# 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 results 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, exposure of long-lived animals to human-induced stressors will induce non-lethal alterations of individual behavior and physiology, before any lethal effects occur. Therefore, external stressors 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, defined as a deviation in an animal’s physiology or behavior from patterns occurring in the absence of predators or humans (Frid and Dill, 2002; Pirotta et al., 2018). Natural predators cause nonlethal disturbance by inducing antipredator behavior 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 behavior) (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 behaviors 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). 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 of 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 exposure is small, the aggregate effect of multiple exposures could have a chronic effect on individual health, with consequences for individual vital rates (Pirotta et al., 2018). For example, a lactating whale that suffers from reduced prey intake might reduce milk provisioning to her calf or abandon it entirely.

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 a 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 return 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 conceptually by linking 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 human-induced stressors on wildlife populations.

Predicting the population consequences of disturbance for long-lived animals is further complicated by the large time-scale differences between the relevant processes. Events involving exposure to the disturbance source can last a few hours, while 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, effects on health may be compensated or aggravated by other events. Although limited by small sample size, 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 lost foraging 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.

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 source 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. 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 (Fig. 1; Jones‐Todd et al., 2022; Joyce et al., 2019; Schorr et al., 2014). To model the effect of behavior on energetics and life history, an energy budget model for the long-finned pilot whale (*G. melas*) (Hin et al., 2021, 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 in each location (SCORE and AUTEC) from which whales feed. Area-specific differences in habitat quality are reflected in the catchability of prey (parameterized as prey encounter rate). 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., 2021). This leads to negative density-dependent population growth as an emerging property of the model, 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 at stationary state 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).

## 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 1,800 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, 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, based on MFAS use and habitat quality. Areas were categorized as either high- or low-quality habitat to minimize the number of spatial units per location and ensure convergence of the estimation of transition rates (see *movement* section). Assessments of spatial variation in the quality of beaked whale habitat at SCORE and AUTEC are presented in Southall et al., (2019) and Benoit-Bird et al. (2020), respectively. Specifically, both ranges were divided into a western, high-quality area and an eastern low-quality area. Because of the specific topography of the Tongue of the Ocean, there were three areas outside the AUTEC range which encompassed all locations of tagged individuals (Fig. 1a). 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, and a single low-quality off-range area south of AUTEC (Benoit-Bird et al., 2020). For SCORE, we modelled single off-range area that was free of sonar and of low quality (Fig 1b).

## 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 as an estimate for . 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 low-quality 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; Fig 1). 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., 2022). 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., 2022). 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* (columns). We did not consider time-dependence of transition rates or dependence on any covariates. If sonar exposure led to displacement from the range, modelled individuals were translocated to an off-range area (see *disturbance* section), but their subsequent transition rates remained unaffected. Therefore, we assumed that the fitted transition rates reflect baseline movement patterns of *Md* and *Zc* around their respective ranges. Calves were assumed to have the same location as their mothers at all times.

## 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 characterized by their 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 length-weight relationship is used to calculate structural mass from structural length.

Either the absolute amount of reserves or its relative extent (*i.e.* the ratio between reserve mass and total body mass, referred to as *body condition*) determine various energetic and life history processes, such as feeding, lactation, mortality and initiation of reproduction. Individual body condition determines prey feeding rate and milk consumption rate (for calves only) through the feeding level (0 – 1), which is a decreasing, sigmoidal function of body condition. As such, the feeding level is higher for whales in poor body condition, which could for example result from disturbance, low prey availability or high energy expenditure (e.g., during lactation). Simultaneously, the feeding level decreases at high body condition, to ensure that reserve mass does not grow out of bounds under favorable conditions. For lactating females, individual body condition affects the milk provisioning rate. Females in poor condition reduce milk supply to their calf and milk supply ceases completely when female body condition drops below a starvation threshold value. Age and structural size also influence the prey feeding rate and the milk consumption rate for calves. Prey feeding increases with age throughout the early years of life (for calves and newly weaned individuals), while milk consumption rate declines with age up to the age at weaning, when lactation stops. In addition, milk feeding rate is proportional to structural surface-area. Prey feeding follows a type II functional response of prey density with area-specific prey encounter rates (attack rate) and a maximum prey consumption rate that is proportional to structural surface area. 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. In addition to natural mortality, whales with a body condition below the starvation body condition threshold suffer from starvation mortality at a rate that increases with declining body condition. Reproduction is initiated when absolute reserve mass exceeds a predetermined pregnancy threshold value, following Klanjscek et al., (2007).

