induced changes in diving behavior might have nonlethal effect on individual health and energetic status (Bernaldo de Quirós et al., 2019). Tagging studies of beaked whales have recorded behavioral responses to sonar that can lead to lost foraging, including avoidance from the sonar source, cessation of foraging and prolonged interruptions between deep foraging dives (DeRuiter et al., 2013; Falcone et al., 2017; Joyce et al., 2019; Miller et al., 2015; Tyack et al., 2011). While the likely effect of a single disturbance is small, the aggregate effect of multiple exposures could have a chronic effect on individual health or energy stores, with consequences for individual vital rates. For example, a lactating whale that suffers from reduced prey intake might reduce milk provisioning to her calf or abandon it entirely. However, the extent to which this happens in beaked whales is currently unknown.

Concerns about the population-level consequences of non-lethal effects of MFAS exposure are especially relevant for beaked whale populations that live in or around navy training ranges, where sonar is used on a regular basis. On the Southern Californian Offshore Range (SCORE) around San Clemente Island, CA, the U.S. Navy regularly employs MFAS in an area that is prime quality habitat for *Zc* (Barlow et al., 2006; Falcone et al., 2009; Macleod and Mitchell, 2006; Moore and Barlow, 2013). Here, MFAS exposure was related to longer time intervals between successive deep dives that are associated with foraging, suggesting that MFAS leads to foraging disruptions in *Zc* (Falcone et al., 2017). A similar setting occurs at the Atlantic Undersea Test and Evaluation Center (AUTEC), which is U.S. Navy training range in the Bahamas used by a resident population of Blainville’s beaked whales (*Mesoplodon densirostris*, hereafter *Md*) (Claridge, 2013). Joyce et al. (2019) studied movement and dive profiles of *Md* at AUTEC during repeated, frequent and intense MFAS exposure associated with naval exercises and found clear and sustained displacement away from the core MFAS areas in the majority of tracked whales. Dive profiles during exposure were comparable to post- and pre-exposure profiles, although the proportion of time spent at depths consistent with foraging decreased during initial exposure to MFAS (Joyce et al., 2019). Passive acoustic monitoring using bottom-mounted range hydrophones at AUTEC also indicated that *Md* leave the range, or cease vocalizing, upon exposure to sonar (Moretti et al., 2010; Tyack et al., 2011), and that it may take 1 – 3 d post-exposure before call rates are back to pre-exposure levels (McCarthy et al., 2011). Taken together, these are strong indications that MFAS use disrupts behavior of beaked whales, leading to ‘lost foraging dives,’ either through cessation of foraging or displacement of whales away from preferred foraging areas.

Assessing the impact of federal activities on marine mammal populations is required by the United States’ Marine Mammal Protection Act, but translating short term behavioral responses to population level consequences has traditionally been difficult. The Population Consequences of Disturbance (PCoD) framework (New et al., 2014; Pirotta et al., 2018) addresses this challenge by conceptually linking disturbance-induced changes in individual behavior and physiology to changes in vital rates, potentially through chronic changes in individual health (broadly defined as all the internal factors that affect fitness or homeostasis). Modelling these processes requires the formulation of transfer functions that describe how behavior and physiology interact with individual health to determine the vital rates of individuals. However, these transfer functions are complex and often of unknown nature, which makes it challenging to assess potential impacts of environmental change or disturbances on wildlife populations. In addition, there are a number of contextual factors that can modify an individual’s response to disturbances.

For long-lived animals, there are large time-scale differences between the relevant processes. While disturbances can occur over several hours, the effects on vital rates may only become evident on a time scale of years (reproduction and offspring survival) or decades (adult survival). During this time, disturbance effects on health may be compensated or aggravated by other events. For example, although the available sample size was small, Joyce et al. (2019) observed an increase in the proportion of time at depths consistent with foraging during the five days after *Md* at AUTEC were exposed to sonar. Indications of compensation were also found for *Zc* at SCORE (Falcone et al., 2017). Although whales might compensate for disturbance by increasing foraging effort post-exposure, the initial reduction in intake might still lead to a delayed initiation of reproduction or reduced survival probabilities of dependent calves. In addition, the exposure to disturbance over time, and its distribution among individuals, will affect the population impact of disturbance. There are also multiple pathways by which changes in ecological drivers such as prey availability can modify individuals’ physiology and health status, and change their exposure to stressors.

Here we combine data from a variety of different sources to investigate how short-term repeated, behavioral disturbances from MFAS at the AUTEC and SCORE navy training ranges may affect beaked whale population dynamics. We use an individual-based population model in which individuals’ life histories are determined by their energy budgets. Movement patterns of simulated whales around navy training ranges and exposure to MFAS were modelled using telemetry data derived from satellite-tagged beaked whales. Passive-acoustic monitoring data from range hydrophones were used to quantify the impact of MFAS on beaked whale foraging, and to create realistic time series of MFAS that were used as disturbance scenarios in the population model. Lastly, we exploited recent insights into the distribution and abundance of beaked whale prey around navy training ranges to represent spatial variation in habitat quality.

