

Statistical Tools for Fitting Models of the Population Consequences of Acoustic Disturbance to Data from Marine Mammal Populations (PCAD Tools II)

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LONG-TERM GOALS

Our top goal is to build a coherent statistical framework for modeling the effects of disturbance, particularly acoustic disturbance, on different species of marine mammals. We wish to quantify each of the transfer functions outlined in New et al. (2014) in order to link the disturbance to a change in health or behaviour and in turn to a change in vital rates. In addition, we aim to build statistical tools that can be applied to real-world management situations in addition to the case studies we have considered here.

OBJECTIVES

The scientific objectives are to build state-space models – typically in a Bayesian framework – in order to link observed disturbances to changes in underlying health of individuals. In either a predictive or a forward simulation approach, we link underlying health, and changes in health to changes in vital rates. Within these objectives we have outlined specific goals and tasks.

These tasks included:

1. continuing and deepening the 4 case studies:
 - 1.1 elephant seals
 - 1.2 right whales
 - 1.3 bottlenose dolphins
 - 1.4 beaked whales
2. providing ongoing statistical support to the PCAD working group
3. writing manuals that describe how the statistical models are formulated

APPROACH

Our technical approach has involved building and fitting statistical models to marine mammal data in order to quantify our understanding of the impacts of disturbance on health, and in turn the impact on vital rates. We proposed examining 4 different case studies: elephant seals, right whales, coastal bottlenose dolphins, and beaked whales. We have focused much of our energy on fitting hierarchical Bayesian (HB) models to data on the drift rates of elephant seals and on the visual health of right whales. In certain cases, particularly data poor cases, we have turned to expert elicitation as a way to fill in our understanding of these links. At St Andrews, key personnel are Robert Schick, John Harwood, Len Thomas, Cormac Booth, and Cornelia Oedekoven. We also work closely with Erica Fleishman at UC-Davis. At New England Aquarium, we work with Scott Kraus, Rosalind Rolland, Amy Knowlton, Philip Hamilton, and Heather Pettis. Lastly, we are active members of the PCAD working group, and regularly participate in working group meetings.

Within Task 1, we focused extensively on two models: elephant seals (Task 1.1) and right whales (Task 1.2). Both of these models are hierarchical and rely on observations of health to make inference on underlying health. In the case of elephant seals, the observation model linked sub-daily drift rates on individual seals (Figure 1), and the process model provided daily estimates of actual lipid status of individual seals (Schick et al. 2013b, O'Toole et al. 2015). These daily estimates can then be used to calculate putative effects of disturbance (New et al. 2014, Costa et al. 2015).

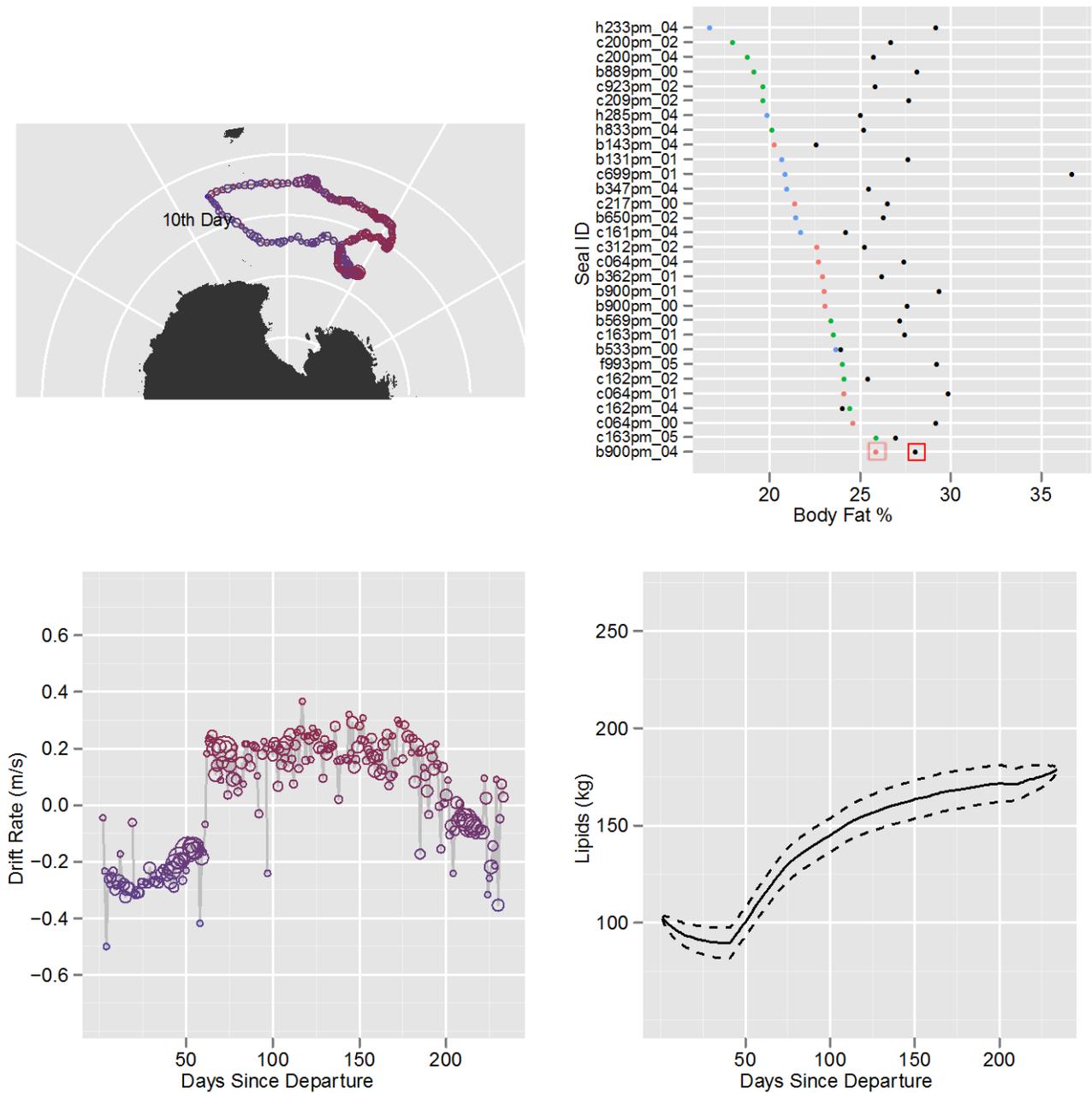


Figure 1. Daily lipid gain/loss in one southern elephant seal tagged in Macquarie Island. Four panels show (clockwise from top left): map of the track, before/after lipid measurements for all seals in the colony (this seal highlighted with red squares), estimated total lipid stores over the course of the trip, and the time series of daily drift rates.

