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14. ABSTRACT

The overall objective of this project is to overcome the most important impediments that have limited the implementation of the PCoD framework. These include:

- the lack of a standard method for assessing aggregate exposure to disturbance over a biologically-realistic time scale;
- the difficulty in choosing an appropriate model structure;
- the lack of a robust, fully-tested protocol for conducting expert elicitation that can provide reliable estimates of associated uncertainty; and
- the lack of data on the relationship between exposure to disturbance and individual health, and between health and vital rates,

We will address these issues by completing five research Tasks. These will deliver a set of research documents that will facilitate the wider application of the PCoD approach.

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PCoD+: Developing widely-applicable models of the population consequences of disturbance

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LONG-TERM GOALS

As part of the permitting process under the Marine Mammal Protection Act and the Endangered Species Act, the Office of Protected Resources is required to determine whether or not a proposed activity will cause negligible impact to the animal species or stocks inhabiting the area. This determination involves examining the potential effects of the activity on the demographic parameters of the species or stocks in question. The Population Consequences of Disturbance (PCoD) framework is designed to provide exactly this information, and this project will explore ways to improve the capabilities of such models and make it easier to develop new models for particular species and stocks. The outputs from this project therefore have the potential to be developed for operational use by the Navy as part of its environmental impact assessments. In future, these assessments will likely be required to provide information on the potential population-level consequences for marine mammals of exposure to anthropogenic noise as well as the number of animals that may show a behavioral response. However, there are still significant uncertainties associated with many of the steps that are involved in predicting these population-level consequences.

OBJECTIVES

The overall objective of this project was to overcome the most important impediments that have limited the implementation of the PCoD framework. These include:

- the lack of a standard method for assessing aggregate exposure to disturbance over a biologically-realistic time scale;

- the difficulty in choosing an appropriate model structure;
- the lack of a robust, fully-tested protocol for conducting expert elicitation that can provide reliable estimates of associated uncertainty; and
- the lack of data on the relationship between exposure to disturbance and individual health, and between health and vital rates,

We addressed these issues by completing five research Tasks, delivering a set of research documents that will facilitate the wider application of the PCoD approach and highlight the next steps for this research field.

APPROACH

We assembled a project team with extensive experience of the development and application of PCoD models to develop a widely-applicable and general approach for assessing the consequences of disturbance for marine mammal populations. The team was supported by an equally-experienced Scientific Advisory Panel, and built on the activities of the PCoD working group and the ONR- and SERDP-funded behavioral response studies.

This project was also conducted in close collaboration with two projects that have been funded by the E&P Sound and Marine Life JIP: "A Bioenergetic Model to Estimate the Population Consequences of Disturbance" (PI Dan Costa) and "Updating the Southall et al. (2007) Marine Mammal Noise Exposure Criteria" (PI Brandon Southall). It was intended that this latter project will provide a new severity scale for behavioral responses more closely linked to the fitness consequences of different behaviors and will attempt to categorize marine mammal species by their ecological sensitivity to noise as well as their hearing capabilities. Members of the team assembled for this project are already involved in those JIP-funded projects.

Task 1. Develop Methods for Assessing Aggregate Exposure. (Lead PI: Thomas)

Develop a standard methodology that can be used in combination with existing Navy tools (3MB and NAEMO) for determining the number of animals likely to be disturbed by a particular training or testing exercise to estimate the aggregate exposure to disturbance of individual marine mammals over a biologically-meaningful period (probably 1 year). An estimate of aggregate exposure is an essential input into any PCoD model that is not provided by existing tools for modeling movement.

Task 2. Develop a PCoD Decision Framework. (Lead PI: Harris)

Researchers are regularly asked for advice on the potential population-level effects of a particular activity, yet there is rarely sufficient data for them to develop a full PCoD model that could be used to provide this advice. Following a thorough review of the literature, we planned to develop a decision framework that can be used to prioritise the development of PCoD models for the populations that may be most affected by disturbance, and to determine what kinds of PCoD model (full PCoD, or simpler models based on bioenergetic modelling, proxy relationships, or expert elicitation) are most appropriate for the high-priority populations.

Task 3. Create Benchmark Models. (Lead PI: Harwood)

We aimed to advance PCoD models, which are based on extensive datasets and detailed information on the potential effects of perturbations, so that they can be used as benchmarks for assessing the data requirements and sensitivities of simpler PCoD models (e.g. those that are based on bioenergetic modelling, proxy relationships, or expert elicitation). We used these benchmark models as case studies in determining which functions, parameters, and processes create the most uncertainty in population growth rate estimates, and investigate the effects of sample sizes, data collection methods, and levels of natural variability on estimates of population growth rate. The aim was that analyses would provide an understanding as to where sample sizes are important, when data collection methods need to be addressed, and when levels of natural variability may overshadow changes in populations due to disturbance.

Task 4. Develop a Standard Protocol for Expert Elicitation in a PCoD Context. (Lead PI: New)
The 'PCoD-lite' (Award: N000141410406) project developed a novel set of software tools that allowed experts to quantify their uncertainty and visually assess whether their response would be appropriate in the context of the relevant model. However, in general in subsequent expert elicitation (EE) exercise have resulted in large amounts of uncertainty associated with the extracted parameter estimates. We believe this is because the experts were unfamiliar with the EE process and that they projected their uncertainty regarding the approach into uncertainty in their parameter estimates. This project intended to build upon what we have learned from the PCoD-lite project and the recommendations of a recent review by the European Food Safety Authority (EFSA, 2014) of EE approaches to construct a more generally applicable and reliable approach to EE in the context of PCoD. We proposed to develop an expert elicitation 'e-learning course' to help train experts in advance of EE workshops and improve the quality of the EE process and consequently, increased confidence in the outputs. We also intended to use expert elicitation tools in expert elicitations to develop, test and improve EE protocols for PCoD.

Task 5. Identify Priorities for Monitoring Programs. (Lead PI: Booth)
Fleishman et al. (2016) identified four elements that should be included in the design and implementation of a monitoring program to investigate the potential effects of human activity on marine mammal behavior and physiology, and the population-level consequences of any behavioral and physiological changes. We planned to investigate how this approach could be used in the design of monitoring program for marine mammals on Navy ranges so that they could inform PCoD models. We used the information generated from the preceding steps to develop observation models that describe the relationship between the chosen response variables and the underlying processes of the PCoD model to help identify early warning signs of population change. Response variables will be chosen on the basis of their sensitivity to the changes in vital rates predicted to occur as a result of disturbance, and the precision with which they can be measured.

WORK COMPLETED

Task 1: We developed a computationally-efficient model fitting and simulation framework for assessing the distribution of aggregate exposure for individuals in a population over an annual time scale. The computational efficiency was achieved in two ways. First, to avoid having to track individual animals at a fine spatial and temporal resolution for an entire year, we have developed both coarse- and fine-scale models; the coarse-scale model operated with a daily time step, and allowed us to determine whether each animal was inside the area where sonar may operate, or outside. Only animals that were inside were subjects for the fine-scale model, which operated at time-scales down to a second and in continuous space. Second, the fine-scale model efficiently approximated the animal's trajectory by considering only the locations of dive starts, the duration of each dive and the depth distribution. To provide realistic tracks, we considered methods of estimating the movement model parameters from data. Case study datasets came from telemetry data on Cuvier's beaked whales and fin whales. See 'Results' and 'Publications' for further details.

Task 2: We developed a decision framework that can be used to prioritize the development of future PCoD models and to identify the most appropriate form of model for a given population, based on likely data availability. Within the framework we first assessed potential risk by mapping the sensitivity of a species to disturbance against the proportion of the population that may be exposed. If a population was identified as being at risk from an activity, then its' susceptibility was assessed. Susceptibility was determined, in part, by the reproductive strategy of the population, the activity state of each life-history stage and any spatio-temporal restriction on range (driven by e.g., prey availability). For highly susceptible populations, data availability can then be used to direct PCoD model choice. In September 2017 we completed a first draft of the decision framework and presented it at a workshop in St Andrews to a group of invited experts consisting of marine mammal scientists and those involved in regulation, impact assessment and policy. The workshop participants applied the decision framework to a series of case studies that had been prepared in advance. This work was also presented at the Society of Marine Mammalogy Conference in 2017 and following that meeting, there was an opportunity for feedback and discussion with Navy and NOAA personnel, allowing refinement of the framework. See 'Results' and 'Publications' for further details.

