A review of literature relevant to the PCAD model for guidance in developing transfer functions

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Introduction

Sound travels efficiently in the ocean, and many marine animals use sound as an important sensory modality. Most marine mammals rely on sound for several important life functions, including communication, navigation and foraging. As we have learned more about the importance of sound for marine mammals, there has been a concomitant increase in awareness of the potential effects of anthropogenic sound on them. Several studies have revealed how human-caused sounds affect marine mammals, reviewed comprehensively by Nowacek et al. (2007), Weilgart (2007) and Southall et al (2007).

The majority of these studies are restricted to short-term observations of individual animals, and demonstrate a variety of reactions ranging from avoidance and attraction, with subsequent demonstrations of both habituation and sensitization. Indeed, most studies address four primary concerns for individual animals exposed to elevated noise levels: permanent threshold shifts (PTS), temporary threshold shifts (TTS), acoustic masking and behavioural effects.

Unfortunately, it is difficult to extrapolate these short terms reactions to potential population level effects, and considering the growing levels of anthropogenic sound in the ocean, such studies are crucial for establishing guidelines and management regimes for anthropogenic noise. To establish how sound may affect populations of marine mammals, we must first understand in detail how sound effects animals behaviourally, physiologically and psychologically, and how these effects could relate to population level effects such as changes in growth and pregnancy rates.

The lack of information on the physiological consequences for marine mammals exposed to sound stressors limits our ability to elucidate population-level impacts. There is, however, a large body of literature that describes physiological effects of noise on terrestrial (including captive) and other species, including links to population level effects. These data and conclusions can be useful for establishing hypotheses and experimental approaches to develop our understanding of how anthropogenic noise can effect marine mammal populations.

At the recent “Effects of Noise of Aquatic Life” conference in Nyborg, Denmark, results from a few studies were presented (Bejder and Lusseau, 2008; Bejder et al., 2006a; Bejder et al., 2006b; Lusseau et al., 2006) that were deemed helpful in the understanding of transfer functions between variables in the Population Consequences of Acoustic Disturbance (PCAD) model (NRC 2005) (Figure 1). These studies did not specifically evaluate possible impacts of sound on cetaceans – but they did identify long-term population level effects of an apparent benign human activity on cetacean populations, i.e., cetacean-watch tourism. Whether or not the documented impacts had an acoustic component was not investigated. The documented impacts were recently acknowledged by the International Whaling Commission’s Scientific Committee (IWC 2006): “[t]here is new compelling evidence that the fitness of individual odontocetes repeatedly exposed to whalewatching vessel traffic can be compromised and that this can lead to population-level effects.”