The second model, was similar in intellectual spirit – namely we used an HB model to estimate health of marine mammals. In contrast to elephant seals, the model for right whales used photographic observations of 4 different visual health parameters (Pettis et al. 2004) to provide monthly estimates of health (Schick et al. 2013a, 2015) (Figure 2).

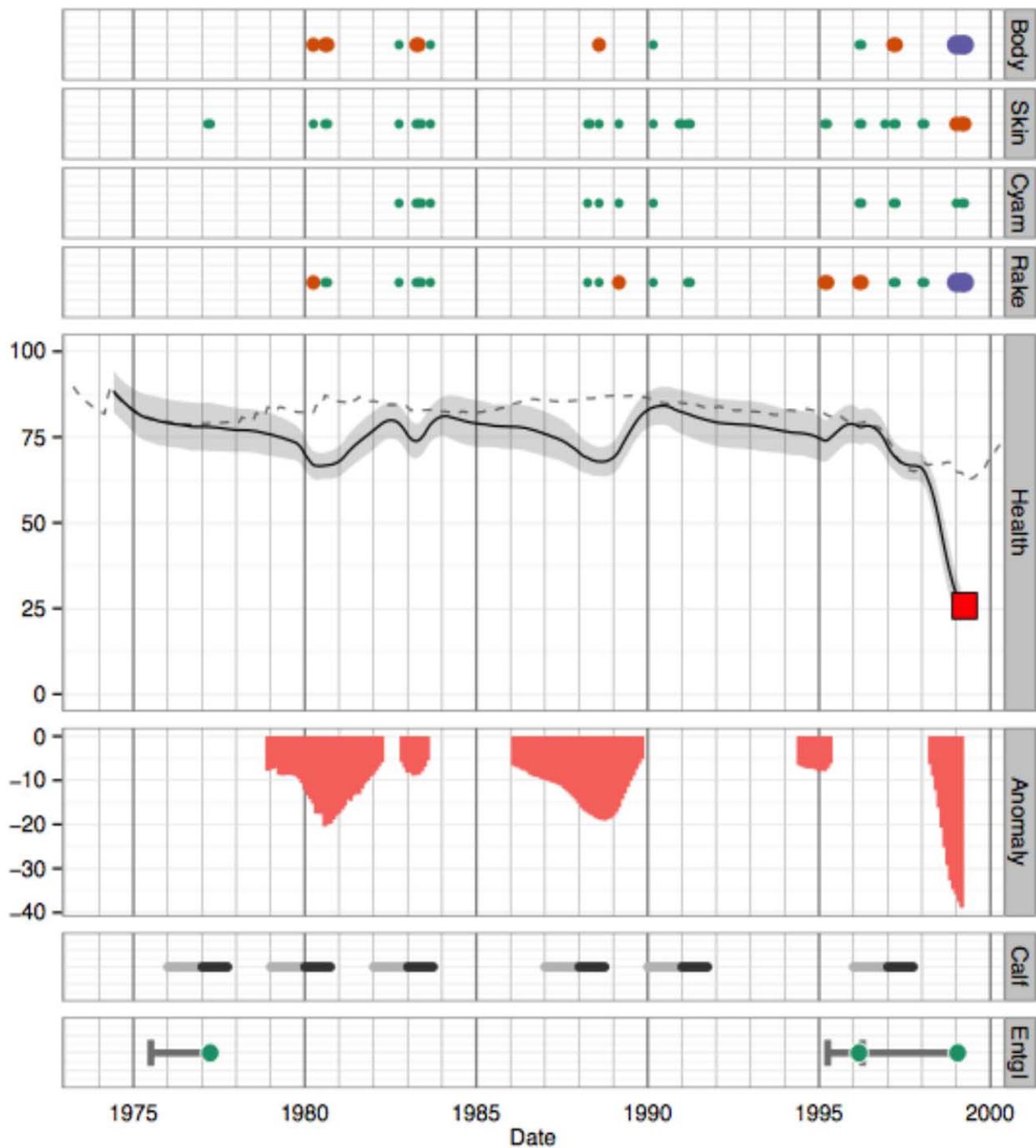


Figure 2. Estimates of health for one right whale with a known death (panel labeled Health). Data used to fit the model are shown in the top four panels. Difference between this individual's health and the population level average is shown in the Anomaly panel. Calving status (grey – pregnant, dark grey – lactating), and entanglement status shown in the lower panels. (Taken from Rolland et al., In revision.)

With the individual health estimates, we can then quantify the impact of disturbance using temporal overlays – extracting health values in two ways: 1) extracting mean health during an entanglement

window and summarizing as a factor of entanglement severity (Figure 3); and 2) extracting health at the start and end of entanglement windows and summarizing changes in health during the window. With these summaries, we can construct Kaplan-Meier curves to assess the impact of entanglement over time (Figure 4, Knowlton et al., *In prep*).