Task 3: Work has been completed on the development of benchmark models for this project. We reviewed and compare other bioenergetics model that are being developed at UCSC and as part of the ONR-funded PCoD+ project. Table 1 summarises the main similarities and differences between these models. The approach originates from the tenet that behavior is an evolutionary trait and and is therefore conditioned on the environment and an individual's physiological state so that fitness is maximised. SDP models involve two primary components, a backwards iteration where behavioral decisions are identified, and an individual-based forward simulation where the state dynamics and behavioral decisions of a set of individuals is simulated. Anthropogenic disturbance can be introduced in the forward simulation under the assumption that it is not in the evolutionary history of the organism, and thus does not influence the behavioral decisions generated in the backwards iteration. The backwards iteration consists of (1) identification of a time horizon, (2) characterization of physiological state variables and how they change in response to the environment and behavior, (3) definition of a function that links the state variables(s) to a measure of Darwinian fitness (referred to as the terminal fitness function), and (4) derivation of the SDP equations that predict the behavior of individuals based on state and time. PDRA Hin described a generalised DEB model for medium-sized odontocetes that he had developed with André de Roos and John. This model combined some features of the beaked whale energetics model developed by New et al. (2013) with the DEB model framework described in De Roos et al. (2009). In these models, density dependence emerges from the interaction between resource consumption and the productivity of the environment. Parameter values were based on the extensive data for North Atlantic long-finned pilot whales documented in Donovan et al. (1993). The form of the functions determining the behavioral and physiological decisions made by a female are chosen by the modeller, rather than emerging from the backward iteration process as they do in SDP. We develoeped the SDP bioenergetic model for pilot whales, and compared with the results by Hin et al. 2019. The aim was to identify the aspects of the model determining the differences between the two approaches and explore their relevance for modelling the population consequences of disturbance. The 'in press' manuscript focused on discussing the influence of reproductive strategy (particularly in terms of risk propensity and fitness maximization) on individuals' susceptibility to disturbance. See 'Results' and 'Publications' for further details.

Task 4: We have completed the online e-learning EE resource and continue to develop the PEEP templates and guidance. We are still developing the manuscript describing past expert elicitations on beaked whales. See 'Results' and 'Publications' for further details.

Task 5: The principal objective of this task, was to identify a suite of suitable response variables that could inform future PCoD analysis of the effects of Navy activities on marine mammal populations. To achieve this, we conducted a review of the existing scientific (published and grey) literature to explore suitable response variables and methodologies. We also carried out a series of simulations (to form a sensitivity analysis) using existing PCoD models (harbour porpoise, bottlenose dolphin and Blainville's beaked whales (the latter developed as part of ONR Award: N000141410406)) to determine if it possible to identify early warning signal of future changes in abundance, by monitoring demographic characteristics of populations. This technical report is finalized and the work went through peer-review and was published in 2020. See 'Results' and 'Publications' for further details.

RESULTS

This project has produced a number of open-access, peer-reviewed publications, which are summarized here. The project website provides a repository for all publicly available publications at the time of reporting preparation: http://www.smruconsulting.com/products-tools/pcod/pcod-plus-home/

Task 1: Assessing the patterns of wildlife attendance to specific areas is relevant across many fundamental and applied ecological studies, particularly when animals are at risk of being exposed to stressors within or outside the boundaries of those areas. Marine mammals are increasingly being exposed to human activities that may cause behavioural and physiological changes, including military exercises using active sonars. Assessment of the population-level consequences of anthropogenic disturbance requires robust and efficient toolsvto quantify the levels of aggregate exposure for individuals in a population over biologically relevant time frames. We have developed a computationally-efficient model fitting and simulation framework for assessing the distribution of aggregate exposure for individuals in a population over an annual time scale. To achieve this efficiency, we divide the task into two components: a coarse-scale model that determines on a per-day basis whether each individual animal is inside or outside a defined region where it may be exposed to sonar, and a fine-scale (minute- or second-level) model that tracks movement and diving of animals that are within the region where sonar exposure may take place. Parameters for the course-scale model can be estimated from data using a discrete-space continuous-time hierarchical Markov model, with transitions between regions modelled as a function of sonar presence and other covariates, and between-animal differences accounted for using a random effect. We are trialing the approach using data from the SOCAL range on Cuvier's beaked and fin whales (data provided by MarEcoTel) and on Blainville's beaked whales from the AUTEC range (data provided by NOAA and BMMRO). The fine-scale model is purely a simulation approach, with parameters "plugged in" from literature values; we are trialing it with data on fin whales in southern California provided by project partners. A simulation exercise confirmed that the method works and is able to detect potential changes in usage.

For coarse scales, we proposed a discrete-space, continuous-time approach to estimate individual transition rates across the boundaries of an area of interest, informed by telemetry data collected with uncertainty. The approach allows inferring the effect of stressors on transition rates, the progressive return to baseline movement patterns, and any difference among individuals. We apply the modelling framework to telemetry data from Blainvilles beaked whale *(Mesoplodon densirostris)* tagged in the Bahamas at the Atlantic Undersea Test and Evaluation Center (AUTEC), an area used by the US Navy for fleet readiness training. We show that transition rates changed as a result of exposure to sonar exercises on the range, reflecting an avoidance response (Figure 1). Our approach will support the assessment of the aggregate exposure of individuals to sonar and the resulting population-level consequences. The approach has potential applications across many applied and fundamental problems where telemetry data are used to characterise animal occurrence within specific areas.

We developed a modelling approach that quantifies the rates at which animals move across the boundaries of a discrete area of interest. The model can therefore be used to describe patterns of attendance to that area. Individual differences in movement and ranging behaviour, which may lead to heterogeneity in area use, are explicitly evaluated. By fitting a movement model to the raw telemetry tracks, uncertainty in animal relocations can also be accounted for. Moreover, because the Markovian component is formulated in continuous time, the approach does not require observations regularly sampled in time. These features are important, because wildlife telemetry often involves irregular relocations with substantial measurement error (Patterson et al., 2017). Crucially, the method we propose can be used to investigate the repulsive (or attractive) effect of a given stressor or activity, operating either within or outside the target area and affecting the propensity of an individual to cross the boundaries in either direction. Our simulation exercise showed that the model performs well at estimating transition rates and any change associated with exposure to disturbance.

For fine-scale movement, we have developed a 3-D movement methodology that uses a sequential Monte Carlo sampler whose horizontal movement is informed by a whale utilisation surface that reflects animal density. This surface weights the acceptance of a proposed “step” in the movement model, where each “step” includes both the vertical and horizontal displacement corresponding to one dive and its associated surface recovery. Noise disturbance is also incorporated wherein the whale response is mediated through a “dose-response” function tailored to the intensity of the noise level. The forward movement model accumulates the number of times individual cetaceans are exposed and respond to disturbance over a biologically-meaningful period. The strength of the response is treated through the magnitude of the “memory” parameter that informs the directional persistence of the whale away from the source of initial or residual noise disturbance. The approach is first demonstrated with an idealised case that applies the movement model to produce a pseudo-track between dive locations to reconstruct the original utilisation surface. Next we applied the movement model to a population of fin whales in a Navy training and testing activities on the Southern California range complex. The horizontal movement is biased to a whale utilisation surface developed specifically for fin whales in this region with the depth dimension of the sampler informed by D-tag dive data. Resulting cumulative exposures are presented (Figure 2). We propose that the tool developed here is a generic 3-D individual-based movement model that could be adapted to any number of disturbances with known impacts on marine mammal populations.