# Model

## General model outline

We present an individual-based population model to simulate behavior (foraging and movement in response to MFAS), energetics and life history of *Zc* around SCORE and *Md* around AUTEC. The model is spatially implicit as simulated whales are assumed to inhabit and move between discrete geographical areas (spatial units) that differ in habitat quality and MFAS use. Movement is modelled as a continuous-time Markovian process with transition rates derived from satellite telemetry data of tagged *Zc* and *Md* at SCORE and AUTEC, respectively (Jones-Todd et al., n.d.; Joyce et al., 2019; Schorr et al., 2014). To model the effect of behavior on energetics and life history, the energy budget model for the long-finned pilot whale (*G. melas*) by Hin et al. (2019) was reparametrized for *Zc* and *Md*. In this model, beaked whale life history emerges from the rules that govern allocation of acquired energy from prey feeding and milk suckling (for calves only) to metabolic maintenance, growth in body size, gestation (pregnant females) and lactation (females with calves).

We consider a single, self-replenishing prey base across all areas per location (SCORE vs AUTEC) from which whales feed. Area-specific differences in habitat quality are reflected in the catchability (parameterized as potential encounter rate) of prey. Consequently, foraging whales deplete prey across all spatial units, although the per capita contribution to the prey depletion rate is larger in high-quality areas. Top-down prey depletion by the whale population suppresses whale vital rates through the energy-budget model (Hin et al., n.d.). This leads to negative density-dependent population growth as an emerging property of the model, as opposed to forms of density dependence that are implemented as a direct effect of whale density on reproduction or survival (Taylor and Demaster, 1993). Because of the predator–prey coupling, an increase in overall prey productivity will increase modeled whale population density, as opposed to prey density, which is top-down controlled. We selected prey productivity values that resulted in undisturbed whale population densities that were close to, or slightly higher than, those estimated for *Zc* at SCORE (+/- 100 individuals) and *Md* at AUTEC (+/- 40 individuals) (Claridge, 2013; Curtis et al., 2020; Hooker et al., 2019).

Use of MFAS can disturb whales that reside in areas located on the navy training range only. The probability that exposure leads to disturbance is given by a statistical description between a measure of sonar intensity and the beaked whale dive count rate, as derived from data from passive acoustic monitoring using navy range hydrophones on AUTEC and SCORE (McCarthy et al., 2011; Moretti et al., 2010). We simulate the following behavioral responses to MFAS: 1) cessation of foraging for a certain period of time, 2) displacement to an off-range area and 3) both cessation of foraging and displacement. Data from range hydrophones are used to create time series of MFAS use, which served as input to the population model.

## Navy ranges

The SCORE range is located off the coast of California, west of St Clemente Island and is part of the broader United States military’s Southern California Range Complex (SOCAL) (DiMarzio et al., 2021; Falcone et al., 2017). The range is approximately 1800 km2 and instrumented with an array of 177 bottom-mounted hydrophones used for navy training purposes (DiMarzio et al., 2021). Although navy exercises involving MFAS are concentrated on the range, MFAS exposure can occur throughout the entire SOCAL (Falcone et al., 2017). The SCORE range and surrounding areas support densities of *Zc* that are considered high for this species (Moore and Barlow, 2013). *Zc* individuals are regularly detected both acoustically and visually on SCORE and display a high site fidelity to the area (Falcone et al., 2017, 2009; Schorr et al., 2014).

The AUTEC range is located east of Andros Island, The Bahamas, in the Tongue of the Ocean (TOTO), which is part of the Great Bahama Canyon, a deep-water trench that extends south from the Northwest Providence Channel (Claridge, 2013). This range is approximately 1,500 km2 and equipped with 91 bottom-mounted hydrophones (McCarthy et al., 2011; Moretti et al., 2014). The resident population of *Md* at AUTEC has one of the highest densities of *Md* that has ever been estimated (Marques et al., 2009; Moore and Barlow, 2013; Moretti et al., 2006) and is subject to a long-term photo-identification program (Claridge, 2013).

## Division of spatial units

For each location (SCORE and AUTEC) we modelled a number of spatial units, which were determined based on MFAS use and assessments of habitat quality. We assumed MFAS use was restricted to the instrumented range areas only, and that whales in off-range areas were not exposed to MFAS. Furthermore, we only categorized areas as high- or low-quality habitat. These simplifying assumptions were required to minimize the number of spatial units per location, in order to ensure convergence of the estimation of transition rates between these areas (see *movement* section).

