Introduction and Progress of a Working Group on the Population Consequences of Acoustic Disturbance

PCAD working group[1]
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ABSTRACT

This paper describes the recent progress of a working group on the formalisation of the Population Consequences of Acoustic Disturbance (PCAD) framework. The working group was convened by the University of California, Santa Barbara with support from the Office of Naval Research. The working group was created to address conceptual challenges regarding PCAD and to test models emerging from collaborative discussions with a wide range of case studies made available by participants. The first two of an anticipated five meetings of the group focussed on measuring the effects of disturbances on physiological status via physiological proxies that link physiological costs of disturbances to changes in vital rates. The group decided to adopt a state-space modelling approach in which observed behaviour emerges from the interactions of intrinsic and extrinsic factors. Here we introduce the working group's conceptual approach and early results of model implementations to key marine mammal case studies.

Keywords: modelling, behaviour, energetics, whalewatching

INTRODUCTION AND OBJECTIVES OF WORKING GROUP

Background

In 2005, the U.S. National Academy of Sciences convened a National Research Council (NRC) committee that examined how marine mammals respond to anthropogenic sound (National Research Council, 2005). The committee provided a valuable conceptual framework, Population Consequences of Acoustic Disturbance (PCAD), to structure future studies of the potential population-level effects of changes in behaviour of marine mammals. Developments since the committee issued its report, and advances in research that were not considered explicitly by

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the committee, have made it possible to transform this framework into a more formal model structure.

The NRC committee identified several transfer functions, levels at which anthropogenic sound may affect marine mammals via behaviour (e.g., diving, resting, orientation), life functions (e.g., feeding, breeding, migrating), vital rates (e.g. adult survival, reproduction), and population dynamics (e.g., growth rate, structure, extirpation). The Office of Naval Research (ONR) is addressing the first transfer function, or the potential behavioural response of animals to sound exposure, during controlled-exposure experiments. Knowledge of how effects transfer between behaviour and life functions, and between life functions and vital rates, is limited. Improved understanding of transfer functions, whether theoretical or empirical, might help to guide research and management efforts, and to project how marine mammals may respond to alternative future scenarios of anthropogenic sound exposure. Inferences also are directly relevant to assessing the potential effects on marine systems of climate change or changes in human density and development in coastal regions.

Objectives

With support from ONR, the University of California, Santa Barbara (led by Erica Fleishman) convened a collaborative group of researchers (facilitated by John Harwood) who will cooperate from September 2009 to December 2011 to examine the population-level effects of sound exposure on marine mammals. The objectives of that group may include, but are not limited to

- Explore how the conceptual model developed by the NRC committee might be translated into a formal mathematical structure
- Consider how the above model might be parameterized with existing or emerging data on the responses of large vertebrates to disturbance
- Define conceptual approaches for investigating transfer functions (e.g., time-energy budgets, trait-mediated responses)
- Expand work by the NRC to include sensitivity analyses on different transfer functions
- Outline exploratory models that might be used to model transfer functions, synthesize existing knowledge, examine potential mechanisms, or inform research and management efforts

The group has met twice (September 2009 and March 2010). Between meetings, participants in the group conduct work at their home institutions. We feel that the collaborative and modelling approaches followed by this group will be extremely valuable for LaWE and indeed echoes many of the points made in the Bunbury report (IWC/60/Rep6). We hope that presenting this work at the International Whaling Commission Scientific Committee meeting will foster collaboration between the two groups.

During the first meeting, the group examined data from a number of pinniped case studies, several of which were identified in NRC 2005, and developed an analytical approach. Pinnipeds were chosen as the first study group because, for a few species, there are extensive data linking difference in the fitness of individuals (as indicated by growth, survival, and reproduction) to their behaviour (Crocker *et al.*, 2001). The second meeting focused on bottlenose dolphins. We anticipate that the third, and fourth meetings respectively will focus on baleen whales and other local populations of cetaceans. We will convene a fifth meeting to compare outcomes of the four groups of case studies.