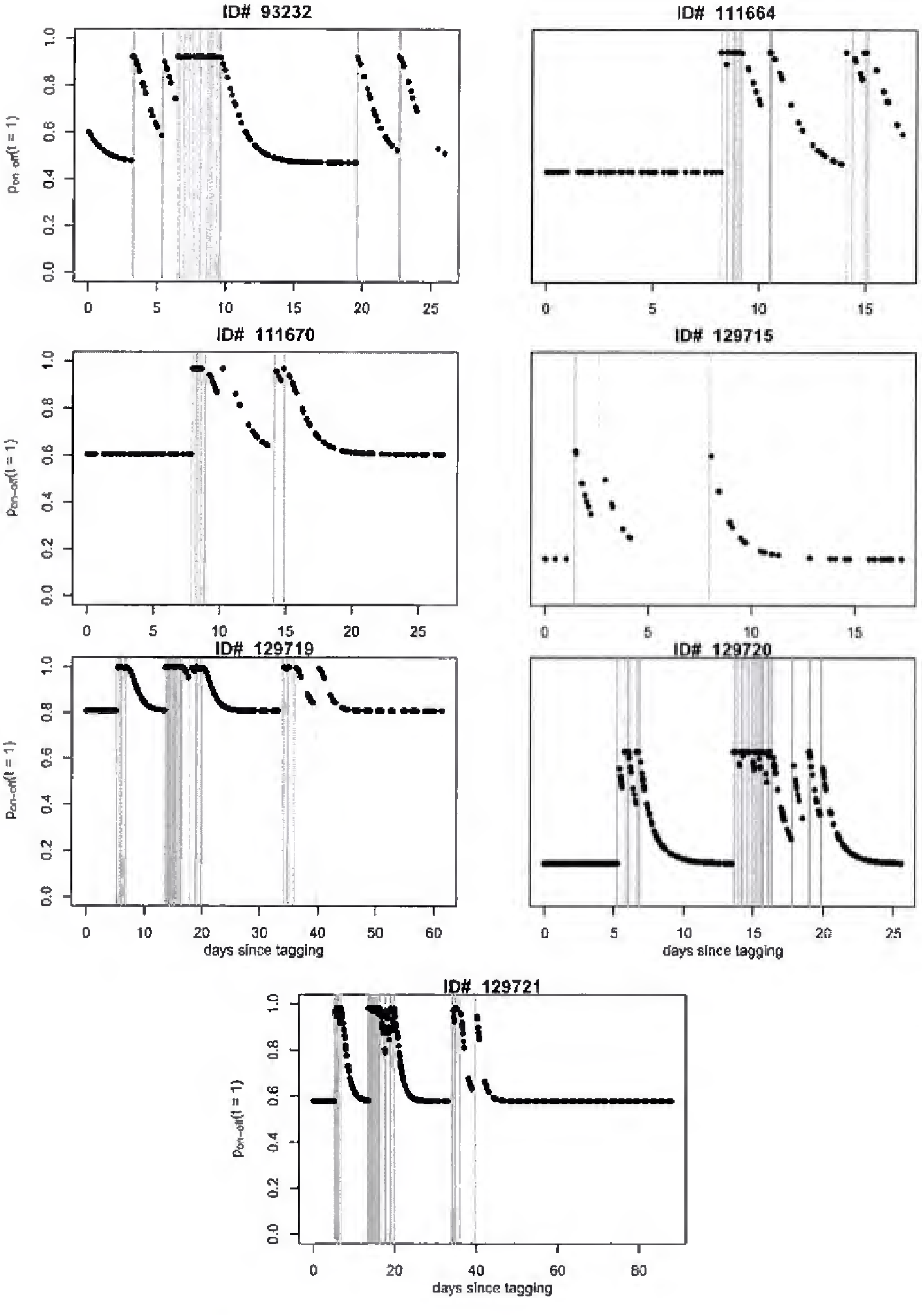

Figure 3: Fitted on–off range transition probabilities, $p_{21}(t = 1)$, for each of the seven Blainville's beaked whales (derived from the corresponding transition rates given by Equation 3). In each plot, the vertical grey lines indicate the time of sonar events; the points represent the time of observed locations (in days) of each individual since tagging. The different horizontal asymptotes in each panel illustrate the differences in baseline transition rates among individuals.

Figure 1 - Figure 3 from Jones-Todd, et al, in review. Full caption above.

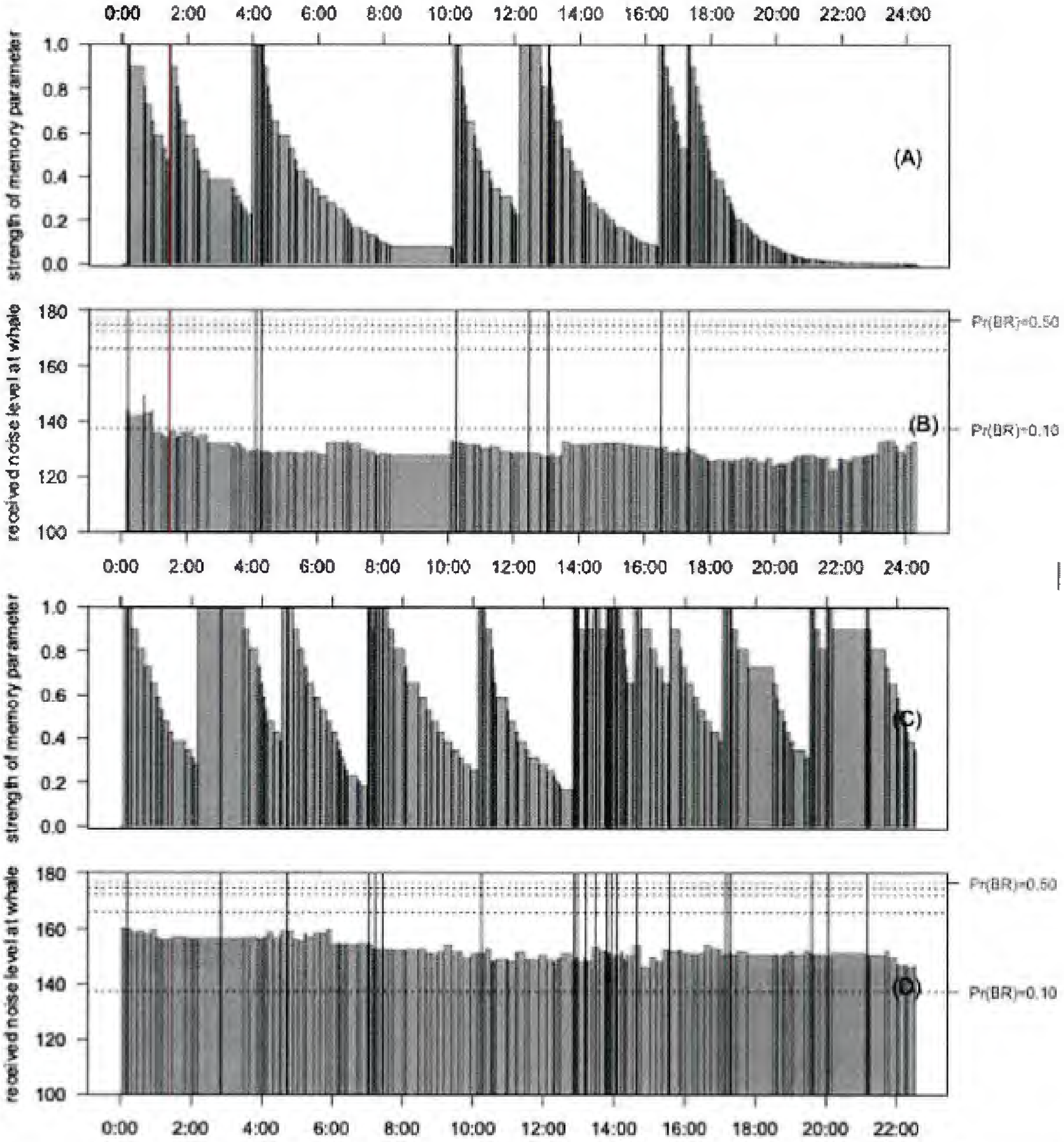

Figure 6: Cumulative exposure over a single day for two different whales. Panels (A) and (B) correspond to a whale that is 49.6 km away from the noise source at the start of the day. Panels (C) and (D) correspond to a whale that is 17.5 km away from the noise source at the start of the day. The horizontal lines in (B) and (D) correspond to the thresholds in probability of a BR ooccurring. The vertical lines denote when they actually occurred in the simulation. In (A) and (C), each bar corresponds to a movement step, on this day of continuous sonar. Notice the higher noise levels (D) than in (B) that corresponds to more BRs in (C) compared to (A).

Figure 2 - From Joy, et al, in prep. Full caption above.

Task 2: We present a decision framework to identify when detailed population-level assessments are required to understand the potential impacts of a disturbance-inducing activity on a marine mammal population and discuss how the framework can be applied to other taxa. Species at high risk of population-level effects can be identified using information on the number of individuals that are likely to be disturbed by the activity, total population size, the probability of repeated disturbance, the species' reproductive strategy, and the life stages (e.g., feeding, pregnant, and lactating)(Figure 3) of the individuals most likely to be exposed. This hierarchical approach (Figure 4) provides those responsible for conducting impact assessments with a time-efficient, cost-effective and reproducible workflow that allows them to prioritize their efforts and assign funds to those species with the most pressing conservation needs. A fully worked case study using marine mammals in the vicinity of a naval training activity is supplied. This case study is for the PACOM exercise in Gulf of Alaska (a discrete two week exercise each year). The use of the decision framework indicates that from a starting point of 41 marine mammal stocks (comprising 22 species) that a total of 10 stocks should be considered further for PCoD model development (seven of these stocks were Endangered Species Act listed species, and so automatically progressed to the further assessment stage). The publication contains the worked example and relevant R code in the Supplementary Information.

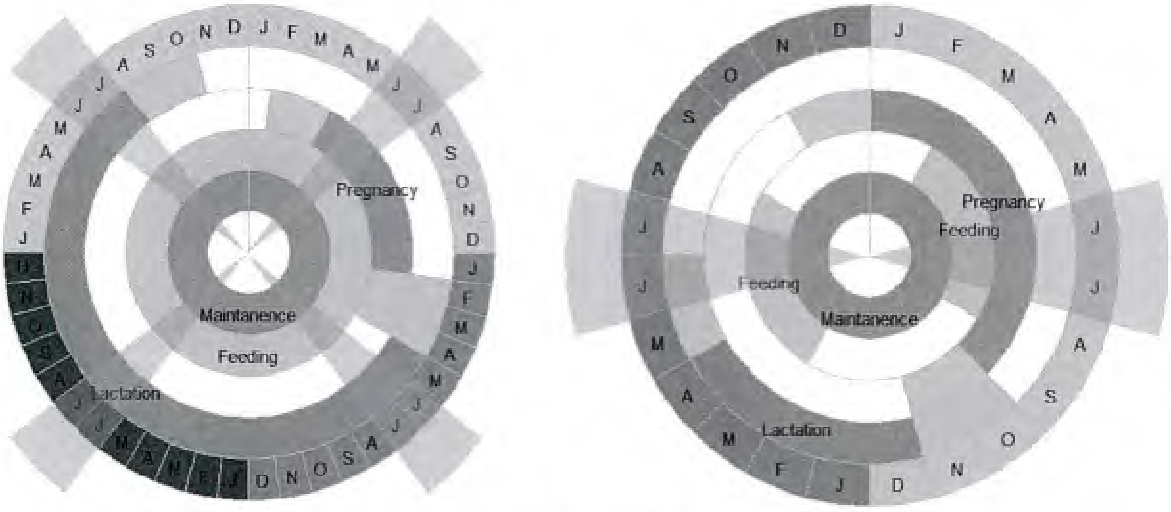

Figure 3 - Life Cycle plots showing the reproductive cycle for Blainville's beaked whale over a four-year period (left) and a fin whale (over a 2-year period). The figures show periods of 'maintenance', feeding and periods of pregnancy and lactation (along with some buffer periods). The green cones indicate user-specified periods of activity, which might be assessed using the decision tree approach.