Assessments of the spatial distribution of beaked whale foraging habitat quality are presented in Southall et al., (2019) for SCORE and Benoit-Bird et al. (2020) for AUTEC. Based on these studies and the above considerations, each range was divided into a western, high-quality area and an eastern low-quality area (Figure 1). For SCORE we considered a single off-range area that was free of sonar and of low quality. Because of the specific topography of the TOTO, we considered three off-range areas around AUTEC. For each on-range area at AUTEC, there was one off-range area to the north that had the same habitat quality as its neighboring on-range area (Figure 1), and a single high-quality off-range area south of AUTEC (Benoit-Bird et al., 2020).

## Habitat quality

Following Southall et al. (2019), habitat quality was quantified as the number of dives per day required to meet the basal metabolic needs of a typical adult beaked whale, with high values indicating low habitat quality. This metric combined data on prey fields, prey energetic content and prey spatial aggregation with estimates of swimming speed and metabolic rate of adult beaked whales. As our model only accounted for a single prey base, differences in habitat quality were reflected in the area-specific prey encounter rates (attack rates), with and denoting prey encounter rates for low and high quality areas, respectively. Without loss of generality, we set and used the relative difference in habitat quality to estimate . For SCORE, the mode for the number of dives per day required to meet baseline daily metabolic requirements of an adult *Zc* equaled 1.5 for high quality areas and 20 for alternate areas (Table 1 in Southall et al. (2019)). For *Zc* at SCORE, we therefore adopted by default. For *Md* at AUTEC the dive rate required to meet metabolic demands equaled 6.0 and 1.2 for low- and high-quality areas (Benoit-Bird et al., 2020) and we adopted for *Md* by default.

## Movement

Transition rates between spatial units were derived from satellite telemetry data of *Md* individualstagged within or near AUTEC (n = 7) and *Zc* individuals tagged around SCORE (n = 12). Details of tag deployment and data collection are described in Joyce et al. (2019) for *Md* at AUTEC and Falcone et al. (2017) for *Zc* at SCORE. The fitting procedure is described in Jones-Todd et al. (n.d.) and in the online Supporting Information. In short, the raw Argos telemetry data were filtered to exclude highly unrealistic animal locations, after which a continuous-time correlated random walk state-space model was used to adjust filtered tracks for Argos uncertainty (Jones-Todd et al., n.d.). Transition rates between spatial units were quantified by fitting a discrete-space, continuous-time Markov model on these filtered, adjusted locations. This procedure resulted in a continuous time transition rate matrix **Q**, each element *qr,s* of which described the immediate risk of moving from spatial unit *r* (rows) to spatial unit *s* (in columns). We did not consider time-dependence of transition rates or dependence on any covariates. In case sonar led to displacement from the range, modelled individuals were translocated to an off-range area (see *disturbance* section), but their transition rates remained unaffected. Therefore, we assumed that the fitted transition rates reflect baseline movement patterns of *Md* and *Zc* around their respective ranges. In the model, calves did not move independently but were assumed to have the same location as their mother.

## Energetics

Details of the energy budget model and derivation of its parameters are presented in the Supplemental Information. The model is based on physiological principles for long-lived mammals, assuming that growth and reproduction proceed at rates that are independent of current food conditions while individuals adapt their foraging rate to maintain a target body condition (De Roos et al., 2009). It contains a number of rules (*i.e.* functions) that describe how the state of the individual influences its survival and the allocation of energy towards growth and reproduction (gestation and lactation). Concerning individual state, reserve mass (metabolizable energy stores) is distinguished from structural mass (non-metabolizable compounds). Furthermore, whales are described by age, structural length and total body mass (sum of structure and reserves). Structural length is directly related to age according to a Von Bertalanffy function. A fixed length-weight relationship is used to calculate structural mass from structural length.

Either absolute amount of reserves or its relative extent (*i.e.* body condition: the ratio between reserve mass and total body mass) determine various life history processes, such as the individual feeding level, initiation of reproduction, lactation rate and mortality rate. The feeding level (0 – 1) influences both rates of prey feeding and milk consumption (for calves only) and is a sigmoid declining function of body condition. It models increased foraging effort for whales with poor body condition, that could for example result from disturbance, low prey availability or high energy expenditure (lactation). Simultaneously, the feeding level ensures that reserve mass does not grow out of bounds under favorable conditions. Reproduction is initiated when absolute reserve mass exceeds a predetermined pregnancy threshold value, following Klanjscek et al., (2007). For females, milk provisioning declines as a function of body condition, and females cease milk supply to their calves when body condition drops below the starvation body condition threshold. Below this threshold, individuals suffer from starvation mortality, which rate increases with declining body condition. Individual age and structural size influence the prey feeding rate and the milk consumption rate for calves. Prey feeding rate increases with age throughout the early years of life (for calves and newly weaned individuals), while milk consumption rate decreases with age up to the age at weaning, at which lactation stops. Both prey and milk feeding rates are proportional to structural surface-area and prey feeding is proportional to prey density and the area-specific prey encounter rate. In addition to starvation mortality applied to whales with poor body condition, all whales suffer from natural background mortality. Calves and weaned females experience age-dependent background mortality according to a Siler model (Barlow and Boveng, 1991; Siler, 1979), while weaned males have constant background mortality rate.