PINNIPED MODEL DEVELOPMENT

Focal data sets

The working group decided to focus on northern and southern elephant seals because existing data are comprehensive, behaviour of elephant seals while at sea is relatively simple, and clear links have been established between mass gain during foraging trips, pup mass, and subsequent pup survival. In addition, both species have been subjected to natural or anthropogenic disturbances that can be used as proxies for the effect of acoustic disturbance. In the mid 1990s, northern elephant seals fitted with telemetry devices were subjected to experimental acoustic disturbance during trials of Acoustic Thermometry of Ocean Climate (ATOC) devices. The impact of changes in the extent of sea ice along the edge of the Antarctic continental shelf on the foraging behaviour and mass gain of southern elephant seals are similar to those that might occur if animals were excluded from certain areas by disturbance (McMahon & Burton, 2005).

Modelling approaches

The working group agreed to develop state-space models of mass gain during foraging trips using a framework proposed by Lusseau in which the behavioural state of an animal is interpreted as an observation of its underlying motivational state (McFarland & Sibly, 1975). These motivational states can be considered as equivalent to the “life functions” in the NRC PCAD model. An underlying process model is then used to describe the transition among motivational states. This transition is likely to be affected by the individual’s physiology, the motivational state of conspecifics in its social group, and its environment (which includes disturbance). The parameters of the underlying process model can be estimated from a time series of observations of an individual’s behavioural state and a matching set of covariate data.

The working group agreed to develop a integrated statistical model of the link between mass gain and demography. The model will facilitate examination of the effects of changes in condition on the breeding and survival of juvenile and adult seals and the effect of maternal condition on pup survival. The model can examine the effects of changes in survival and breeding on demography of southern elephant seals, accounting for the effects of environmental conditions.

Model Structure for Foraging Trips

Elephant seals are ideal for developing a simple, motivational model of the way in which behaviour affects body condition because they spend most of the time between consecutive breeding episodes at sea, only returning to land once in order to moult, when they are easy to recapture. The body composition of an animal (fat, protein, water content) can be estimated at these times using isotope -dilution techniques. While at sea, elephant seals exhibit a very small repertoire of behavioural states that can be identified on the basis of the data provided by satellite tags. These states are foraging (when a significant proportion of the dive is spent at one depth), moving between locations, and sleeping (which occurs during certain dives). Animals sometimes also conduct predator avoidance by diving for extended periods at the same depth. In addition, there is a period during some dives ("drift" dives) when animals descend without propulsion. In these dives, the rate of descent reflects the animal's buoyancy and can be used to estimate its body composition (i.e., the ratio of fat to protein). Data from southern elephant seals indicate that the drift rate observed on the first day before or after their body composition has been measured is correlated with their total body fat.

On the basis of this information the working group developed a process model that could be used to describe the way three states (motivation to feed or move, total body fat, and total body protein) changed over time during a foraging trip. This state process is constrained by the initial and final states of the animal (i.e., its total body fat and protein when it left and returned to its breeding colony). The amount of time an animal spends at depth on a particular day provides an observation (with error) of its motivational state, and the drift rate provides an observation of body fat and protein. Motivational state is likely to be a function of previous motivational states, the rate at which body fat changes, the duration of the trip, and the animal's distance from its breeding colony. Body fat is likely to be a function of the time spent at depth and the rate at which prey are encountered. Some animals have been fitted with stomach temperature sensors, which can be used to infer the occurrence of successful encounters with prey. Although this was not discussed at the meeting, some other measure of prey encounter rate, perhaps some measure of area-restricted searching, will be required for animals that were not fitted with stomach temperature sensors, or whose sensors were no longer functioning.

Following the development of the model above, a simpler model was found to fit the data extremely well. This simpler, linear version of this model was fit with a Kalman filter to obtain a reasonable fit to data on drift rate (an index of relative body composition; total body protein / total body fat) from a single animal. Transit rate (the horizontal displacement of the animal over a 48 hour period) was used as a measure of prey encounter rate. However, the modelled daily increases in fat levels were unrealistically large during some time periods. The unrealistic values appeared to be associated with a change from negative to positive buoyancy. More realistic results were obtained if separate functions relating drift rate to fat reserves were applied when the animal was negatively buoyant versus positively buoyant.