Depending on an 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 are negligible. The mass of the fetus is included in the maintenance body mass of pregnant females, and 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 decreases when the opposite is true. The difference in metabolic efficiency between storing (anabolism) and mobilizing (catabolism) reserve mass is taken into account.

## Exposure to MFAS

For both ranges, information on MFAS use and beaked whale echolocation were derived from passive-acoustic monitoring of range hydrophones. Data consisted of hourly counts of beaked whale dive starts per hydrophone and hourly 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, during which no monitoring occurred, were excluded. This 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 (western vs eastern areas/spatial units; Fig. 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 the two years for each range. This resulted in a standardized measure of sonar use, which we refer 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 model the number of dive starts per spatial unit per hour as a function of a series of covariates. Specifically, each GAM tested for the effects of 1) standardized sonar area; 2) spatial unit within the range (western vs eastern areas); 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 or 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 predicted effect of standardized sonar area on beaked whale dive start rate provided an estimate of the relative decrease in beaked whale foraging activity (*z*) as a result of sonar use. Here, *z* = 1.0 indicated 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, such that each event was characterized by a starting time (d), a *z*-value and a duration (in multiples of one hour). For each location, the time series of events for eastern and western areas were merged and served as input to the individual-based population model. In model scenarios with sonar, we repeated the same time series of sonar use ad infinitum.

## Disturbance

Whales were assumed to be exposed to sonar if they were present on a range area at the onset of a sonar event. Upon exposure, the *z*-value of that particular event was used to calculate the number of disturbed whales. We simulated three different 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. To clearly distinguish between effects of displacement and cessation of foraging, we assumed that displaced whales did not loss foraging time and continued foraging in the area they were displaced to. In cessation of foraging scenario, we calculated the number of 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 by a previous sonar event were included in *Ni,d* , 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 , which resulted in a default mean disturbance duration of 1.5 days with a standard deviation of 1.06 days. The disturbance duration was used to set the future time at which the whale would resume foraging: *t + td*.

In the displacement scenario, the number of whales displaced was calculated relative to the stable distribution of individuals across areas. This distribution followed from the baseline movement pattern as dictated by the transition rate matrix **Q**. More specifically, the number of whales displaced equaled: *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. As for the cessation of foraging, 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 displaced whales were moved to the off-range area directly to the north. 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 MFAS 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) (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.

We simulated the onset of MFAS use on a previously undisturbed population residing at its stationary state, distinguishing between the three different behavioral response to MFAS. Because prey productivity rates were adjusted to match observed low beaked whale population abundances, there were considerable effects of demographic stochasticity. Therefore, we ran 100 replicate simulations for each behavioral response scenario and present mean (+/- sd) of population density. We inferred the rate of population decline from the dynamics of total population abundance. For the cessation of feeding scenario, we studied how fast the population would recover once use of MFAS stopped. In addition, we studied the effect of varying 1) the prey attack rate parameter in high-quality areas () and 2) the transition rate matrix **Q**. For each of combination of these, we readjusted the parameter describing maximum prey density (*Rmax*) to ensure a population abundance of around 100 *Zc* individuals, or 60 *Md* individuals. The sensitivity to the transition rate matrix **Q** was explored by applying a 10-fold decrease to all rates that described transitions from on-range areas to off-range areas. We furthermore studied the effect the pattern of MFAS use and the mean disturbance duration on population abundance. In addition to the effect on population abundance, 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, the mean duration was 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 five 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 (mean of 11 hours). 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 are on the western part of the range (24% vs 5.5%). The north-western off-range area hosts the largest percentage of the *Md* population (31%). The north-eastern and southern off-range areas host similar percentage of the population (19% and 21%, respectively).