Depending on individual’s reproductive state, energy expenditure can consist of four different costs. For all individuals, field metabolic costs are a ¾ power-law function of maintenance body mass, which accounts for the lower mass-specific metabolic costs of reserves relative to structure. For all individuals, growth costs are given by the change in structural mass multiplied by a cost-of-growth parameter. For fully-grown individuals, growth costs will be neglectable. For pregnant females, gestation costs are proportional to structural growth of the fetus. For lactating females, lactation costs are proportional to milk consumption of their calf. Together with the rates of energy intake, the rates of energy expenditure determine reserve mass dynamics. Reserve mass increases when total energy intake exceed total energy expenditure and decrease when the opposite is true. The different efficiency of storing (anabolism) and mobilizing (catabolism) reserve mass is taken into account.

## Exposure to MFAS

For both ranges, information on MFAS use was derived from passive-acoustic monitoring of range hydrophones. Data consisted of hourly counts of beaked whale dive starts per hydrophone and presence/absence of sonar per hydrophone across two years (2013 – 2014 for AUTEC and 2014 – 2015 for SCORE) (DiMarzio et al., 2021; Falcone et al., 2017; Kates Varghese et al., 2020; McCarthy et al., 2011). Data gaps in which no monitoring occurred were excluded, which resulted in 16,400 hours of data for AUTEC (1.87 years) and 11,925 hours for SCORE (1.36 years). Hydrophones were assigned to their spatial unit within each range (west vs east; Figure 1) and a tessellation algorithm was applied to each hydrophone to obtain the area covered by that hydrophone. Within each spatial unit, the areas associated with hydrophones on which sonar was detected were summed and scaled by the maximum area over which sonar was detected across each entire range and time period. This resulted in a standardized measure of sonar use, referred to as the ‘standardized sonar area’. Hourly detections of beaked whale dive starts were summed across all hydrophones within each spatial unit. We fitted separate Generalized Additive Models (GAMs) for each range to estimate the response of the number of dive starts per spatial unit per hour. Each GAM tested for the effects of 1) standardized sonar area; 2) spatial unit within the range (west vs east); 3) year; 4) hour (time of day); 5) julian day; 6) time since onset of sonar and 7) duration of the sonar bout. The response variable was assumed to follow a Poisson distribution, with a log link function and the size of the area as an offset on the link scale. The continuous covariates were modelled using thin plate splines except for hour and julian day, which were cyclic cubic regression splines (so that the estimated effects at the beginning and end of the day/year matched). Smoothness was estimated by minimizing an unbiased risk estimator (UBRE) criterion (Wood, 2017). Estimation was done with the ‘mgcv’ package in R (R Core Team, 2020).

After back-transformation to the original scale, the GAM predictor for the effect of the standardized sonar area on beaked whale dive start rate provided an estimate for the relative decrease in beaked whale foraging activity (*z*) as a result of sonar use. Here, *z* = 1.0 resembled no reduction in beaked whale foraging in a particular area, while *z* = 0.0 indicated complete reduction of foraging. For each hour we calculated area-specific values of *z* based on the standardized sonar area within that hour. This resulted in two time series of MFAS use per location: *z­w* and *z­e* for the western and eastern range areas, respectively. These time-series were condensed by grouping consecutive hours of identical *z*-values into sonar events using run-length encoding. Each event was characterized by a starting time (d), a *z*-value and a duration (in multiples of one hour). Per location, the time series of eastern and western areas were merged and served as input to the individual-based population model.

## Disturbance

Whales were exposed to sonar when present on a range area at the onset of a sonar event in that area. Upon exposure, the *z-*value of that particular event was used to calculate the number of disturbed whales, depending on the disturbance scenario (cessation of foraging, displacement from range or both). For cessation of foraging, we calculated the number whales that ceased foraging as *Ni,d* = (1 – *zi*) *N­i*, with *Ni* being the number of whales in area *i* at the onset of the sonar event. Whales already disturbed from a previous sonar event were discounted from *Ni,d* and could not get disturbed again. This was done to ensure that the fraction of disturbed whales within each area (*Ni,d / Ni*) matched the observed sonar-induced decrease in beaked whale foraging activity (*z*) as predicted by the GAM. A number of *Ni,d* whales were randomly selected amongst the undisturbed whales. For each selected whale, the prey foraging rate was set to zero and a disturbance duration (*td*) was calculated. This duration was assumed to follow an Erlang distribution (a common waiting time distribution) with shape parameter *k* = 2 and scale parameter (Figure 1). The disturbance duration was used to set the future time at which the whale would resume foraging: *t + td*.