Modelling the Demographic Consequences of Weight Change

The aim of this model is to examine the effects of the weight and body composition of female elephant seals when they return from a trip on their survival, fecundity and the mass of their pup. Mark Hindell and Clive McMahon already have a project that will examine lifetime reproductive success of individual female southern elephant seals using 13,500 individual capture histories of animals marked as weaned pups. Data on birth and weaning mass of pup and mother's mass is available for a subset of these animals. These data will also be analysed by New using the same approach that has been applied to examine the relationship between body condition, survival and fecundity in grey seals. In addition, information is available on the birth and weaned mass of all pups born to most of the 124 female southern elephant seals that have been tracked, and the subsequent recapture history of these pups.

McMahon found a clear relationship between the mass of female southern elephant seals when they return to Maquarie Island and the weaned weight of their pup. He also found a clear relationship between the weight of a pup at weaning and its subsequent survival (McMahon *et al.*, 2000). Similar data are available for the Heard Island colony. The group agreed that conducting a comprehensive analysis of similar relationships for northern elephant seals is a high priority. Analyses for northern elephant seals have been complicated by the need to estimate rates of tag loss for these animals. Lisa Schwarz will analyze tag loss information for three populations (Macquarie Island, Marion Island, California colonies) and then conduct an integrated analysis of the relationship between pup survival, pup condition, and maternal condition for both southern and northern elephant seals. The results of this analysis will serve as a foundation for a demonstration model of the relationship between female foraging success and elephant seal colony dynamics that will be developed by New.

COASTAL POPULATIONS OF BOTTLENOSE DOLPHINS

Focal data sets

Doubtful Sound

Lusseau described studies of bottlenose dolphins that have been conducted at Doubtful Sound on the South Island of New Zealand. There are three distinct populations of bottlenose dolphins in the local fjord system, but there appears to be little or no interaction between them. The Doubtful Sound population has declined from 68 to 53 individuals since 1995 (Currey *et al.*, 2008). Individuals live in mixed-sex schools and have spatially fixed activities (i.e., some activities typically are observed in certain locations, probably reflecting a patchy distribution of prey that are associated with reefs). Three species of large sharks occur in the area, and there is convincing evidence that predation shapes group behaviour.

Data are available on the behavioural state of all school members at 15-minute intervals and on the school's geographic distribution, location, and composition (the sex of all individuals is known). Data for individual dolphins also are available from 161 focal follows, with 2-43 samples in each sequence, and there is additional information on dive intervals for males and females.

The population is subject to disturbance associated with tourism. Disturbance results in increased time spent travelling, an increase in the length of travelling bouts, and a decrease in time spent resting. These responses varied between sexes. The dive interval for males increased sharply when a school was approached closely, whereas the dive interval for females (which have a shorter dive interval than males) increased gradually.

Calf survival has declined from 86% to 34% coincident with an increase in the number of tour boats, but no change in adult survival has been observed. Lusseau believes that the decrease in calf survival is caused by change in the maternal energy budget. He suspects that an increase in feeding cannot compensate for the additional energetic cost of increased travelling time and reduced resting time, which leaves less energy available for the calf.

Sarasota Bay

Wells summarized data collected by the Sarasota Dolphin Research Program that were relevant to the working group's objectives.

The Sarasota Dolphin Research Program began as a pilot tagging project in 1970. Radio-tagging and tracking have been conducted since 1975. However, the primary source of information is sightings of photo-identified animals. There is a catalogue of 3512 individuals for the west coast of Florida and there have been over 100,000 individual sightings and 38,000 group sightings of known animals. Some individuals have been resighted more than 1,000 times. These data have allowed female reproductive success to be monitored from 1970 to present, facilitating study of extended lineages. The birth date, sex, age of mother, and duration of association of 314 calves born to 106 resident females have been recorded. Some females have had as many as 9 offspring. Naive females have lower calving success than older females. The inter-calf interval is initially high, decreases as the animal ages, and then increases when mothers are older. Substantial mortality occurs when young leave their mother and become sexually active; male mortality is higher than female mortality.