## Exposure and response to MFAS

Within the two years of data analyzed, MFAS was used more frequently on SCORE than on AUTEC, with sonar events occurring in 8.4% and 2.9% of all recorded hours on each range (Fig. 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 for all hours with sonar on the western range areas was higher for AUTEC than for SCORE (0.537 vs. 0.384, respectively), but not so 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 of beaked whale foraging activity (Fig. 2). On AUTEC, there was little effect on beaked whale dive count rate at low sonar intensity, but the relative decrease in dive count rate on AUTEC at the maximum recorded MFAS use was larger than on SCORE (0.71 vs 0.53; Fig. 2). For AUTEC, the GAM 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 (Fig. 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 (Fig. S4). There was also an effect of the duration of the sonar bout, but this effect disappeared when temporal autocorrelation was accounted for. 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 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 rapid initial decline of *Zc* population abundance and a subsequent slower approach of the population to a new stationary state (Fig. 3). This decline occurred across all three behavioral response scenarios but was greatest if MFAS led to both displacement and cessation of foraging, in which case the *Zc* population went extinct in all replicate simulations. Either displacement or cessation of foraging alone led to an approximately 50% reduction of population size. For cessation of foraging behavioral scenario, half of the decrease in population abundance occurred within the first 5 years after the onset of MFAS, while it took another 26 years before mean population abundance was within 1 per cent of the mean disturbed population abundance. Among females in the different reproductive classes, the decline in abundance was most pronounced for lactating females. Because of the coupling between predator and prey dynamics, prey density increased in response to the relaxation of foraging pressure caused by the decline in whale population abundance (Fig. 3). The magnitude of the increase in prey density mirrored the reduction in abundance of the *Zc* population following the onset of MFAS use. Disturbance from 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 the intervals between MFAS events. Recovery of the *Zc* population when MFAS ceased was slower compared to the initial population decline. It took on average approximately 66 years for the *Zc* population to recover from MFAS disturbance that led to cessation of foraging (Fig. 3). During the first 30 years of recovery, the population growth rate equaled 1.13% per year.

For *Md* at AUTEC, the effect of disturbance from MFAS on mean population abundance was largest for the cessation of foraging behavioral response, with an approximate 45% reduction of mean population size (Fig. 4). MFAS-induced displacement of *Md* individuals from the AUTEC range led to a slight increase of mean *Md* population abundance (from 59 to 65 individuals). The cessation and displacement behavioral response induced an effect on mean population abundance that was in between the effect of the two responses in isolation. The decline of mean *Md* population abundance was much slower compared to *Zc* at SCORE; half of the initial decrease occurred within around 24 years, on average, and it took another 123 years before the population was within 1 per cent of the mean disturbed population abundance (Fig. 4). The onset of MFAS at AUTEC also changed prey density and its variation, but the size of this effect was much smaller compared to SCORE. The recovery of the *Md* population after MFAS has ceased was slower than for *Zc* and took approximately 156 years. The initial 50% of mean population recovery took around 59 years, corresponding to a yearly growth rate of 0.59%.

The sensitivity of model outcomes to movement patterns were investigated by adjusting the matrix with transition rates between areas (**Q**) and changing the attack rate ratio . With the adjusted **Q**-matrix, a larger fraction of the population was present on the range under baseline condition with 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 66% and 15% in the western and eastern range areas (Table 1).

For both species, the relative pattern of population abundance across the different disturbance scenarios was robust against changes in **Q** and . For *Md*, MFAS-induced cessation of foraging had the largest negative effect on population abundance, while displacement by MFAS led to a slight increase in population abundance. However, for , in which case there are no differences in habitat quality between areas, displacement did not affect *Md* abundance and the other two scenarios had a similar effect. For , the adjusted **Q** – matrix led to extinction of the *Md* population in case the response to MFAS disturbance included cessation of foraging. For *Zc* displacement from SCORE had a larger impact on population abundance than cessation of foraging and this pattern was especially pronounced for the adjusted **Q–** matrix. The combination of displacement and cessation led to extinction of *Zc* population. For , MFAS-induced displacement did not affect population abundance, but displacement did reduce the effect of cessation of foraging.