If disturbance led to displacement the number of whales displaced was calculated relative to the stable distribution, which followed from the baseline movement pattern as dictated by the transition rate matrix **Q** (see Supplemental Information). More specifically, the number of whales displaced equalled: *Ni,d =* max(*Ni – Mi zi* , 0). Here, *M­i = p­i Ntot* is the number of whales in area *i* according to the stable proportion *pi*, with , *n* being the number of areas and *Ntot* total population size. Again, this calculation ensured that the modelled decrease in foraging activity within an area matched its observed counterpart as predicted by the GAM fitted on range dive start data. The randomly selected *Ni,d* whales were displaced to an off-range area, but their baseline transition rates remained unaffected. At AUTEC all displaced whales were moved to the off-range area north of each range area. At SCORE there was only a single off-range area that whales could be displaced to. This same procedure was adopted in the scenario where disturbance led to both displacement and cessation of foraging, but in addition, the prey foraging rates of displaced whales were set to zero for a randomly selected period as drawn from the Erlang distribution described above.

## Model simulation

The Escalator Boxcar Train (EBT) software package (https://staff.fnwi.uva.nl/a.m.deroos/ EBT/Software/ index.html) (de Roos, 1988) was used to simulate the individual-based population model. This package contains numerical integration routines to compute the dynamics of the individual-state variables (Table S1) of all individuals in the population, together with the Ordinary Differential Equation (ODE) that describes prey dynamics (Table S2). Model implementation files for use with EBT-software are available online (*link to repository*). The movement of each individual between different geographical areas was simulated by calculating for each area *s*, other than the individual’s current area *r* (*r s*), the future time of moving to area *s* as a random draw from an exponential distribution with rate *qr,s*. The individual was assigned to move to the area with the earliest future time of moving. During each numerical integration step, all individuals whose future time to move was exceeded by the current time were relocated at once. Lactating calves were assumed to always follow their mother and did not move independently.

We simulated the onset of MFAS-use on a previously undisturbed population residing at its stationary state, distinguishing between the three different disturbance scenarios. Because of the natural low abundance of beaked whale populations, we ran 100 replicate simulations for each disturbance scenario. In addition, we assessed the effect of varying 1) the prey attack rate parameter in high-quality areas (), 2) overall prey productivity (*Rmax*), 3) the transition rate matrix **Q** and 4) the mean disturbance duration *td* on beaked whale population density at stationary state for each disturbance scenario (including no disturbance). The sensitivity to the transition rate matrix **Q** was examined by applying a 10-fold decrease to all rates that described transitions from range areas to off-range areas. All effects are presented relative to the undisturbed scenario. Apart from population density, disturbance effects on female life history are presented.

# Results

## Movement and stable distribution

The transition rate matrices estimated from beaked whale telemetry data are shown in Table 1. For *Zc* around SCORE, the estimated mean duration that a whale stayed off range was 7 days, it stayed on average 2 days on the western part of the range, and less than 1 day (~16 hours) on the eastern part of the range. According to the associated stable distribution, at any time 64% of the *Zc* whales at SCORE are off range, 30% are on the western part of the range and only 6.5% inhabit the eastern part of the range (Table 1).

For *Md* at AUTEC, the movement analysis involved 5 different areas and there was less variation in mean residency times among areas compared to those for *Zc* at SCORE (Table 1). The longest residency time occurred in the area south of the range (mean of 3.7 days) and the shortest in the eastern range area (11 hours on average). The associated stable distribution (Table 1) indicated that on average 29% of the *Md* population can be found on the AUTEC range, the large majority (81%) of which reside on the western part of the range (24% vs 5.5%). The north-western off range area hosts the largest fraction the *Md* population (31%). The north-eastern and southern off-range areas host a similar fraction of the population with respectively 19% and 21%.

## Exposure and response to MFAS

Within the two years of data analyzed, MFAS was used more frequently on SCORE than on AUTEC, with sonar occurring in 8.4% and 2.9% of all recorded hours on each range (Figure 2). On AUTEC there were longer time intervals between sonar events, but there were more days with high MFAS use (as quantified by the daily sum of the standardized sonar area). Mean standardized sonar area of all hours with sonar was higher on AUTEC than on SCORE for the western range areas (0.537 vs. 0.384, respectively), but not for the eastern range areas (0.411 vs 0.456). For both ranges, the hourly sonar count (number of hydrophones on which sonar was received) was strongly correlated between eastern and western areas (Pearson correlation coefficient equaled 0.848 for AUTEC and 0.863 for SCORE).