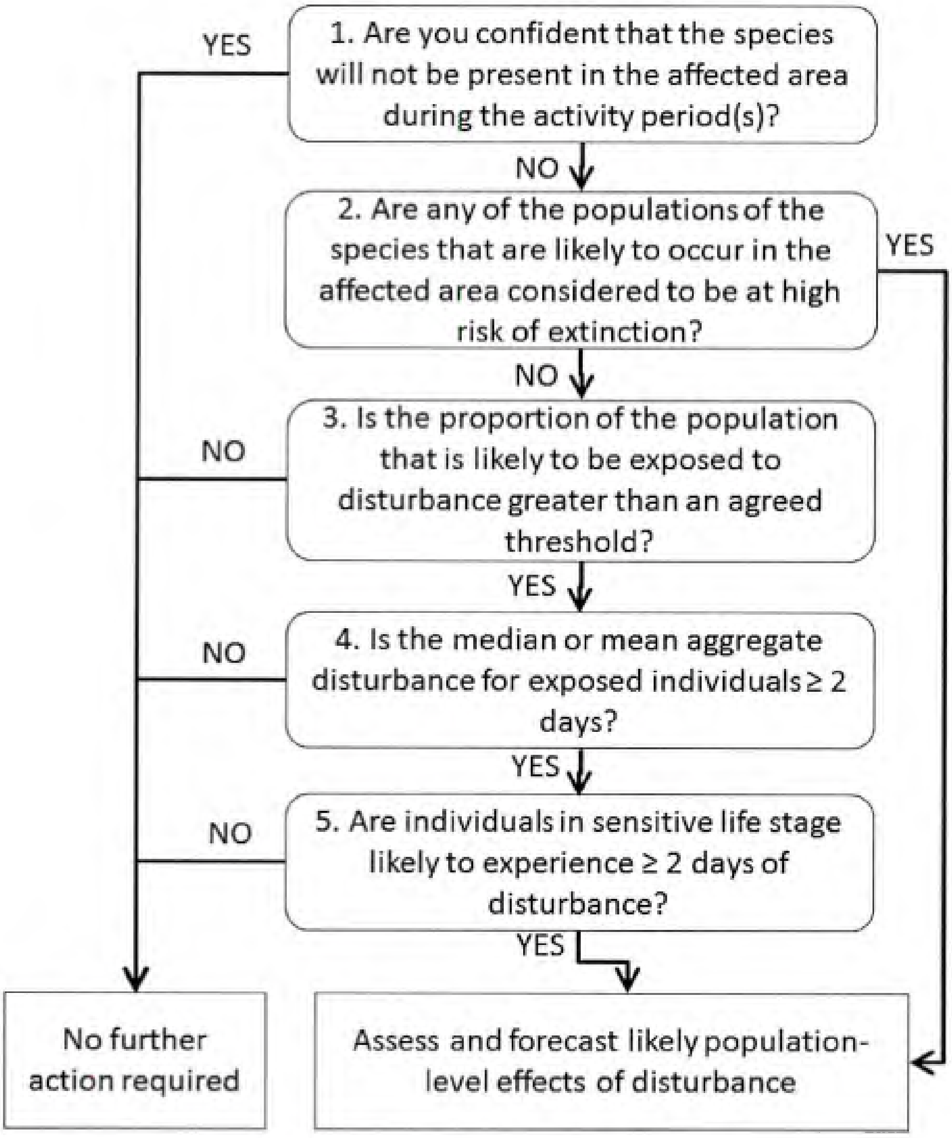

Figure 4 - A decision framework to identify when disturbance-inducing activities are most likely to have population-level consequences. From Wilson et al 2019.

Task 3: The objective of this task was to develop a series of benchmark models for use throughout the PCoD+ project. The majority of modelling efforts were successful (the exception was model efforts on elephant seals and bottlenose dolphins by PI Schwarz) and both DEB and SDP approaches were investigated further. Papers were published summarizing the PCoD modelling efforts to date (Pirotta, et al 2018 – Figure 5), presenting a lifecycle SDP for blue whales in the Eastern Northern Pacific (Pirotta, et al 2019a&b – Figure 6) and a generalized medium odontocete DEB model, parameterized for pilot whales (Hin et al 2019 – Figure 7). These models allowed the assessment of myriad disturbance scenarios, examining both anthropogenic disturbance and the effect of a variable quality environment on survival and reproductive success (Figures 6-7). We reviewed and compared DEB and SDP models that are being developed at UCSC and as part of the ONR-funded PCoD+ project. Table 1 summarizes the main similarities and differences between these models

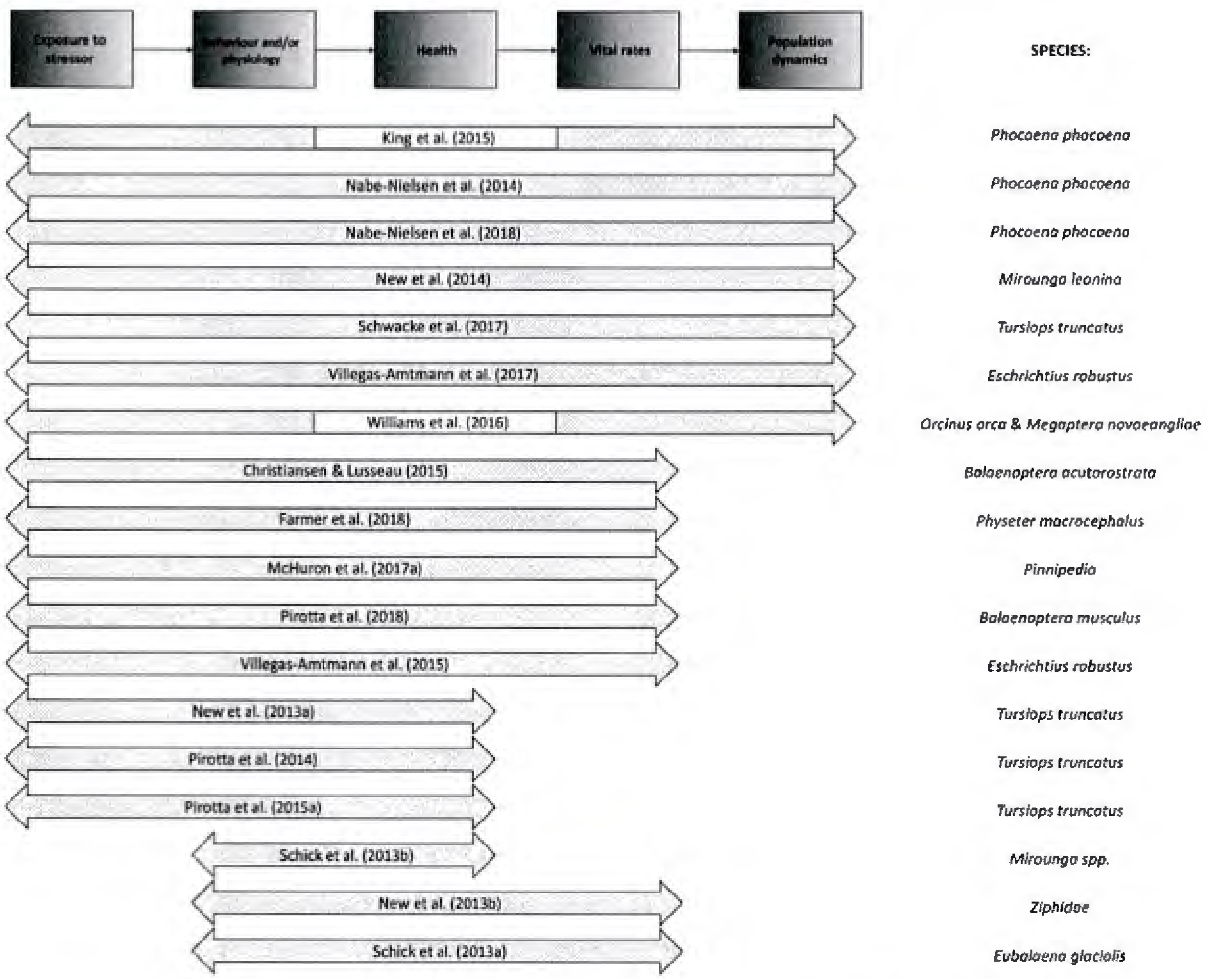

FIGURE 2 Studies investigating the Population Consequences of Disturbance (PCoD) on marine mammals, updated from Nowacek, Christiansen, Bejder, Goldbogen, and Friedlaender (2016). The arrows indicate the functional steps of the framework (simplified on top) that were included in each study. White gaps in the arrows indicate studies that evaluated the link between behavior and vital rates directly, without estimating health

Figure 5 - Summary of PCoD models on marine mammals from Pirotta, et al 2018.