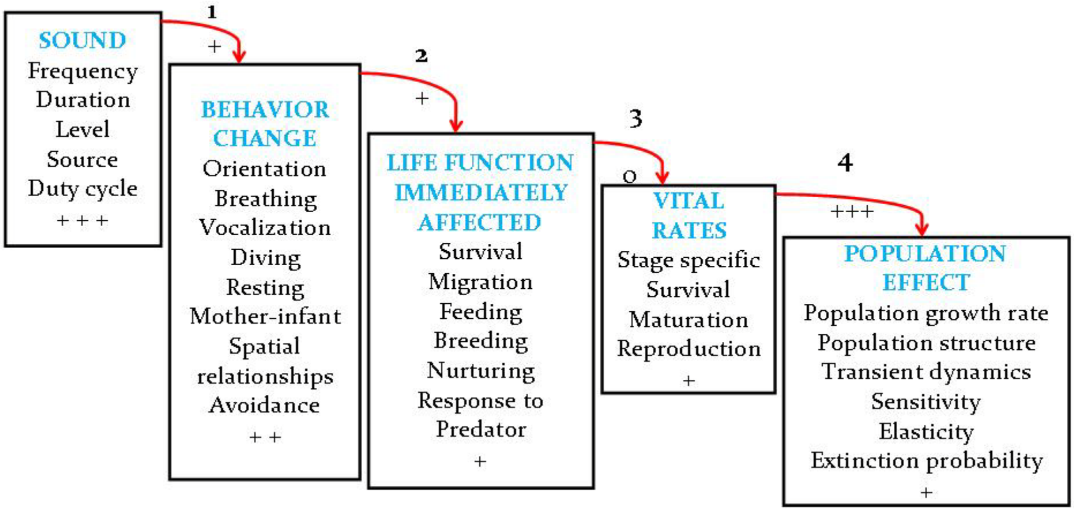

Figure 1. Population Consequences of Acoustic Disturbance (PCAD) Model (NRC 2005). The model involves fives levels of variables (Sound, Behavior Change, Life Function Immediately Affected, Vital Rates and Population Effects) that are related by four "transfer functions".

Detecting population-level effects of whale watching was based on long-term population monitoring and availability of information on cumulative exposure on individuals (Bejder and Lusseau 2007). The influence of such impacts on population viability was inferred using the dose-response relationships these studies describe. Early individual-based models show that the documented impacts are highly likely to endanger the viability of small populations, which have restricted immigration/ emigration because of the increased cumulative exposure they incur. So, while these studies did not study acoustic disturbance, they demonstrated a population level consequence of a periodic, sub-lethal stressor (i.e., vessel traffic); such investigations are the goal of the PCAD model using sound as the stressor.

The PCAD model was developed as part of a U.S. National Research Council Panel specifically convened to assess the population level consequences of acoustic exposure on marine mammals. The PCAD model aimed to create a framework that clarifies where different kinds of information fit in and identifies processes that need study' (NRC 2005). The Panel described their work as a status report and the PCAD model as a 'roadmap' for the critical longterm project of turning a conceptual model into a predictive model useful for science-based management of marine mammals and their exposure to sound. Our review follows this map, specifically elucidating the areas where there is solid existing information and where the critical gaps exist with respect to sound exposure and the transfer functions described in the PCAD model.

The specific aims of this literature review were to:

a) identify papers that report on links between the five levels of variables outlined in the PCAD model;
b) identify links between variables that are well documented;
c) identify links between variable that are not well studied;
d) identify papers that can be used to produce quantitative links between levels;

e) to further develop the PCAD model by inclusion of a broader taxonomic range;

f) use the results from a-e above to focus future studies to further assist transforming the conceptual PCAD framework into a predictive model that would be more useful for marine mammal management.

Methods

Given the thorough and relatively recent reviews of the behavioural responses of marine mammals to noise (Nowacek et al 2007, Southall et al 2008), our intent was not to revisit these reviews but instead to explore the literature from the perspective of the PCAD model, specifically links between how noise exposure may be linked to the other four levels of variables in the PCAD model. Our approach to this review was to use targeted search methods to be confident that the results of our search represented the structure of the PCAD model while also being broad enough so as to avoid missing appropriate literature.

We did not limit our review to marine mammals; indeed our review included terrestrial mammals as well as fish, amphibians, reptiles and birds. Invertebrates were not included in our review. We recognize that significant differences exist between these taxonomic groups in behaviour and physiology, but we wanted our review to provide a comprehensive search for effects of noise exposure as they relate to one or more aspects of the PCAD model. We included in our search direct physiological responses to acoustic disturbances, which were not explicitly part of the PCAD model, though their inclusion was discussed in the early stages by the Panel (Appendix D of NRC 2005). The NRC Panel did recognize the need to measure physiological responses, e.g., hearing loss, steroid hormone concentrations, and they recommend that additional effort be devoted to developing methods for measuring glucocorticoids and other steroid hormone metabolites, such as increasing the capability of data logging devices (NRC 2005). Our review revealed many studies linking acoustic disturbances with physiological responses including hormone changes as well as a host of other physiological responses. Evaluating the severity of these responses in the context of population consequences is beyond the scope of this review, but we felt it important to identify and catalogue them.