Standardized sonar area had a negative effect on the number of dive starts per hour, a measure for beaked whale foraging activity (Figure 2). On AUTEC, there was little effect on the beaked whale dive count rate at low sonar intensity, but at the maximum recorded MFAS use, the relative decrease in dive count rate on AUTEC was larger than on SCORE (0.71 vs 0.53; Figure 2). For AUTEC, the GAM furthermore revealed significant effects of ‘area’ and ‘year’, with higher dive count rates in the western area and in 2013 (Table S4). There was fluctuation in the dive count rate throughout the year and day and a weak pattern of increasing dive count rate with increasing time since last MFAS use (Figure S3). For SCORE, the results from the GAM were similar (Table S5). The dive count rate was higher in the western SCORE area and in 2014 (compared to 2015). There was also significant variation throughout the day and year and a weak effect of time since last MFAS use (Figure S4). There was also an effect of the length of the sonar event, but this effect disappeared when accounting for temporal autocorrelation. Because our main study objective was to explore potential population effect of MFAS use, we only used the mean effect of the standardized sonar area on the beaked whale dive count rate in the individual-based population model and did not consider the effects of the other terms incorporated in the GAMs.

## Population consequences of disturbance

The onset of MFAS use led to a decline of *Zc* population density and a subsequent stabilization of the population at a lower density (Figure 3). This decline occurred across all three disturbance scenarios but was greatest if disturbance led to both displacement and cessation of foraging. Among females in the different reproductive classes, the decline in density was most pronounced for lactating and resting females and less steep for pregnant and waiting females. This corresponded to the observation that body condition of resting and lactating female is generally lower than that of waiting and pregnant female (Figure S?), and females in the former reproductive classes are therefore more likely to suffer from increased starvation mortality after the onset of MFAS use. Because of the coupling between predator and prey dynamics, the prey density increased in response to the relaxation of foraging pressure caused by the decline in population density (Figure 3). The magnitude of the increase in prey density mirrored the reduction in density of the *Zc* population following the onset of MFAS disturbance. Disturbance by MFAS also increased variation in prey density, with temporal peaks corresponding to disturbance-induced reduction of beaked whale foraging, followed by a decline in prey density in between MFAS disturbance events.

The effect of MFAS disturbance on mean population density of *Md* at AUTEC was less pronounced compared to that of *Zc* at SCORE (Figure 4). Cessation of foraging combined with displacement led to the largest decline in population density, but contrary to *Zc* at SCORE, displacement alone had a marginal effect on *Md* population density. For *Md*, disturbance by MFAS mainly reduced population density through a disruption of foraging behavior. The onset of MFAS at AUTEC also increased the (variation in) prey density, but the size of this effect was much smaller compared to the increase in prey density following MFAS use at SCORE.

Regardless of the decrease in mean population density from 100 replicate simulations, there was considerable overlap in the distribution of population density between different disturbance scenarios (for *Zc*) and between undisturbed and disturbed populations (*Md*) (Figure 5). The least overlap in the distribution of population density occurred between the ‘undisturbed’ and ‘cessation of foraging’ scenarios for *Zc* at SCORE.

## Movement and habitat quality

With the adjusted **Q** – matrix, a larger fraction of the population was present on the range under baseline condition (no MFAS). For *Zc* this adjustment meant that 85% of the population was on-range (70% and 15% in western and easter range areas; Table 1). For *Md* 81% of the population was on-range with the adjusted **Q** – matrix, with 66% and 15% in the western and eastern range areas (Table 1). Although a considerably larger fraction of both populations was exposed to MFAS, this did not lead to a markedly larger population impact of disturbance (comparing top and bottom panels in Figure 6). On the contrary, for *Zc* under low prey productivity, the adjusted **Q** – matrix even increased population persistence at low prey encounter rates, as the population was able to persist at lower - values compared to the default **Q** – matrix.

The relative effect of disturbance on population density decreased with increasing difference in habitat quality (Figure 6). Habitat quality was represented by the prey encounter rate (attack rate) of the high-quality area () with the prey encounter rate in the low-quality area set to 1. Increasing therefore also increased the mean prey encounter rates across all areas, which increased population density, irrespective of the disturbance scenario (Figure S8). Vice versa, decreasing resulted in the extinction of the beaked whale populations.

Increasing prey productivity increased population density across all disturbance scenarios (Figure S8). For *Zc*, the high prey productivity considered (*Rmax*­ = 3.0) led to a mean undisturbed total population density of 560 whales, versus 104 at low prey productivity (*Rmax*= 1.0). This difference was even greater for *Md*, where the high prey productivity value (*Rmax* = 2.0) resulted in around 1044 whales (versus 73 whales at *Rmax* = 0.5). These high productivity levels resulted in densities of beaked whales that are far beyond those estimated for *Md* and *Zc* at their respective sites (Hooker et al., 2019). Increasing prey productivity decreased the relative effect of disturbance on population density (Figure 6). Furthermore, at high prey productivity there was hardly an effect of changing on the relative effect of disturbance and the beaked populations persisted when there was no difference in habitat quality (.