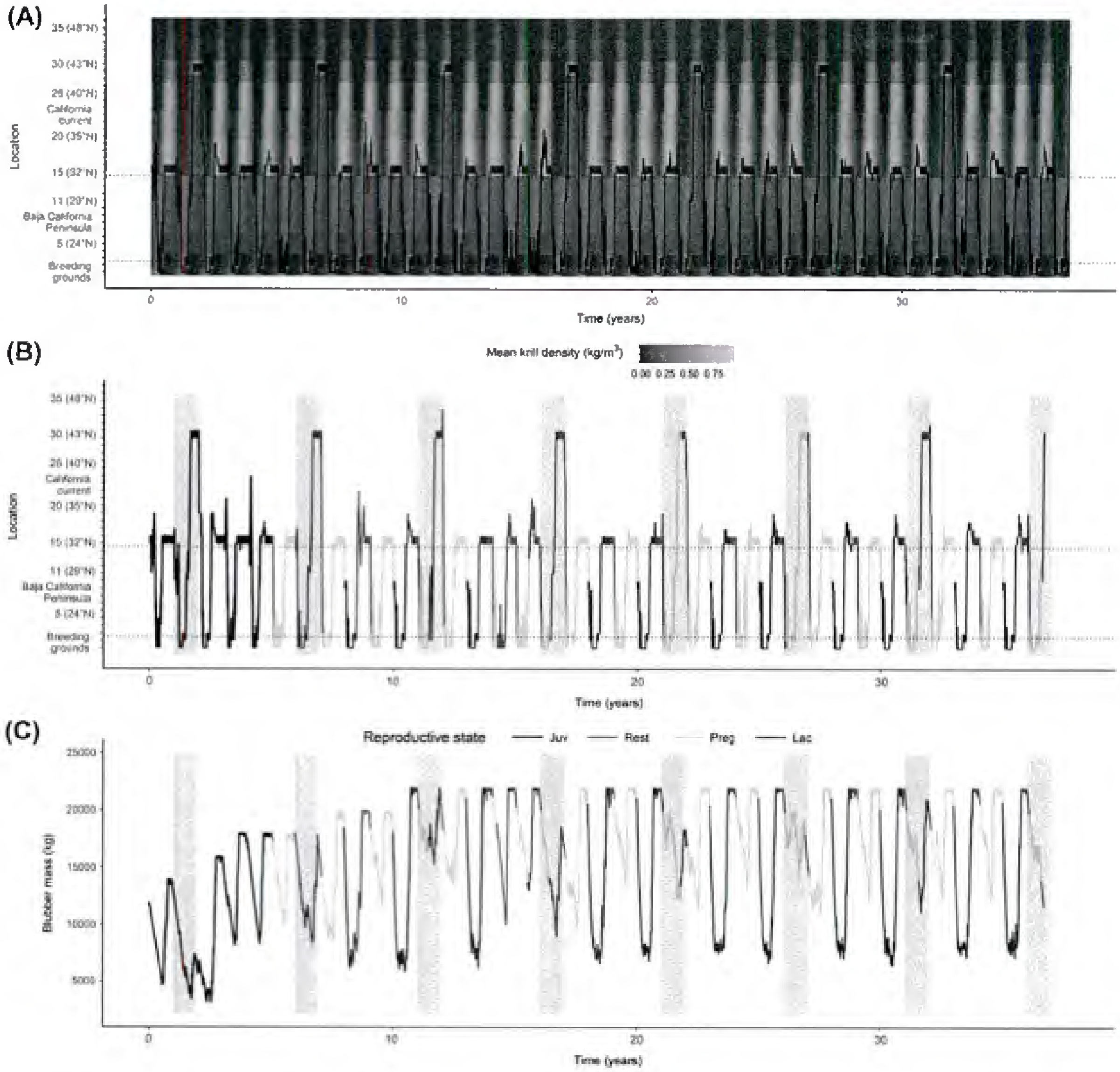

Figure 2. An example of the time series of location (A–B) and blubber mass (C) for one female. In (A), the time series of location is overlaid on a heat map of the spatiotemporal variation in mean krill density (as derived in Pirotta et al. 2018b from the upwelling index). In (B) and (C), the time series is coloured by reproductive state. Possible reproductive states are juvenile (Juv), not pregnant and not lactating (Rest), pregnant (Preg) and lactating (Lac). The grey shaded areas represent unfavourable years. Locations are numbered progressively from south to north from 1 to 36. The corresponding latitude is reported in brackets.

Figure 6 - From Pirotta, et al 2019. Full caption above.

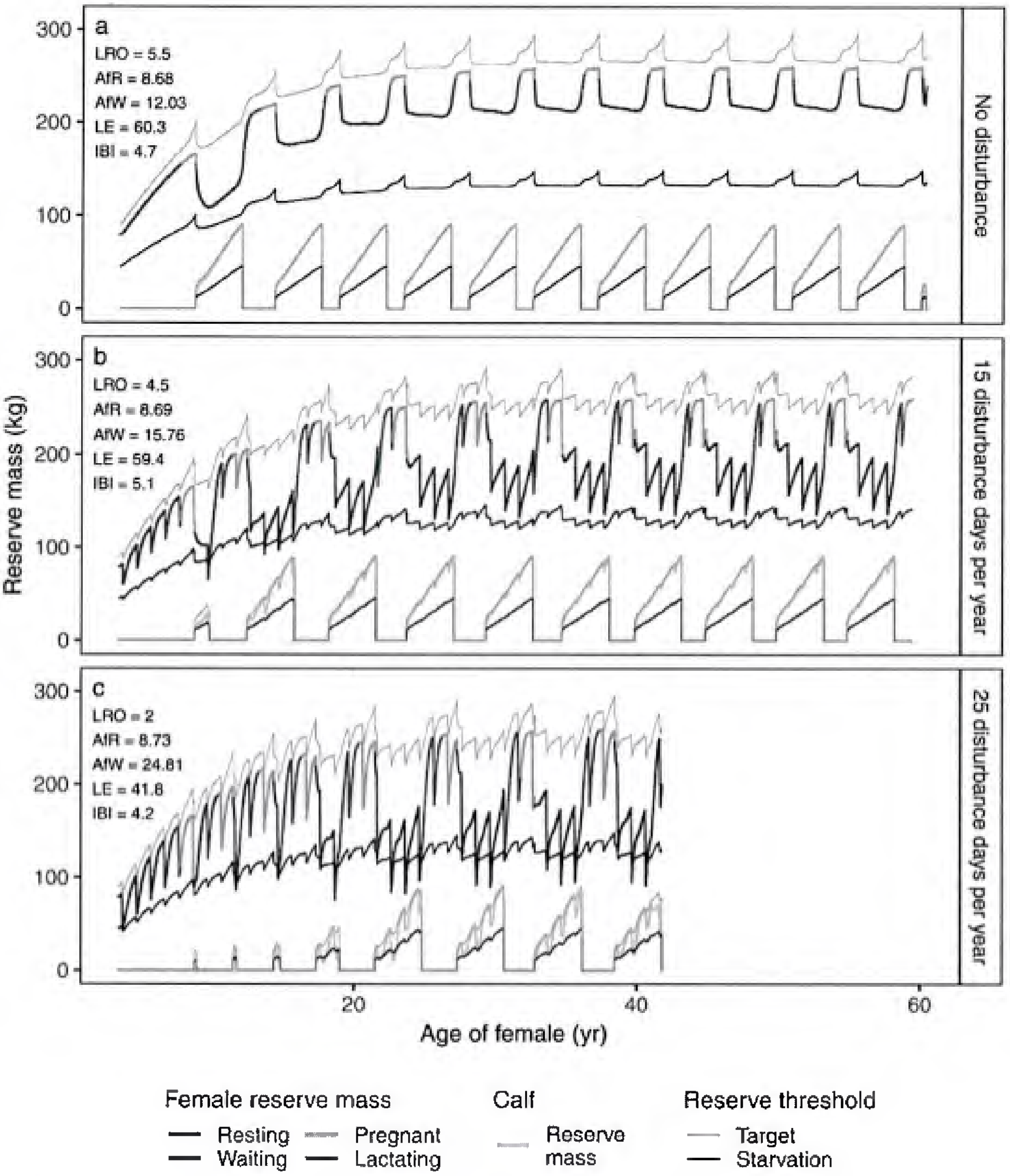

FIG. 2. Reserve mass of the female and her calves as a function of female age for different disturbance periods (0, 15, and 25 d/yr). Female reserve mass is colored according to reproductive status (as indicated). A non-pregnant and non-lactating female is coined "waiting" when her reserve mass is above the pregnancy threshold (not shown) and she awaits implantation, otherwise she is coined "resting." Target and starvation reserve thresholds are plotted for both the female (upper lines) and calves (lower lines) and are equal to total body mass multiplied by $\rho = 0.3$ and $\rho_s = 0.15$, respectively. LRO, lifetime reproductive output (female offspring only); AfR, female age at first reproduction (yr); AfW, female age at which first calf is weaned (yr); LE, life expectancy (yr); and IBI, inter-birth interval (yr). A fixed life expectancy at birth of 60 yr was used, which can only decrease due to additional starvation mortality. Mean annual resource density $\bar{R} = 1.8$ and all other parameters at default values (Appendix S1: Table S1).