We used several tools and databases in an effort to make our review as comprehensive as possible. Keywords (Table 1) were chosen on the basis of locating literature relevant to linking outcomes of noise exposure to the five levels of variables within the PCAD model. Specifically, the keywords ‘noise’, ‘sound’ OR ‘auditory exposure’ were used in all searches and combined with each search terms listed in Table 1.

Table 1. Terms used in database searches, all were combined individually with 'noise', ‘sound’ and 'auditory exposure' when searching each database. * indicates a ‘wildcard’ to reduce the chances of missing relevant literature in the database search. Parentheses indicate a paired search in which both terms were searched against a required term, e.g., ‘noise’ searched with hormon* or cortisol

Keywords			
Stress	(eat or forag*)	Fecundity	Stress & (hormon* or cortisol)
Physiology*	Heart rate	Energet*	Endocrine* & effect*
Endocrine*	Blood pressure	Vigilance	(mate or mating) & behav*
			(reproduct* & success)

These keywords were then searched in six databases: Web of Science, BIOSIS previews, CAB Abstracts, ASFA, Google Scholar (searched only for reports and conference proceedings, which were later omitted) and PsycINFO (this search engine was abandoned due to the high number of duplicate papers retrieved). These databases were chosen because: i) we believed that their focus (field) was conducive to our area of interest; ii) the coverage of the database was sufficient, i.e., the level of redundancy between databases indicated that we were not missing papers, instilling confidence in our results. See Table 2 for coverage and information of the databases searched. We utilized the database access for both Duke and Murdoch Universities, providing exceptional coverage.

Table 2. Attributes of the databases used in our search.

Database & platform	Coverage	Years available to Murdoch & Duke Universities	Number of papers
WOS Web Of Science – Web of Knowledge platform	10,000 authoritative journals – multidisciplinary science, social science, arts, humanities	1900 onwards	40m records from 1840 onwards; records from 1840-1900 not available to Duke or Murdoch
ASFA - CSA platform	5,000 journals + books, reports, proceedings in marine, brackish, freshwater environments	1971 onwards	1m records from 1971 – present
BIOSIS Previews – OvidSP platform	5,000 journals in biosciences + meetings, books, patents	1926 onwards	18m records from 1926 - present
CAB Abstracts – OvidSP platform	400 journals + books, theses, proceedings in agriculture and applied life sciences	1910 onwards	7.1m records from 1910 – present

Due to the scope of this review, the following reference types were excluded: i) any papers which were not peer reviewed; ii) literature reviews); iii) conference proceedings and meetings; iv) all reports (e.g. government, NGO etc.); v) any paper where the abstract was not written in English. References concerning invertebrates were not included. Some keyword searches were further refined if the number of hits were too large; refined results are shown in Appendix 1.
Once searches were concluded and refined, 769 papers were archived in EndNote®, and this became the working bibliography. In an attempt to focus review efforts in relation to the PCAD model, a subsection of papers (n=138) pertaining to the neurophysiological effects of noise was kept in a separate EndNote folder and not

included in the review framework. This subset incorporated any papers found on the auditory processes of the brain, excluding those referring to hearing sensitivity, threshold shifts or localisation. We excluded them from further analyses because critically evaluating them is beyond our expertise, and furthermore they concern neurophysiological processes that are well beyond what is currently known for marine mammals.