## Disturbance duration

Increasing the mean duration of cessation of foraging had a stronger effect on population density at low prey productivity compared to high prey productivity (Figure 7). At high prey productivity, mean *Md* population density decreased by 4% (from 1045 to 999 individuals) across a mean disturbance duration of 6 days for the cessation of foraging scenario. The decrease in *Zc* population density across the same range was slightly higher: 10% (from 556 to 503 individuals). Increasing mean disturbance duration led to the extinction of the *Md* population at a mean disturbance duration of 5.2 and 4.2 days for cessation of feeding only and cessation and displacement, respectively. The *Zc* population went extinct at a mean disturbance duration of 4 days, likely due to the effects of demographic stochasticity, which had a large impact on simulated population dynamics at low prey productivity.

## Life history effect of disturbance

Within each species, life history statistics were similar across all disturbance scenarios (Table 2, Figures S9 & S10). Irrespective of disturbance, modelled *Zc* females initiated reproduction earlier in life compared to *Md* females. Because these data represent females from populations at stationary state subject to a certain disturbance regime, mean lifetime reproductive output was equal to 2 (counting male and females calves born to each female). Mean number of calves weaned per female was slightly higher for *Zc* compared to *Md*, indicating that calf survival was slightly lower in the latter species (0.65 vs 0.55).

# DISCUSSION

We have integrated various data sources, including telemetry data, spatial prey distributions, passive acoustic data on the temporal pattern of sonar use and its relationship to beaked whale foraging activity, with a bio-energetics model to estimate the consequences of aggregated exposure to navy sonar on two beaked whale populations that inhabit navy training ranges. Individuals in our modeled population where hence repeatedly exposed to navy sonar during their lifetime. We considered three different behavioral responses to sonar – cessation of foraging, displacement from range areas, and a combination of both – on both population density and individual life histories. There was an effect of disturbance on population densities of both species, although this effect was much larger for *Zc* than for *Md*. For both species, the disturbance effect on population density was comparable between the three different behavioral responses considered, with the largest effect in case of both cessation of foraging and displacement. There was no clear effect of sonar disturbance on our selected life history variables, which related to the onset of reproduction and to the number of calves produced or weaned during a female’s lifetime.

The relative effect of disturbance was larger at low prey productivity (*Rmax*) and for lower area-specific differences in habitat quality, as quantified by the prey encounter rate in high quality areas (). Both parameters influenced modelled population density, with whale density increasing with higher prey productivity and larger prey encounter rates. The low prey productivity was chosen to reflect the low natural densities of beaked whales, but resulted in our modelled population being close to the parameter boundary that marked population persistence. This was illustrated by the fact that a decrease in at low productivity led to the extinction of the modelled whale population. At low whale density there is weak top-down control of prey. Because prey growth rate decreases with prey density, weak top-down of prey implies that there is only a weak increase in prey density during disturbance events and this reduces the opportunity for compensatory feeding by whales post disturbance. Potentially this mechanism drives the stronger relative effect of disturbance at low whale density.

After the initiation of a constant disturbance regime, we found an initial rapid decrease of population density and a subsequent slower approach to a new stationary state (Fig. 3). Regarding the response of *Zc* in the ‘cessation of foraging and displacement’ scenario, half of the initial decrease in population density was reached after 2.5 years on average, while it took another 12.4 years before the population was within 1 per cent of the mean disturbed population density. This indicates that there is a least one decade of persistent population decline that could potentially be observed with a monitoring program of sufficient scale and intensity. Recovery of the *Zc* population when MFAS disturbance ceased was slower compared to the initial population decline and took approximately 25 years for *Zc*. This was equal to a mean population growth rate of 0.015, which is equivalent to a yearly increase factor of 1.5%. The combination of slow estimated population growth at low population density implies that it would require long-term monitoring (several decades) with high scale and intensity to detect any potential signs of population recovery once sonar disturbance ends.