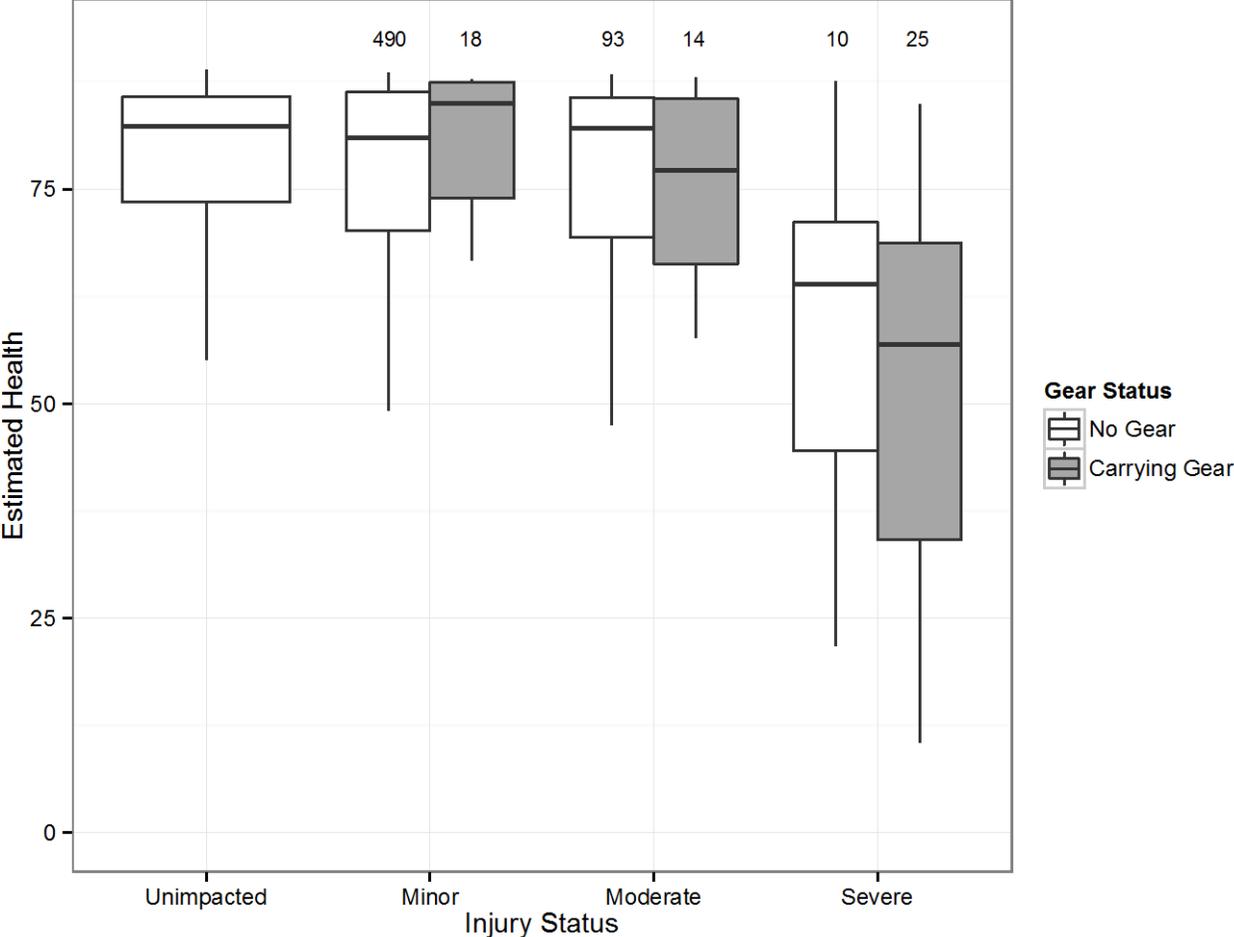


Figure 3. Median health of individuals entangled in fishing gear during the entanglement period compared to unimpacted whales. Health of entangled whales decreases as entanglement severity increases; the added impact of carrying gear can be seen in the moderate and minor entanglements.