From the remaining papers in the library (630), the first 113 references were evaluated using the original search framework (Figure 2) by reading the entire publication. Using the headings under the framework, which was designed around the PCAD model, the relevant data were extracted from each publication and inserted into the framework. However, due to time constraints the framework was condensed (Figure 3). To ensure little loss of critical data we undertook a comparison exercise. The consistency of the review between 'original' (full papers) and 'refined' (abstracts only) search frameworks was verified by taking twenty (of the 113) randomly selected papers reviewed with the original framework and re-reviewing them based only on the abstract using the refined framework. The integrity of the review was not compromised (Appendix 1, '20 refs check' tab). As well as this change, the rest of the publications (497) were categorised using only the abstracts; full papers were read if there was insufficient information in the abstract. Additionally, 20 papers were not categorised due to either the paper being in a non-English narrative, inaccessibility to either the abstract, or, if it was not possible to categorise a publication from the abstract alone, the full paper.

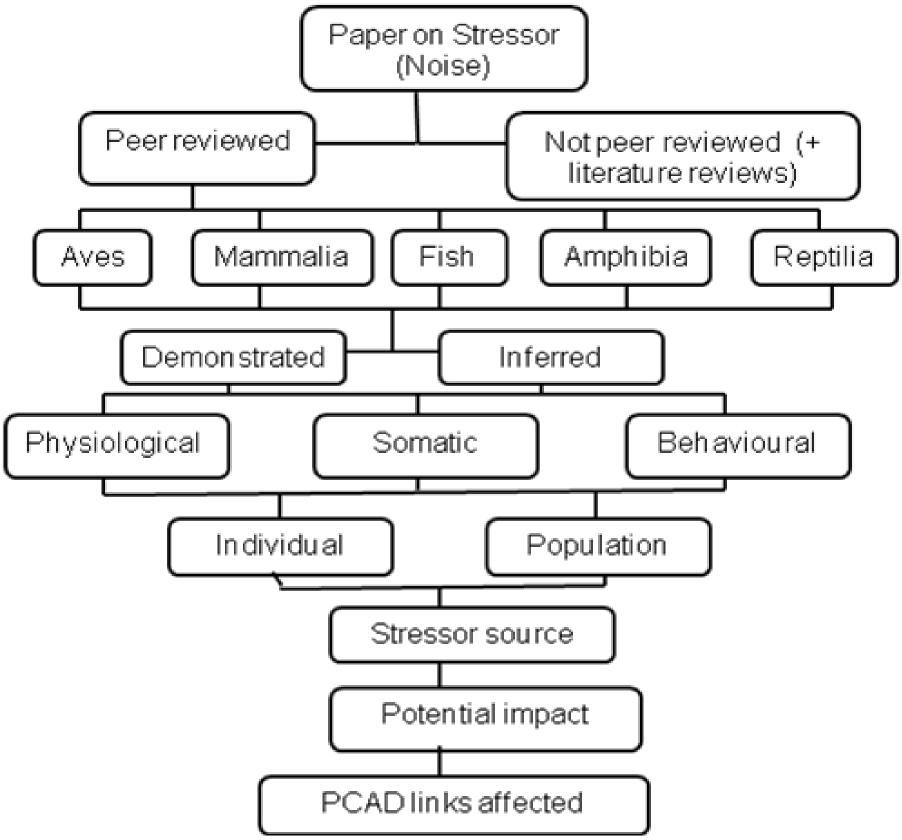

Figure 2. Original search framework.