Figure 7 - From Hin et al. 2019. Original caption above. N.B: The modelled disturbance events are continuous and result in no energy intake on those days. As such they are unlikely to represent real-world disturbance scenarios.

Table 1 - Comparison of models developed by UCSC and those being developed as part of Task 3 of PCoD+.

Model characteristics	Blue whale (SDP)	California sea lion (SDP)	Gray whale (SDP)	Pilot whale
Environment	Spatial and temporal variation in prey field explicitly modelled	Homogeneous prey field	Spatial and temporal variation in prey field explicitly modelled	Relative prey field affected by predator consumption, with or without seasonal variation
Time horizon	Single reproductive cycle (as published) and cradle-to-grave	Cradle-to-grave and multigenerations	Foraging season	Cradle-to-grave and multigenerations
Population level	Yes	Yes	No	Yes
Density dependence included?	Yes, but exogenous	No	NA	Yes, w/ resource coupling via predator consumption
Structural growth curve	Length determined by fixed growth curve. Linear for fetus length	Length determined by fixed growth curve which sets maximum reserves. Linear for fetus length	None for adults, Gompertz for fetal length	Length determined by fixed growth curve. Linear for fetus length
Field metabolic rate	Depends on size and activity budget	Depends on size, activity (ashore or at sea) and age class	Depends on activity budget?	Depends only on size
Energy reserve metric	Female lipid mass, calf relative condition	Female and offspring lipid mass	Female lipid mass	Female and offspring lipid mass
Compensation for decreased energy reserve	Emergent property	No	Emergent property	Foraging motivation determined by energy reserves
Relat. bet/w foraging efficiency and age	No	No	NA	Yes
Onset of reproduction	Length threshold, facultative	Age threshold, facultative	Already pregnant	Lipid mass threshold but precise timing stochastic
Abortion possible	Yes, facultative	Yes, facultative	No	No
Offspring size var.?	No	Yes	Yes	No
Milk delivery	Exogenous, allocation dependent on mother and offspring states	Exogenous, allocation dependent on mother and offspring states	NA	Exogenous, allocation dependent on mother and offspring states
Early weaning/calf abandonment	Facultative	Facultative	NA	Obligate
Background mortality	Age class specific	Age class specific	Constant (only one age class)	Age specific Siler model
Starvation mortality	Certain if lipid reserves falls below a defined threshold	Fixed, age dependent	Occurs at fixed lipid mass	Mortality risk increases progressively if proportion of lipid falls below a defined threshold
Disturbance response	Can move away, or stay with reduced foraging efficiency	Has to stay with reduced foraging efficiency which extends foraging trip duration	Can move away, or stay with reduced foraging efficiency	Has to stay with reduced foraging efficiency

Although the SDP and DEB models differ in their detail, they model the same basic bioenergetic processes in a similar way. The most important differences are in the way interactions between the predators and their resources are modelled, and the way in which parameter values and the functions describing behavioral and physiological decisions are chosen. We concluded that a high priority should be given to the development of matched SDP and DEB models for the same marine mammal population. To explore the trade-offs between internal state, external resource availability and reproduction, we applied State-Dependent Life-History Theory (SDLHT) to a Dynamic Energy Budget (DEB) model for long-finned pilot whales (*Globicephala melas*)(Figure 8). We investigated the reproductive strategies emerging from the interplay between fitness maximization and propensity to take energetic risks, and the resulting susceptibility of individual vital rates to disturbance. Without disturbance, facultative reproductive behavior from SDLHT and fixed rules in the DEB model led to comparable individual fitness. However, under disturbance, the reproductive strategies emerging from SDLHT increased vulnerability to energetic risks, resulting in lower fitness than fixed rules. These fragile strategies might therefore be unlikely to evolve in the first place. Heterogeneous resource availability favored more cautious, and thus more robust, strategies, particularly when knowledge of resource variation was accurate. Our results demonstrate that the assumptions regarding the dynamic trade-offs underlying an individual's decision-making can have important consequences for predicting the effects of anthropogenic stressors on wildlife populations.

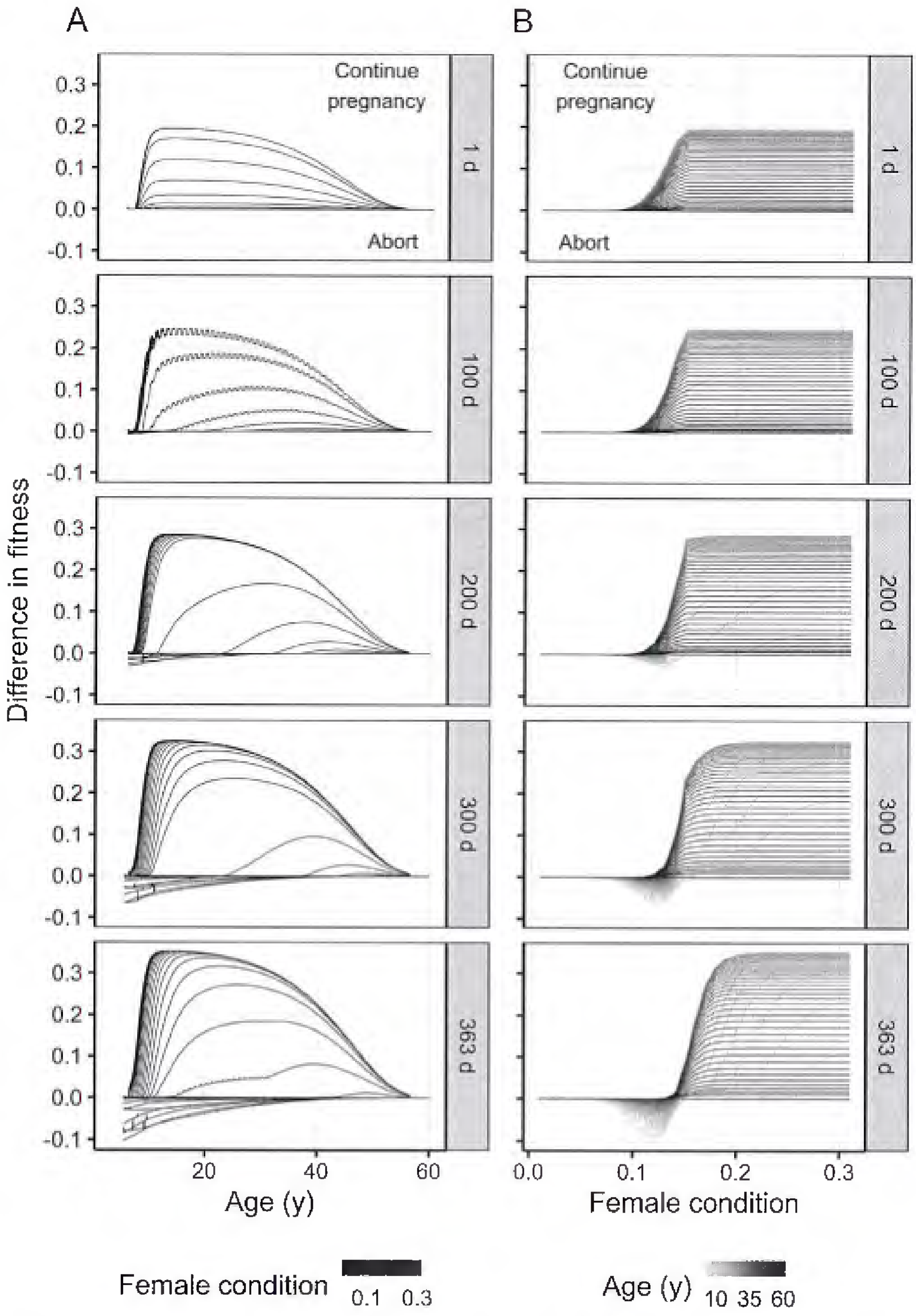

Figure 8 - Figure 3 from Pirotta et al., in press (American Naturalist). Difference in fitness value in model V1 between the decision to continue a pregnancy and the decision to abort the fetus, highlighting the costs or benefits of continuing pregnancy as a function of age by condition of the female (A) and as a function of condition by age (B), at five stages of gestation (after 1 d, 100 d, 200 d, 300 d or 363 d of gestation). The oscillations in fitness benefits in A emerge from the constraints on the timing of reproduction, and depend on which timings ensure weaning a calf on the last day of life. For some gestation stages, these oscillations are more apparent because of the relative size of the associated fitness (there is either a greater benefit of continuing pregnancy or a greater cost of interrupting it, depending on the energy that has already been invested).