Adult males range more widely than females but still are primarily associated with Sarasota Bay. Males form alliances that are an important part of the social structure and can be maintained for the life of an individual. Females have multiple partners during their lifetime and some paternities cannot be attributed to resident males, suggesting that genetic exchange is occurring. Most paternities have been attributed to animals that are 13-40 years old. The paternal group includes both large and small animals, although animals that are part of an alliance appear to be more successful in fathering young than solitary individuals.

Defining the Sarasota Bay population for the purpose of estimating vital rates is difficult because although the population largely is resident within the Bay, it is highly mobile. There is some genetic exchange, likely with populations with slightly overlapping ranges to the west, north, and south. Work recently has been conducted to define the population more accurately.

The program has archived information from focal follows of the behaviour of individual animals from the 1980s to the present. The data include at least 1158 follows of 102 different individuals. Information associated with these follows includes distance to nearest neighbour, location, water depth, habitat, activity, group size, and the number of dolphins within a defined distance. Not all projects collect exactly the same data.

The program has established a health assessment database on the basis of samples collected at least once a year. The database includes a maximum of 689 sets of measurements per individual (n = 219). Individuals have been sampled as many as 15 times. Blood samples are collected to evaluate basic hematology, immune system function, occurrence of pathogens and biotoxins, environmental contaminants, and stress and reproductive hormones, and to conduct retrospective studies of disease by analyzing antibodies. Faeces, milk, urine, and blubber also are collected. Blubber thickness and reproductive status are determined by ultrasound. A tooth is collected to determine an animal's age if it has not been followed since birth. Blubber thickness changes substantially among seasons. Unpublished measurements of the metabolic rates of free-ranging animals and mortality patterns suggest that the detrimental effects of heat stress are greater than those of cold stress.

On average, bottlenose dolphins in Sarasota Bay come into contact with boats every 6 minutes. More than 45,000 boats are registered in the area. Most collisions occur within a two week window around the 4 July powerboat races. Animals change their behaviour in response to boats: they form tighter groups, dive more frequently, and change their vocalization patterns. At least 31% of animals have scars from shark bites although the abundance of sharks has declined considerably over the past few decades. Changes in vital rates have been driven more strongly by environmental events (e.g., severe red tides) than by disturbance. The size and weight of 2-year old calves (the youngest age at which animals are handled) decreased following severe red tides. In 2006, the year following the most extensive recorded red tide, 50% of calves died, significantly more than in any other year. The mortality followed dramatic reductions in abundances of prey fishes (>90% for some species) in response to the red tide. Dolphin abundance decreased as a result of temporary and permanent emigration and reduced immigration. The behaviour of the animals changed. Foraging rates were lower, group size increased, and animals ranged over a larger area.

Shark Bay

The population of Indian Ocean bottlenose dolphins in Shark Bay has been studied intensively since the mid-1980s, primarily via photo-identification. Over 1,200 individuals have been identified, and there are more than 15,000 sightings in the database. Different kinds of focal follows of schools and individuals have been conducted. In the mid-1990s biopsies were conducted to analyze relatedness and paternity.

Compared to the dolphins in Sarasota Bay, Shark Bay dolphins are smaller and less sexually dimorphic. They mature later and have an inter-calf interval of 3–6 years (typically greater than 3 years). They appear to have lower adult survival and a higher population density (approximately 2.4 animals / km^2).

The group size, range size (7.2–101 km^2), and foraging tactics of females vary. Foraging behaviour appears to be vertically transmitted and specific to certain microhabitats. Males vary in alliance strategies, ranging tactics, and foraging tactics. During the breeding season, individual females are herded for up to several weeks by 2-3 males that belong to larger teams of 4-14 individuals. Teams attack each other to take females and defend against attacks. The size of the group is correlated positively with the size of its home range, which varies from 27.5–216.8 km^2. Mating opportunities seems to be shared amongst first order alliances. The distribution of females determines that of males. There is very high predation pressure, mostly from tiger sharks: over 70% of dolphins have shark bite scars.