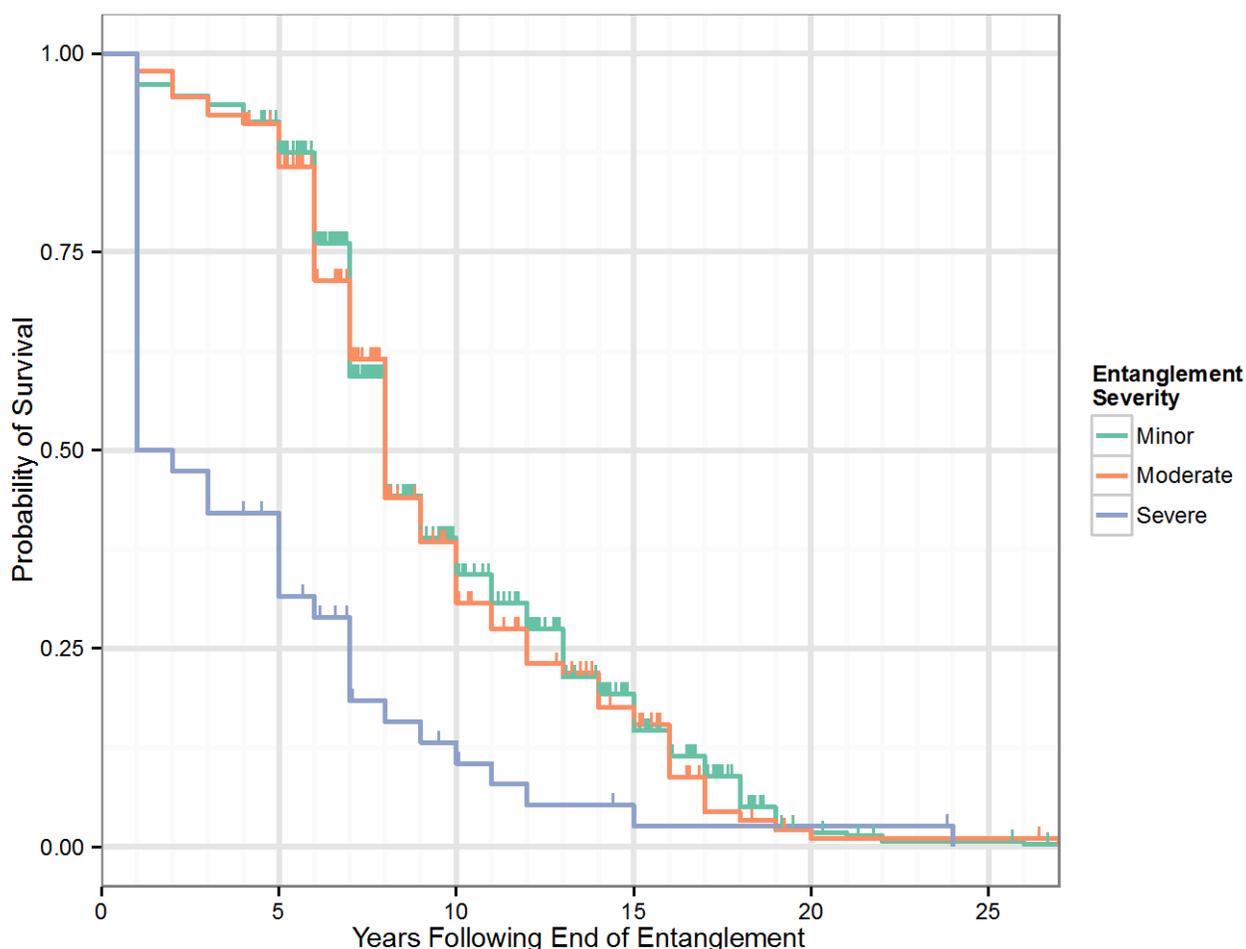


Figure 4. Kaplan-Meier survival curves for right whales that have experienced an entanglement; survival is shown as a function of entanglement severity following the last entanglement experienced by individuals. Small vertical tick marks indicate when an animal was censored. Fifty percent of animals with a severe entanglement die within one year. Median survival for these whales is 7 years shorter than those who have experienced minor or moderate entanglements.

We can also place the individual health profiles in context of overall population trends to see times when the animals are in worse or better condition than overall average (Figure 2, Rolland et al., *In revision*). Lastly, using the individual data and population level summaries, we can generate annual population report cards that depict individual health, population summaries, and estimates of survival (Hamilton et al., *In prep*).

Within Task 1.3, we decided as a working group that the analysis for the Sarasota Bay dolphins would be carried out by Lisa Schwarz from UC-Santa Cruz.

For the beaked whale demographic model (Task 1.4), our technical approach was to construct a age- and sex-structured population dynamics model (Caswell 2001), and to use this to integrate observations on population stage (calf, juvenile and adult) and demographic parameters (fecundity and

survival), as well as modelled estimates of effect of disturbance based on an energetic analysis when available. We focused on two sites in the Bahamas. The first was Abaco, which has been the focus of a long-term study by the Bahamas Marine Mammal Research Organization (BMMRO), with whom we collaborated on this work. Observations of population structure and estimates of demographic parameters from the long-term study are available in Claridge (2013) (reproduced in Tables 1 and 2). Abaco was assumed to be the reference site. The second site, AUTEK, has been the subject of more recent population study by BMMRO, and was one of our PCAD case study populations. Observations of population structure are available in Claridge (2013) (reproduced in Table 1), but the site has not been studied for long enough yet to produce reliable estimates of demographic parameters. Ongoing work by staff at NUWC, as part of the PCAD working group, is constructing an energy-based assessment of the effect on demographic parameters of disturbance at this site; this builds on previous work documented by New et al. (2013).

Table 1. Blainville’s beaked whale population stage structure from visual observations at Abaco and AUTEK, based on Claridge (2013).

Site	Calves	Sub-adults	Adult females	Adult males
Abaco	0.17	0.25	0.37	0.21
AUTEK	0.10	0.15	0.59	0.16

Table 2. Estimates of Blainville’s beaked whale demographic parameters at Abaco, based on Claridge (2013).

Fecundity	Calf survival	Subadult female survival	Subadult male survival	Adult female survival	Adult male survival
0.1351	0.9283	0.962	0.807	0.984	0.823

Here, we have focused on modelling females, since it is females that drive population dynamics. We constructed a matrix population model (Caswell 2001) with an annual time step and 10 age classes: age 0, 1 and 2 females, assumed to be calves, age 4, 5, 6, 7 and 8 females, assumed to be juveniles and age 9+ females, assumed to be adults. The resulting Leslie matrix is shown in Figure 5.

$$\begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi_a \alpha \\ \phi_p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_p & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_j & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_j & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \phi_j & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \phi_j & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi_j & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi_j & \phi_a \end{pmatrix}$$

Figure 5. Leslie matrix for female beaked whale population dynamics model. Ages 0-2 are calves, 4-8 juveniles and 9+ adults. Parameters ϕ_p , ϕ_j and ϕ_a are female calf, juvenile and adult survival, and α is fecundity of female offspring (i.e., annual probability that an adult female gives birth to a female calf).

Given demographic parameters, eigenanalysis allows prediction of the stable age structure (Caswell 2001). We used an optimization approach based on minimizing the least-squares difference between observations of age structure and predictions to estimate demographic parameters. The optimization included the constraint that adult female survival be greater than or equal to subadult female survival and that this in turn be greater than or equal to calf survival.

We also constructed an integral projection model (IPM) (Coulson 2012) using health in right whales as a continuous covariate explaining survival and fecundity (Harwood et al, *In prep*). This approach will allow us to test scenarios to quantify how putative changes in individual health affect population trajectories.

For Task 2, we decided as a working group not to implement the motivational state model for elephant seals.