At low densities, demographic stochasticity can have a significant effect on whale population dynamics, and this will make it hard to detect disturbance effects on beaked whale abundance, especially for *Md* where the predicted effect of disturbance on population density was small. In our model there are various sources of stochasticity that influence individual life histories, including random life expectancy and fetal mortality, random waiting period before onset of pregnancy and random sex determination at birth. In addition, movement between the discrete spatial units is modelled as a continuous-time Markovian processes (Jones-Todd et al., n.d.). The combined effect of these random processes leads to substantial fluctuations of population density around a carrying capacity level. These fluctuations will likely be enhanced by sources of environmental variability or seasonality that are currently not considered in our model. For example, productivity in the bathypelagic is shown to vary considerably in time and space, and strongly influenced by shifting deep-water currents that bring in nutrient rich waters. (Benoit-Bird et al., 2020, 2016; Southall et al., 2019). Incorporating variability or seasonality in the productivity of prey will likely further increase the variability in population density, and thereby clouding the effect of disturbance on population density.

Besides the effect of disturbance on population density, we did not find any long-term effects of disturbance on individual life history, although this relates to a comparison of females from stationary populations that are either disturbed or undisturbed. During the initial decline in population density after the onset of sonar, females will have reduced reproductive output and experience increased mortality. According to our results, responses to disturbance on individual vital rates will likely only be detectable during the first few years after the onset of disturbance, when the population is still declining. Monitoring programs that focus on individual vital rates of health measures would therefore need to start well in advance of any planned disturbances, to ensure that sufficient baseline observations are available.

Density-dependent population models reveal that non-lethal disturbances effectively decrease population ‘carrying capacity’ (this study, (Hin et al., n.d.)) and that compensatory effects on individual life history can occur through a disturbed-induced release in top-down control of prey (Hin et al., n.d.). Using the same energy budget model, but parameterized for long-finned pilot whales, Hin et al. (n.d.) showed that non-lethal disturbances which resulted in cessation of foraging for multiple, consecutive days each year led to increased mortality among young females that were lactating their first calf and increased reproductive output of older females. In addition, non-lethal disturbance increased population mean body condition and led to earlier first reproduction. The fact that we did not find any effect of disturbance on individual life history probably relates to the specific disturbance scenarios used here, which involved multiple disturbances of short duration throughout the year that only affected a subset of the population. In contrast, Hin et al. (n.d.) purposely used extreme disturbance scenarios, in which the entire population was exposed to long-lasting disturbances that continued for tens of days (up to 40 days) each year. It is very unlikely that beaked whales will cease foraging for such period of time.

Although our model represents one possible effect of MFAS disturbance on beaked whale populations at navy ranges, we cannot conclude anything about the probability of this outcome being true as there are uncertainties in our model on many levels and a full sensitivity analysis of all these uncertainties is unfeasible at this point. However, the finding that populations can be stable under continued disturbance if that population is operating under density dependence is likely to be general. This will especially hold for long-lived species, such as beaked whales, that tend to have stable population dynamics around a carrying capacity level.

Apart from uncertainties relating to model parameters, we didn’t consider that there might be whales living off-range that never come on range but are still foraging and therefore competing for prey with whales that are being disturbed. To test this, one would need to do surveys off-range to check density and in addition tag animals off-range to see if any come on range.

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Table 1: Transition rate matrices and stable distributions of *Md* around AUTEC and *Zc* around SCORE.

|  |  |  |
| --- | --- | --- |
|  | *Mesoplodon densirostris* | *Ziphius cavirostris* |
| Areas | [south, western range, northwest, northeast, eastern range] | [off range, western range, eastern range] |
| Transition rate  matrix (**Q**def) |  |  |
| Stable distribution **Q**def | [0.21, 0.24, 0.31, 0.19, 0.055] | [0.64, 0.30, 0.065] |
| Fraction on-range **Q**def | 0.29 | 0.36 |
| Adjusted transition rate matrix (**Q**adj) |  |  |
| Stable distribution **Q**adj | [0.057, 0.66, 0.084, 0.052, 0.15] | [0.15, 0.70, 0.15] |
| Fraction on-range **Q**adj | 0.81 | 0.85 |

Table 2: Mean (sd) of several life history variables of modelled *Md* and *Zc* females.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | *Mesoplodon densirostris* | | *Ziphius cavirostris* | |
|  | *Undisturbed (n = 9464)* | *Disturbed*\* *(n = 9505)* | *Undisturbed (n = 7238)* | *Disturbed*\* *(n = 5393)* |
| Age at first receptive | 7.7 (0.34) | 7.7 (0.37) | 5.7 (0.35) | 5.7 (0.36) |
| Age at first reproduction | 10.3 (1.6) | 10.3 (1.6) | 8.4 (1.7) | 8.2 (1.6) |
| Age at weaning first calf | 16.1 (3.9) | 16.0 (3.8) | 11.6 (2.9) | 11.5 (2.9) |
| Number of calves born | 2.0 (3.0) | 2.0 (3.0) | 2.0 (3.2) | 2.0 (3.2) |
| Number of calves weaned | 1.1 (1.8) | 1.1 (1.8) | 1.3 (2.3) | 1.3 (2.3) |
| \*Disturbance leads to cessation of foraging and displacement | | | | |