The number of tourist vessels has increased since 1995 and the number of trips per day has increased from 4 to 8, although tour boat activity is confined to a relatively small area. There has been some emigration of animals from the area over this time, and calf survival to age 3 has decreased in proportion to vessel exposure. There has been no observed effect of tourism on inter-calf interval or on adult survival.

Model development

Results from all three study sites suggest that predation is the dominant cause of adult mortality and that dolphin behaviour reflects the trade-offs between predation risk and foraging costs, as well as competition among males for females. Adult dolphins rarely appear to change their behaviour, even when exposed to relatively high levels of disturbance. The only documented effects of disturbance and environmental perturbation on vital rates of bottlenose dolphins are reductions in the survival and condition of calves. This change appears to be caused by reduced availability of energy to adult females in response to behavioural changes associated with disturbance or altered prey availability (for example, as a result of a red tide event). The working group therefore agreed to focus on a model of the effect of behavioural changes on individual energy budgets and the potential effect of changes in energy budgets on calf condition and survival.

Modelling approaches

Lusseau presented a revised version of the model of motivation he had described at the working group’s first meeting. He believes the model could be applied to marine mammals, like bottlenose dolphins, that are social and are income breeders. Income breeders rely on continuous energy acquisition during the calf-rearing period, whereas capital breeders (such as elephant seals and most other phocids) are able to acquire and store energy outside the calf-rearing period. In Lusseau’s model, the activity of an individual at a particular moment in time is determined by a number of internal motivational states (e.g., body condition, desire to socialize, and fear), the behaviour of other members of its social group, and a range of external covariates. However, it is not always possible to assign the observed behaviour of an individual to a particular activity because the behaviour may not be clearly visible or because certain activities (e.g., travelling and fleeing) cannot always be distinguished by a human observer. In addition, observations often concentrate on the behaviour of entire groups, rather than on the behaviour of individuals within a group.

There was considerable discussion of the merits of this and alternative models. The model that emerged from group discussions (see section 3.4) follows the structure outlined by Lusseau (Figure 1).

A mathematical model linking activity budgets and energy budgets

Here we provide a simple verbal description of the model and discuss its application to bottlenose dolphins and other income breeding marine mammals. The purpose of the model is to infer changes in the energy levels of individual dolphins, particularly females and their calves, from a set of behavioural observations. The state-space framework of the model distinguishes between actual biological processes and indirect observations of the outcome of those processes. The group used the following conventions to describe the components of this model. **States** are a set of characteristics for each modelled individual that affect its activity. In the bottlenose dolphin model these states include the individual's energetic status (i.e., whether it is in net energy balance, an adult, or, if it is a calf or juvenile, has acquired sufficient energy for growth), and a number of "motivational" states that reflect the individual's propensity to perform particular activities (in this case socializing and fleeing). The values of these states will change over time depending on the individual's 'activity' (defined below), the states of other members of the individual's social group, and some characteristics of the environment (e.g., prey density). Changes in the values of states over time are determined by an underlying process model. At a particular time step, an individual may perform one of a number of different **activities** [search, feed (i.e., consume a prey item), travel, socialize, nurse (performed by mothers and calves only), and flee]. Each of these activities will have different effects on the animal's state, particularly its energetic status, at the next time step. For example, we assume feeding will have a positive impact on energetic status, resting will have a moderate negative impact, and fleeing will have a large negative impact. The negative costs can be estimated independently on the basis of experimental results, theoretical relationships, observed respiration rates (which are available for all three bottlenose dolphin populations considered here), and telemetry data. An observer will assign a dolphin that is performing a particular activity to a **behavioural** category that may or may not accurately reflect the true activity of that animal. The uncertain relationship between the recorded behaviour and the actual activity of the individual is reflected in an observation model.