For Task 3, we submitted one software paper describing the elephant seal code. This paper was rejected, and has not been reworked at present as other components of the case studies, e.g. right whale survival, were deemed higher priority. On a related project, we did publish a software manual that described how to assess the impacts of acoustic disturbance on harbour porpoise (Harwood et al., 2014).

Though not explicitly one of the tasks outlined in the original proposal, following a working group meeting in 2012, we have used expert elicitation in three different case studies: right whales and ship strikes, right whale movement through the mid-Atlantic migratory corridor (MIDA), and the putative effect of disturbance on sperm whales. In a related project, we have explored the effects of disturbance from the construction of offshore marine renewables on harbour porpoise in UK waters (Harwood et al. 2014, King et al. 2015). In each of these case studies, we have been data limited, and the time required to collect the data would be prohibitive. In some cases, we sought the links between disturbance and vital rates (e.g. harbour porpoise, sperm whales), and in some we sought to better inform the knowledge of movements through the MIDA.

In the latter two elicitations (sperm whales and right whales) we have used a graphical user interface-generating system called shiny (Chang et al. 2015) to build interactive web-based apps that have an R engine (R Core Team 2015) (Figure 6). This allows direct and easy access to necessary statistical distributions, without requiring the user to know any R. Elicitations typically have two rounds in this sequence: a private first round where experts enter their answers to the elicited questions, a group level conversation whereby experts review and discuss their answers in common, followed by a private second round where experts can modify their answers based on the conversation. Within the shiny framework, we dynamically updated the apps using results from round 1 in advance of round 2. This allowed the user to visualise their answer along with other experts. We will continue to use and refine this approach in future elicitations.

Question 14, Round 2. Movements of Adult Male Right Whales into and out of the mid-Atlantic region (MIDA)

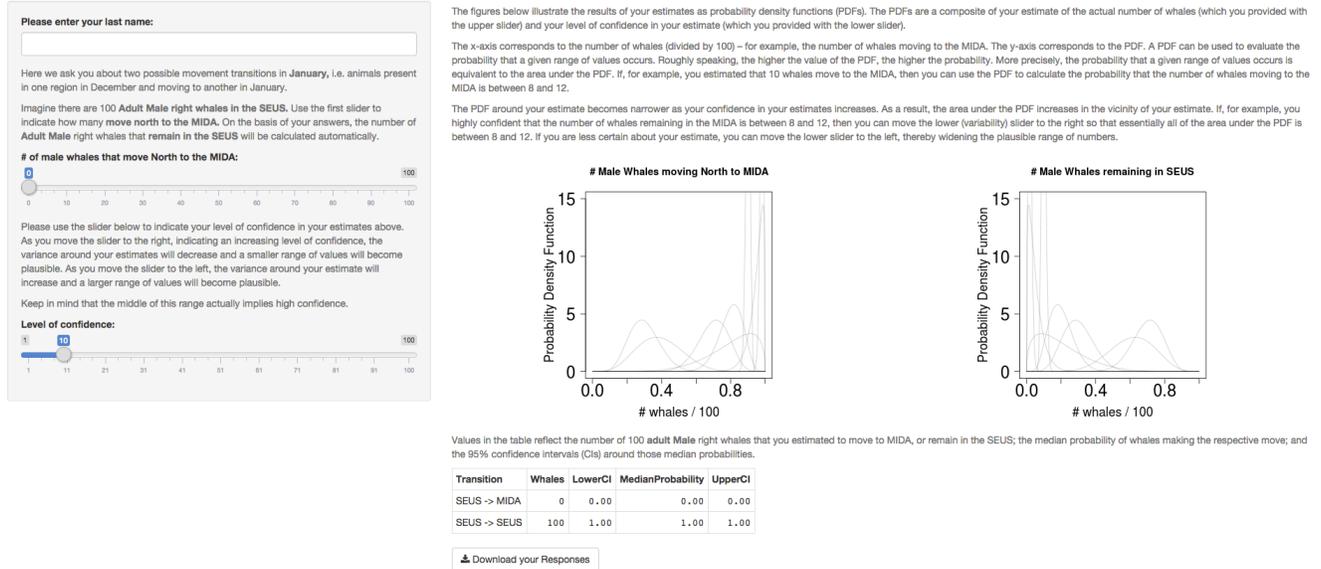


Figure 5. Screenshot of the shiny web-based application (with R as the underlying analysis engine) we developed to conduct two expert elicitations. Here we were asking about the probability of adult male right whales moving North from the mid-Atlantic habitat. Experts opinions about these transitions were harvested as Beta distributions. Shown is how the view an expert sees at the start of Round 2 of an elicitation, with all answers from Round 1 shown in light grey lines.

WORK COMPLETED

Elephant seals were the first case study. Within this task we have successfully built and fit to data models to estimate daily lipid stores for each individual seal as a function of environmental covariates (Schick et al. 2013b, New et al. 2014) for both the post-moult trip and the post-breeding trip (O’Toole et al. 2015). We have used these results to generate estimates of the effects of disturbance on lipid gain, and ultimately on juvenile survival (New et al. 2014, Costa et al. 2015). This has given us the first link within the PCAD framework from disturbance through to vital rates.