Task 4: We have developed a Protocol for Expert Elicitation for PCoD (PEEP) to guide expert elicitation efforts in support of PCoD models. The PEEP guidance document is not intended to be read in a linear fashion, beginning to end. Instead, the first two chapters (1. Introduction and 2. Expert Elicitation and PCoD) are intended to provide the core background information needed to implement the PEEP. The next two chapters relate to specific case studies to highlight issues within expert elicitation (EE) that are specific to the different types of Population Consequences of Disturbance (PCoD) models (3. PCoD Case Study and 4. Interim-PCoD Case Study). In contrast, the final chapter (5. Practicalities) contains information on common challenges to be considered across almost all elicitations. We suggest that everyone read Chapter 2, since it will be referenced in the other chapters. The remaining components of the guidance document are intended to be modules that can stand on their own, provided that readers are comfortable in their understanding of EE and PCoD. As a result, people should feel free to pick and choose which of the chapters are most helpful to them, without concern that they are missing necessary information. The guidance document was developed via a series of student workshops and tested at expert elicitations on beaked whales and blue whales. The guidance document and protocols are in draft form and current iterations can be found here:
PEEP templates: https://smrumarine.box.com/s/hlwi5sccas917ss772h4ptaeob8wurs6 and
PEEP Guidance Document: https://smrumarine.box.com/s/dfwtql99natsl06g1k97rfxqmzf6ky9a

An online tool for 'e-learning training course' for experts to participate in expert elicitation has been developed and is now freely available online at: http://www.smruconsulting.com/products-tools/pcod/pcod-project-outputs/online-expert-elicitation-course/ . This course has been widely used to support recent EE (for PCoD and other applications – see 'Related Projects' below) and experts have fed back that this has been an excellent primer to aid them in advance of elicitations. Similarly, it has been notable that the process of experts providing their judgements is expedited.

A draft manuscript comparing the outputs of the PCoD Lite (Award: N000141410406) beaked whale elicitation (2015) and the beaked whale elicitation from this project (2018) is currently in preparation (led by Dr Leslie New).

Task 5: Investigating the sublethal effects of disturbance and their consequences at a population-level remains a significant ecological challenge. It requires extensive baseline knowledge of foraging patterns, life-history and demography. However, for most marine mammal populations, this knowledge is currently lacking and it could take many years to fill these gaps. During this time, undetected population declines may occur. Typically, marine mammal populations are monitored via surveys to determine their size or density. Whilst there are well established methods – such as line-transect surveys for cetaceans (e.g. Wade and Gerrodette, 1993) or telemetry-corrected haulout counts for pinnipeds (e.g. Thompson and Harwood, 1990) - for estimating the size of marine mammal populations, these are expensive, particularly in the case of cetacean populations. They also tend to provide imprecise estimates, because marine mammal populations are often spread over wide areas and individuals are often submerged, when they cannot be sighted. Consequently, monitoring programs based on these methods typically only have the power to detect large declines (Taylor et al., 2007; Jewell et al., 2012). Additionally, it may take many years before changes in vital rates manifest themselves as changes in population size if a species is long-lived. There may, therefore, be merit in monitoring demographic characteristics (such as the age- or stage-structure of the population) and indicators of individual health that can provide an early warning of population level effects and help to identify some of the drivers of changes (National Academies of Sciences Engineering and Medicine (2017)).

Booth et al (2017; 2020) present a technical report and peer reviewed publication respectively which summarize the results of the literature review (Figure 9), an exploration of the methods and/or techniques required to collect appropriate datasets and the feasibility of using them to monitoring different species and populations (e.g. Figure 10). Using existing PCoD models, we explore the potential utility of different demographic parameters to provide early warning indicators of population decline (e.g. Figure 11). We also summarized an external assessment of US Navy marine mammal monitoring and assess the potential for current monitoring practice to inform a PCoD analysis using the lessons learned from the literature review and sensitivity analysis phases. Booth concluded the report with recommendations for how to inform future PCoD analysis of the effects of Navy activities on relevant marine mammal populations.

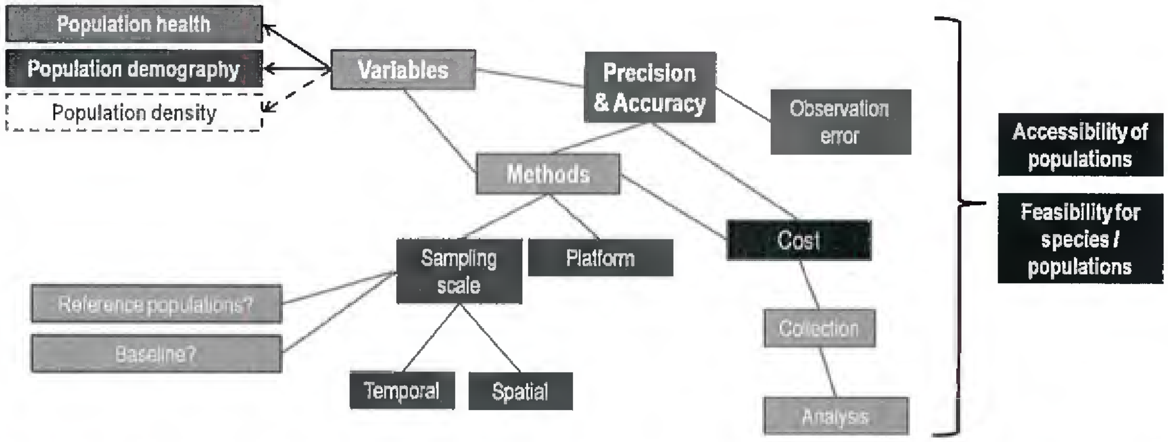

Figure 9 – Schematic of elements to be considered in monitoring program for identifying variables that be collected practically and might inform future PCoD analyses of the effects of Navy activities on marine mammals.

Using the results from the literature search and the workshop exercises, we identified a set of currently available and developing methodologies for monitoring demographic variables and individual health that are reviewed in section 2.4. At the workshop, we agreed to follow a multiple lines of evidence (LoE) approach (e.g. Amidan et al., 2015) to assess the value of these methodologies for monitoring marine mammal populations. This involved making a judgement on the feasibility and the utility of each methodology for following marine mammal groups: deep-diving cetaceans, baleen whales, coastal dolphins and porpoises, oceanic dolphins, land-breeding pinnipeds and ice-breeding pinnipeds. In this report 'feasibility' captured the readiness of the methodology for use in a monitoring program, the likelihood that it could be applied to each marine mammal group, and its potential for collecting demographic / health information as new analytical techniques become available. It should be recognized that feasibility was assessed on a relative scale for each class of response variable, so that a feasibility score of 3 applied to a methodology for measuring demographic variables cannot be equated directly with a score of 3 applied to a methodology for monitoring health measures. 'Utility' captured the number of demographic variables and/or health measures that could be monitored with a specific method. For the 'Feasibility-Utility' assessments (e.g. see Figure 4) experts also ranked the demographic variables in terms of their potential value as early warning indicators and these ranks were used to weight the value of variables (as not variables are equally valuable in informing demography or health). Following the workshop, we developed a similar value ranking index (not reviewed by the health experts but following the approach undertaken by demography experts in the workshop) for health variables. The ranking combined an assessment of the current feasibility of collecting information on each variable and how informative the variable was likely to be in a health monitoring context and this was used to weight as described above.

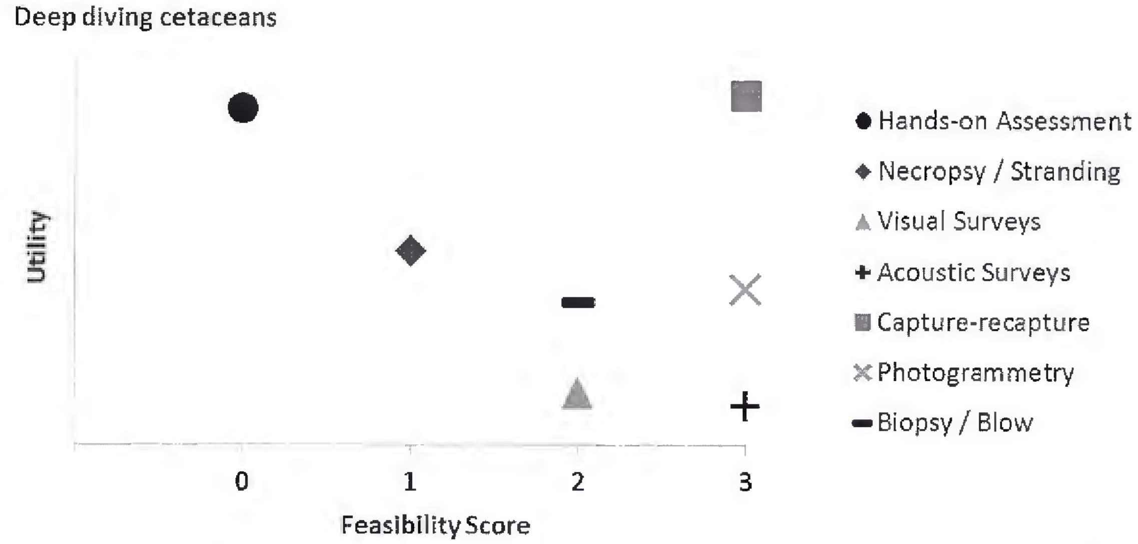

Figure 10 – Feasibility-Utility plot for methods to monitor demographic variables for populations of deep diving cetaceans. Feasibility indicates which methods are most practicable for this species group (higher score = greater feasibility) and Utility Score indicates the weighted number of variables that might be measured using a given technique. Methods with the best combination of scores appear in the upper, right-hand side of the figure.