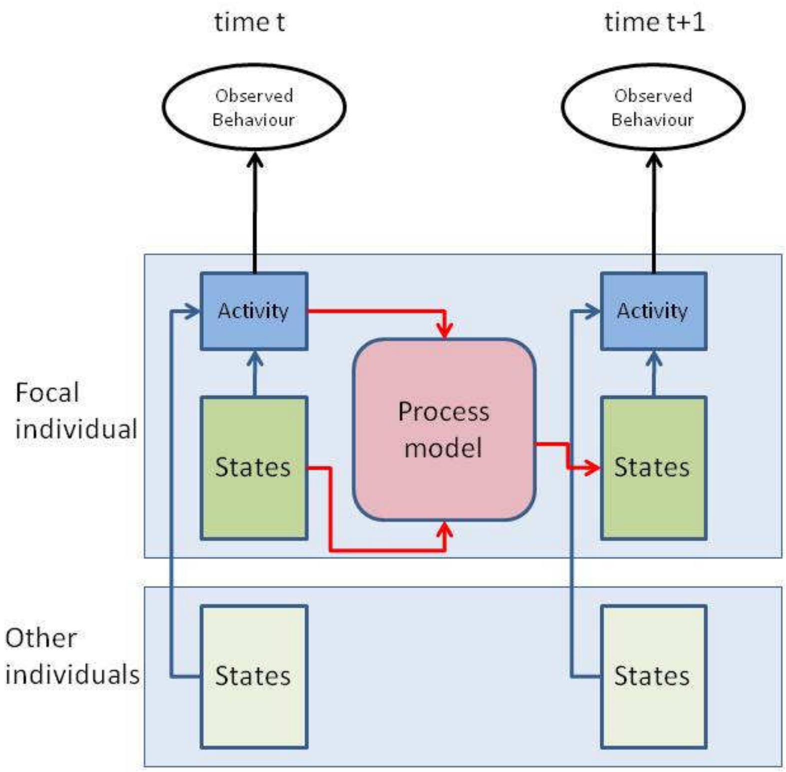

Figure 1. A state-space model of the evolution of the behaviour of a single dolphin in a school. States that could be included in this model are energy level, body size, motivation to socialize, and fear. Possible activities include searching, feeding, travelling, resting, socializing, fleeing, and nursing. The dolphin's activity at time t is determined by the values of the different states for the individual and the other members of its school, and by the values of external covariates such as environmental quality and disturbance. The process model uses information on the dolphin's state values and its activity at time t to predict its state values at time t+1.

The working group developed a formulation that can be used to model the effect of other members of an individual's social group on that individual's activity. This formulation can reflect an unshared consensus decision-making process, in which a small number of individuals determine the activity of the entire social group; a shared consensus decision-making process, in which the activity of the social group reflects the state values of the majority of the group; or a decision-making system that is intermediate between these extremes.

In principle, this model can be fit to data from focal follows of individual animals or schools. However, the model will be more effective when behaviours can be ascribed to individuals or particular age and sex classes (e.g., mothers and calves, adult males, adult females, juveniles) rather than entire schools. Additional information on the energy status of animals, for example from observations of relative condition or telemetry, likely will increase the power of the model and may in fact be essential for fitting the model accurately.

The working group identified three sets of bottlenose dolphin data that could be used almost immediately for testing this model: data from focal follows of dolphin schools in Doubtful Sound when tour boats are present and absent, data from focal follows of mother-calf pairs in Sarasota Bay in a year when a red tide occurred and in other years, and data from focal follows of mother-calf pairs in areas of Shark Bay where exposure to tour boats varies. Several members of the group will attempt to develop a model appropriate for the first of these data sets during the boreal summer of 2010.

The working group also noted that the same model structure could be applied to income breeding pinnipeds, such as fur seals and sea lions. In fact, this might be a particularly useful application of the model because there are extensive telemetry data on these animals that could provide information on changes in their energetic status as well as their behaviour over time.

Energy budgets and vital rates

The model described in section 3.4 does not provide a clear link between the energy status of an individual and any vital rates. However, it can provide an estimate of how the energy status of a calf changes over time in relation to its mother’s behaviour. This information can then be used to infer the relationship between a female’s behaviour, disturbance and the probability that a calf will survive to age 3, the typical age at separation from mother (nutritional weaning occurs earlier).

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