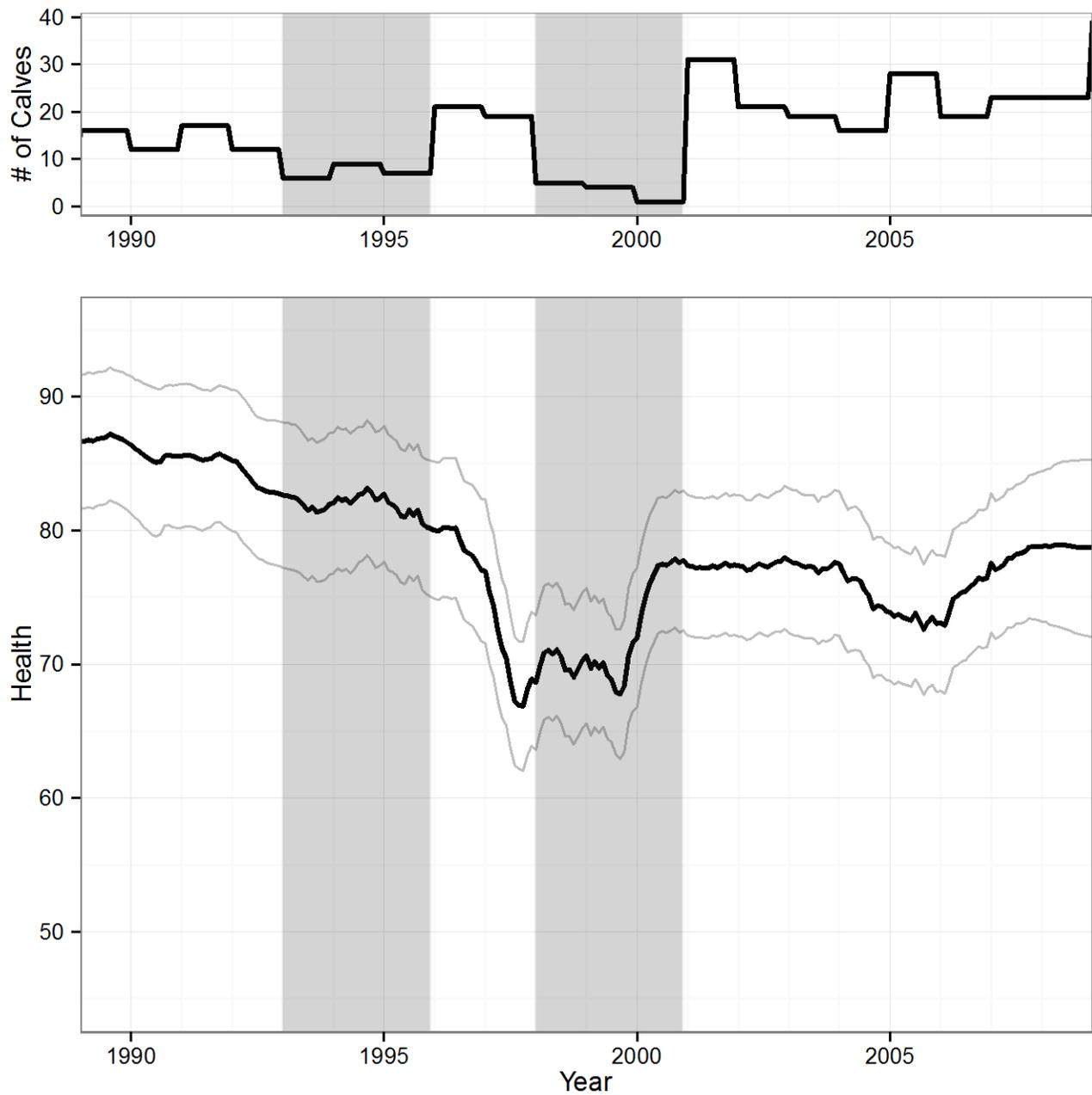


Figure 6. Average health of the representative segment of the right whale population, aggregated from individual health profiles (Figure 2). Periods of population-wide low fecundity are shown in light grey. Upper panel depicts actual numbers of calves born each year. (Taken from Rolland et al., In revision.)