For both species, the pattern of MFAS use at SCORE had the largest effect on population abundance (Fig. 6). Applying the MFAS time-series from SCORE to the *Md* population led to extinction of *Md* in the cessation of foraging scenario, and to an even higher increase in population abundance in the displacement scenario (Fig. 6). Conversely applying the MFAS time-series from AUTEC to the *Zc* population decreased the disturbance effect on population abundance and ensured persistence of *Zc* under all behavioral scenarios considered.

Increasing the mean duration of cessation of foraging led to a further decrease in population abundance of both species, but did not change the relative pattern of the effect of MFAS disturbance (Fig. 7). For *Zc*, cessation and displacement led to lower population abundances than cessation of foraging alone, irrespective of the mean disturbance duration. For *Md*, displacement by MFAS relaxed the effect of cessation of foraging across all disturbance durations considered.

## Disturbance effects on life history and body condition

For both species, life history statistics relating to the onset of reproduction were not affected by disturbance from MFAS and were similar across all behavioral response scenarios (Fig 8). Note that these results relate to females from stationary populations subject to a certain disturbance regime, and not to the transient phase of population decline right after the onset of MFAS. Regarding the onset of reproduction, we distinguished between female age at first receptive, female age at first reproduction and female age at weaning first calf. Because these data represent females from stationary populations, mean lifetime reproductive output was equal to 2 (counting male and females calves born to each female). The 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.

Disturbance from MFAS did not affect body condition of females from stationary populations (Fig. 9) subject to a certain disturbance regime. For both species, body condition is lowest for lactating females and highest for calves, although variation is large in this latter class (Table S6 and Figs. 9). For *Zc*, resting females have lower body condition than pregnant and waiting females. Females with low body condition are more likely to suffer from increased starvation mortality after the onset of MFAS use.

# DISCUSSION

We integrated a wide range of data sources, including telemetry data, information on spatial variation in habitat quality, 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 were repeatedly exposed to navy sonar during their lifetime. We considered the effects of 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. The effect of disturbance on population densities was much larger for *Zc* than for *Md,* because of the larger number of sonar events per year on SCORE. For both species, cessation of foraging and displacement had the largest effect on population density. There was no clear effect of disturbance by MFAS 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 when there were 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 that a decrease in 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 control of prey implies that there is only a weak increase in prey density during MFAS events and this reduces the opportunity for compensatory feeding by whales post disturbance. This mechanism could be driving the stronger relative effect of disturbance at low whale 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. This slow estimated population growth 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 use ends (Taylor et al., 2007).

At low densities, demographic stochasticity can have a significant effect on whale population dynamics, and this will make it hard to detect effects of non-lethal disturbances 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 carrying capacity. These fluctuations will be enhanced by environmental variability or seasonality, neither of which were 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 these sources of uncertainty into the model will likely further increase the predicted variability in population density, and thereby mask the effect of disturbance on population density.

Besides the effect of disturbance on population density, we did not find any effects of disturbance on individual life history once the simulated populations had attained a stationary state. However, females will have reduced reproductive output and experience increased mortality during the initial decline phase following the introduction of sonar. These effects on individual vital rates will likely only be detectable during the first few years after the onset of disturbance. Monitoring programs that focus on individual vital rates would therefore need to start well in advance of any planned disturbing activities, 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., 2021)) and that compensatory effects on individual life history can occur through a disturbance-induced release of top-down control of prey (Hin et al., 2021). Using the same energy budget model, but parameterized for long-finned pilot whales, Hin et al. (2021) showed that non-lethal disturbances that resulted in cessation of foraging for multiple, consecutive days each year led to increased mortality among young females that were nursing their first calf and increased reproductive output of older females. In addition, non-lethal disturbance increased mean body condition in the population 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. (2021) 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.

Although we used realistic patterns of MFAS disturbance derived from passive acoustic data and direct measurements of movement rates and prey availability, there are many sources of uncertainty in our model and a full sensitivity analysis is unfeasible at this point. However, the finding that populations that are subject to repeated disturbance rapidly attain a new, stable population structure if there is 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 did not 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.

# References

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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 |