We identified that changes in demographic characteristics are strongly correlated with changes in abundance or population status, and therefore can provide some early warning of future changes in abundance. However, the probability of failing to detect a large decline may be high if only one characteristic is monitored (Figure 11). As such it is important to identify multiple approaches and the value of monitoring these characteristics will depend on the precision with which they can be monitored, and the practicality and cost of this monitoring. In addition, the literature review identified that demographic parameters tend to come from established approaches (e.g. visual surveys, mark-recapture (Photo-ID), photogrammetry) and that monitoring individual health/physiology has lots of possibilities but that many methods still being explored for links to health / vital rates. From the health measures, body condition might provide a way to identify unhealthy animals (though causes hard to ID) and few efforts to date have established a clear link between body condition and vital rates (i.e. demographic parameters).

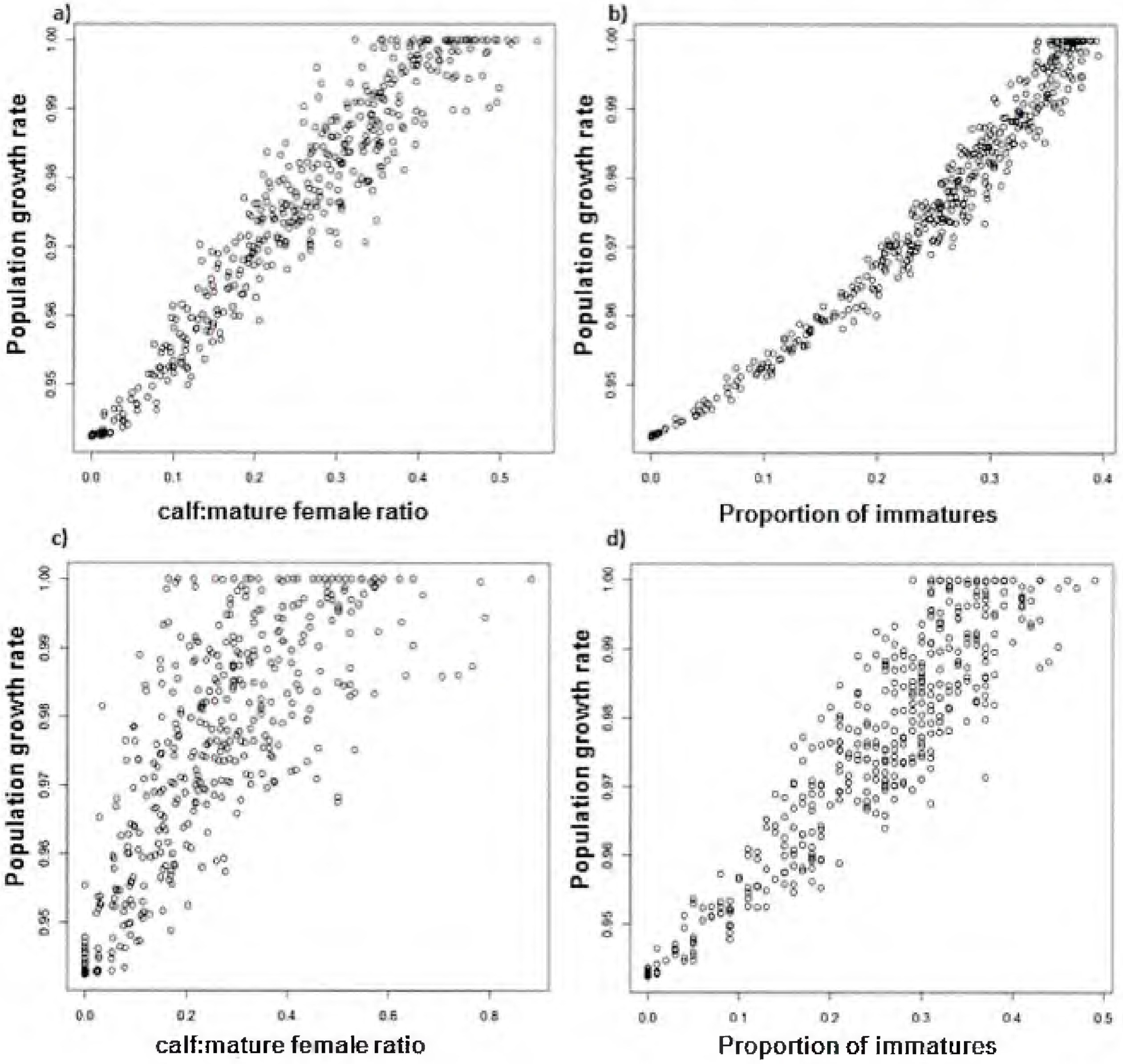

Figure 11 - Relationship between the long term growth rate of a Blainville's beaked whale population and (a) the ratio of calves to mature females estimated from a random sample of 1,000 animals, (b) the proportion of immature animals estimated from a random sample of 1,000 animals (c) the ratio of calves to mature females estimated from a random sample of 100 animals, (d) the proportion of immature animals estimated from a random sample of 100 animals.

IMPACT/APPLICATIONS

The approaches developed in this project have the potential for operational use by the Navy as part of its environmental impact assessments. In future, these assessments will likely be required to provide information on the potential population-level consequences of exposure to anthropogenic noise from Navy activities as well as the number of animals that are exposed. The Office of Protected Resources is required to determine that an activity will cause negligible impact to the animal species or stocks inhabiting the area as part of the permitting process; this involves examining the potential effect of the impact on demographic parameters. The PCoD framework is designed to provide exactly this information, and this project will explore ways to improve the capabilities of such models and make it easier to develop new models for particular species and stocks. Work carried out under Task 5 has provided advice on the scope of monitoring programs that can provide data for identifying population level effects (or the pre-cursors to such effects) and is being further investigated under N39430-19-C-2175: 'MSM4PCoD' – Marine Species Monitoring for Population Consequences of Disturbance.

RELATED PROJECTS

The products and concepts arising from this award have been utilized in a number of related projects:

Office of Naval Research

- N000141912464: 'BRS4PCoD': Integrating the results of Behavioral Response Studies into models of the Population Consequences of Disturbance
- N0001419WX00431: Integrating Information on Displacement Caused by Mid-Frequency Active Sonar and Measurements of Prey Field into a Population Consequences of Disturbance Model for Beaked Whales
- N000142012392: Advancing PCoD Efforts Through a Marine Mammal Bioenergetics Workshop

Living Marine Resources

- N39430-19-C-2175: 'MSM4PCoD' – Marine Species Monitoring for Population Consequences of Disturbance.

Selected others

- Scottish Government: Exploring the utility of Dynamic Energy Budget models for potential integration into the interim PCoD model. (June 2019-April 2020)
- GoMRI: "Consortium for Advanced Research on Marine Mammal Health Assessment (CARMMHA)

The expert elicitation e-learning course has been used in at least eight expert elicitation workshops since it was publicly available. The PCoD+ project website has been viewed 2,500 times since June 2017 and the online expert elicitation training course has been run >600 times (as of June 2020).

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- Hin, V., Harwood, J., and De Roos, A.M. (2019). Bio-energetic modeling of medium-sized cetaceans shows high sensitivity to disturbance in seasons of low resource supply. Ecological Applications, e01903. [published]
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Booth, C.G, Plunkett, R & Harwood, J. 2017. Identifying Monitoring Priorities for Population Consequences of Disturbance. Report Code SMRUC-ONR-2017-017, Technical Report submitted to the Office of Naval Research – Marine Mammal & Biology program, Nov 2017 (unpublished). Available at: http://d92381143ccd30809f56ed62.smruconsulting.netdna-cdn.com/wp-content/uploads/2017/05/Boothetal2017-Identifying-monitoring-priorities-for-PCoD.pdf

Protocol for the use of Expert Elicitation for PCoD:

- Draft PEEP templates: https://smrumarine.box.com/s/hlwi5sccas917ss772h4ptaeob8wurs6
- Draft PEEP Guidance Document: https://smrumarine.box.com/s/dfwtql99natsl06g1k97rfxqmzf6ky9a

Software

Expert elicitation online course: http://www.smruconsulting.com/products-tools/pcod/pcod-project-outputs/online-expert-elicitation-course/