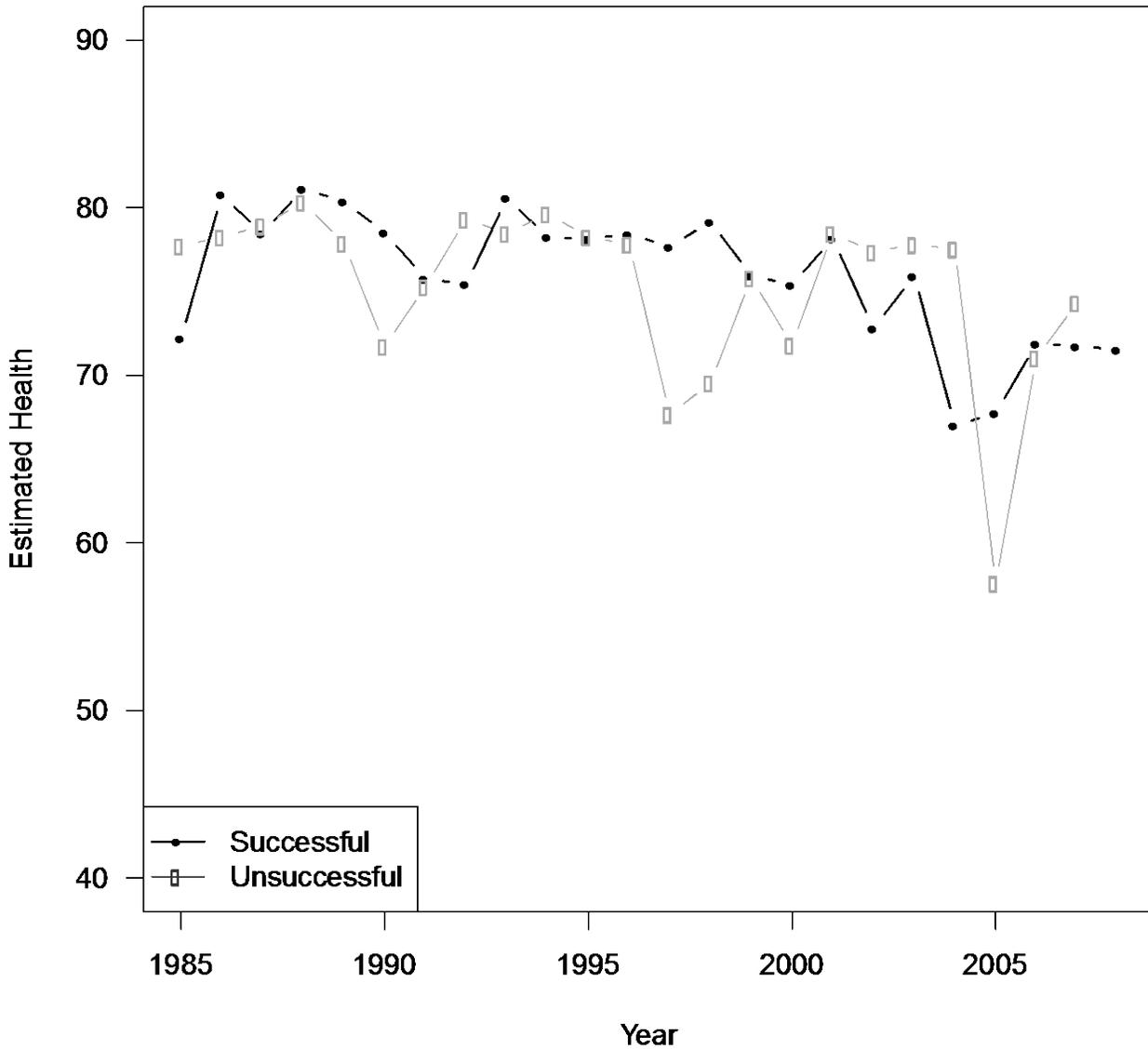


Figure 7. Relationship between health in years when adult females are available to become pregnant. Animals that became pregnant are depicted with solid circles; animals who were unsuccessful are depicted with open circles.

For Task 1.2, we have fit the model developed in Schick et al. (2013a) to 30+ years of individual sightings data of right whales (Figure 2). We have scaled up from these individual estimates of health to understand population level health (Figure 7), health of critical sub-populations, and the link between health and reproduction (Figure 8, Rolland et al., *In revision*). We have also intersected health estimates with data on entanglement to understand how this disturbance impacts the health of individuals. This provides us with insight into how health changes over the time frame of the entanglement (Figure 3), as well as how that change in health is linked to changes in survival (Figure 4). We have also outlined how the right whale health metric can be used to investigate population

dynamics with an IPM framework (Harwood et al., *In prep*) (Tasks 1.2 and 1.4). Lastly, we are using the estimates of health and survival from the model to provide an annual snapshot of the status of the right whale population (Hamilton et al., *In prep*).

Using expert elicitation, we have estimated prior movement probabilities in and around the MIDA migratory corridor. We have iterated our elicitation process and developed interactive apps to facilitate the data gathering process (Figure 6). We are currently using these data to estimate posterior movement probabilities. In conjunction with seasonal distribution probabilities (Oedekoven et al., *In press*), we can provide further technical guidance to managers on the critical periods when right whales are likely to be in the MIDA. We have also gathered expert knowledge on the probable impact of naval activity in Hawaii and AUTEK on vital rates in sperm whales. Lastly, we participated in an initial elicitation in the right whale community to estimate the likely impact of ship speed restrictions on vital rates (Fleishman et al. 2015).

Schick participated in a workshop at the IMCC in Glasgow, 2014, which was organised by Leslie New. He focused on the use of the PCAD approach to monitoring disturbance and health in marine mammal populations. This workshop paper was published earlier this year (New et al. 2015).

For beaked whales (Task 1.4) initial modelling focussed on the Abaco population, where we investigated whether the values for demographic parameters and stage structure from the field data (Tables 1 and 2) are mutually compatible, given the population model. We then investigated what the observed stage structure data at AUTEK (Table 2) implies for demographic parameters at that site, assuming population stability. We undertook a sensitivity analysis for the AUTEK study by testing whether fixing some demographic parameters (e.g., adult female survival) to those from Abaco led to reasonable values for the other parameters at AUTEK.

RESULTS

Of the four case studies (Tasks 1.1 – 1.4) here we focus discussion on the right whales and beaked whales; this is in part because for right whales the results quantify the links from disturbance through to change in vital rates. For right whales, we had four related achievements that all build upon one another: 1) placing individual right whale health in context of larger sub-population and population level groups (Figure 2); 2) linking health status of adult females that are available to calve to their pregnancy status (Figure 7); 3) documenting the impact on health of entanglements of increasing severity (Figure 3); and 4) translating that decrease in health to a decrease in individual survival (Figure 4). In so doing, we have fully linked the transfer functions in the PCAD diagram about which we know least, and are now prepared to carry these forward to assess the impact of changes in vital rates on population dynamics. Critical to this result were two factors: the first was estimation of the underlying health status of individuals – an approach we have used throughout the PCAD project; and the second was calculating and accounting for uncertainty at each of these three levels.

What we have shown is that starting with estimates of health and the entanglement window, i.e. the timeframe during which the animal must have been entangled, we can assess the health status at the beginning and end of the window. Animals typically start the entanglement in similar health status; however, at the end of severe entanglements with and without gear, individuals are in significantly worse health (Figure 3). Based on the revised PCAD flowchart, we are now tracking the chronic impact of entanglement on health and changes in health on survival. Figure 4 shows the stark reduction in survival for animals with severe entanglements. Together with the result linking poorer health status

to reduced probability of giving birth, we have documented how health can be linked to vital rates. We have shown how to apply modern inferential approaches to data in order to management ready outcomes.

Outside of the right whale community, this approach can be modified and applied to other similar systems. While the modelling approach we have used (Schick et al. 2013a, 2015) is currently very closely tied to right whales, it can be modified and extended to systems and species where photographic evidence of health exist.

For beaked whales, we have results from two the different populations – Abaco and AUTEK.

Abaco population.

Male and female subadults cannot be distinguished in the field, but our demographic modelling requires an estimate of the proportion of subadult females in the population. Hence an initial task was to determine what proportion of subadults was female. Using the subadult survival rates given in Table 1 and assuming a stable age structure, the female sex subadult ratio was estimated to be 0.593. Using this value and assuming that 50% of calves are female, the female age structure at Abaco was therefore estimated as 0.140 calf, 0.248 subadult and 0.612 adult. Using the demographic parameters shown in Table 2 together with the Leslie matrix from Figure 5 an eigenanalysis gave the female stable age structure as 0.19 calf, 0.25 subadult and 0.56 adult, which is close to the above values. However, the implied rate of population change using these demographic parameter values was 1.04 (i.e., increasing by 4% per year); the population is not thought to be increasing in nature. We therefore performed an analysis to determine which demographic parameters were consistent with the observed female stage structure (0.140 calf, 0.248 subadult and 0.612 adult) and a population growth rate of 1.00, using the optimization method under Approach. The best fitting values for calf, subadult and adult survival were 0.928, 0.962 and 0.984, with fecundity being 0.135. These are well within measurement error of the observed values. Our conclusion was that the demographic and stage structure values observed at Abaco are broadly compatible with one another, and with the observation of no discernible population trend.

AUTEK population

Assuming the same subadult sex ratio at AUTEK as that at Abaco leads to an estimated female stage structure of 0.072 female calves, 0.114 female subadults and 0.814 female adults. Repeating the optimization exercise, using these female stage structures from AUTEK and assuming a population growth rate of 1.00 gave estimates of calf, subadult and adult survival rates of 0.946, 0.951 and 0.98 with fecundity of 0.032. This corresponds with one female calf every 15.74 years, on average.

We performed a sensitivity analysis to test whether other explanations for the observed age structure were feasible apart from low fecundity. We repeated the above analysis, fixing the fecundity parameter to the value of 0.135 estimated for Abaco (and removing the constraint for survival rate to increase with stage). This produced unrealistic estimates of female calf, subadult and adult survival of 0.11, 3.97 and 0.58 respectively. Note that the subadult “survival” rate far exceeds 1.0, but this can be interpreted as immigration of subadults. We then added a further constraint, that the adult survival was that of Abaco (0.984), but it then became impossible to find a stage structure that matched the observed structure at AUTEK.

Our conclusion was that, if the population is stable and the subadult sex ratio matches that of Abaco, then low calf fecundity combined with high survival at all life stages is the only plausible explanation for the observed stage structure ratio.

IMPACT/APPLICATIONS

Within the right whale community, knowing the health status of individuals provides us with a baseline to which we can compare future health values. In a shifting climate, and in a time when right whale habitat is increasingly exposed to anthropogenic activities (e.g. offshore exploration for oil and gas deposits), right whales are likely to have their health impacted in unknown ways. This baseline understanding of past health (Rolland et al., *In revision*, Schick et al. 2013a) provides a long-term context against which we can compare future health. With respect to survival, we know that entangled right whales have decreased survival (Robbins et al. 2015). However, here we show the mechanism by which the disturbance acts and now have a health-based understanding of the link between disturbance and vital rates (both survival and fecundity).

We have clearly shown the magnitude and timing of severe entanglements on survival (Figure 4). We now have a fully inferential way to go from data (photographic assessments of condition for example) to estimates of survival. Thus as each year's worth of new data come into the North Atlantic Right Whale Consortium, we can run the model and update current estimates of health and survival across the entire population. This annual update (Hamilton et al., *In prep*) is of critical importance to the right whale community, but also to managers up and down the eastern seaboard of the United States and Canada.

As mentioned in the APPROACH section, we have relied on expert elicitation in the right whale case study and two related (though not explicitly part of PCAD Tools) case studies. These related projects were the harbour porpoise (Harwood et al. 2014, King et al. 2015), and the sperm whale case study – both part of the Interim PCOD approach. In both of these case studies we relied on expert knowledge to link disturbance to vital rates. In the right whale case study (Schick et al., *In prep*), we sought information on two related issues: right whale seasonal density in the MIDA (Oedekoven et al., *In press*), and right whale movement through the MIDA in the months from December to January (Schick et al., *In prep*).

The beaked whale work strongly complements the ongoing work by NUWC constructing an energetic model of the effect of disturbance on individual and population vital rates. That work will produce estimates of fecundity and calf survival that can be compared with the estimates derived here.

We feel our experience with expert elicitation within the PCAD framework can have broader reach outside the PCAD community. At present, there are many ecosystems vulnerable to anthropogenic disturbance, yet the data linking exposure to disturbance to health and to vital rates are typically lacking. Expert elicitation provides a structured, rigorous way to gather data as an interim way to incorporate many sources of uncertainty as management decisions are made. Expert elicitation also highlights the types of data that are lacking, which will be critical to understand the long-term impacts of exposure. Therefore, we feel this approach is useful both to managers who need the information in order to make time-critical decisions, as well as to scientists to gather the state of knowledge about a system and act accordingly with future data gathering and modelling.

In two of these elicitations (sperm whales and right whales) we made use of RStudio's shiny web-based front end to the R statistical language (Chang et al., 2015). While other R based tools exist to perform expert elicitations (Oakley and O'Hagan 2010), we built our own with shiny as this meant the experts did not need to have any knowledge of the R computer language (R Core 2015). With a few minutes of minimal instruction, users were able to interact with the application as part of submitting their answers to the elicitation. In the second round users were able to see their answers along with the answers from other experts (Figure 6). This provided much-needed context for their answer, and experts could more readily revise as they saw fit. Having the real-time interaction greatly facilitated the elicitation because it allowed the user to see the impact of their answer in the correct domain. For example, in the sperm whale elicitation the expert could set their distribution for the response of an individual to a specific disturbance, and then immediately could see the updated estimate – in biological terms – of that distribution, e.g. the number of animals likely to die. Working in both the modelling domain and the biological domain greatly increased uptake of the elicitation process, and one we feel could readily extend beyond PCAD related work.

RELATED PROJECTS

This project is closely related to two other ONR awards: N000141210389 to Scott Kraus (New England Aquarium), N000141210274 to Erica Fleishman (UC-Davis), and N000141410406 to SMRU, LLC.

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