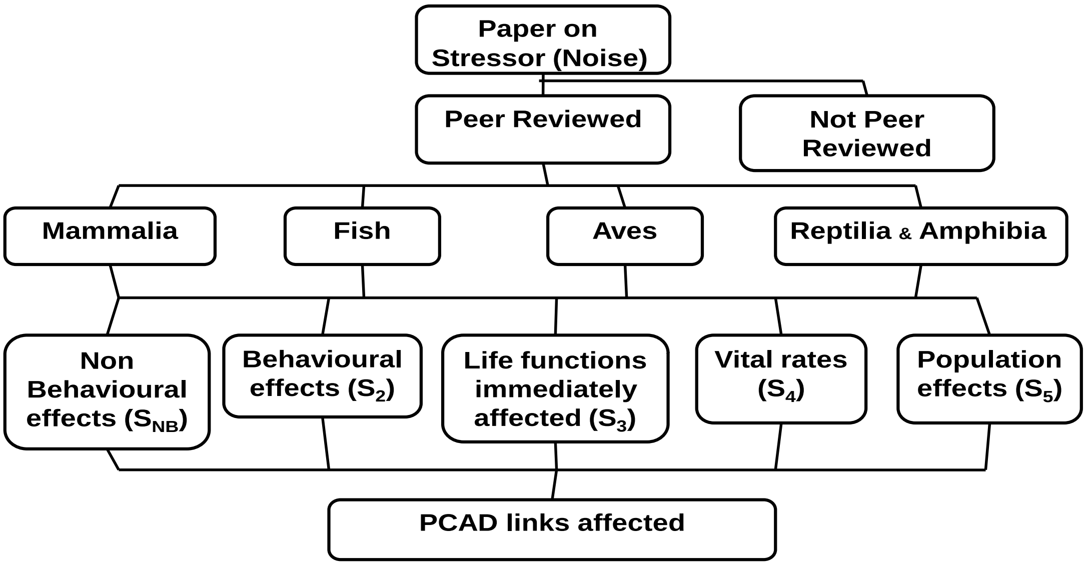

Figure 3. Revised search framework

The framework for reviewing and categorizing the papers was as follows:

- Stressor
    - Single – where noise was the only source of stress on the animal
    - Multiple – the effect of noise was tested with any other stimuli
- Controlled or uncontrolled (omitted in revised framework) – indicates whether the administration of each stimulus was controlled individually
- Measured (omitted in revised framework) – specifies if the noise and other sources of stress were directly measured
- Class
    - Mammalia
    - Mammalia (marine)
    - Aves
    - Reptilia
    - Amphibia
    - Fish
- Experimental outcome (NB: these will be taken into account in the critical review of the individual papers but was beyond the scope of the current review framework)
    - Demonstrated (omitted in revised framework) – the results of the experiment were validated
    - Inferred (omitted in revised framework) – the results were not directly determined through experimental means
- Level of impact (omitted in revised framework)
    - Individual animals
    - Multiple animals
    - Population of animals
- Noise source (S_1) (omitted in revised framework) – the purpose and origin of the sound stress; omitted in the revised framework as it was deemed to be too

detailed for this review, i.e., this review was focused on identifying strengths and gaps in our knowledge and literature with respect to noise exposure having population level consequences. The noise source is certainly a critical factor in individual cases, but we sought to include all noise sources in this ‘higher order’ review

- PCAD Level of Variables (full description of subheading provided in Table 3)
  - Non-behavioural effects (S_{NB}) (physiological and somatic were combined in the revised framework)
    - Change in body processes e.g. biochemical parameters, hormones, heart rate and blood pressure
    - Somatic effects – physical damage to tissues, e.g., damage to ear structure, manipulation of various body organelles
  - Behavioural (S_2) - any behavioural response or lack of response to noise which was documented in the paper
  - Life function immediately affected (S_3), e.g., feeding, mating
  - Vital rate(s) affected (S_4), e.g., growth, reproductive rate
  - Population effects (S_5) – how sound stress on an individual eventually affects the population

Levels of variables (S_2,S_3,S_4,S_5) affected by the noise exposure – as our review was rooted in noise exposures, S_1 of the PCAD model is included by default, but in this stage of the review framework we categorized whether a paper affected one or more of the PCAD levels of variables, e.g., life function (S_3), vital rate (S_4).

Invertebrates were excluded from our review on the scientific presumption that their physiology and behaviour differ substantially from those of vertebrates. The same argument could be made for the differences between mammals and other vertebrates, but we felt it was important to include these groups as they can be removed in later analyses if so desired. Mammals were divided into terrestrial and marine so we could more easily identify gaps in the literature and perhaps recognise the areas where methods and observations may be drawn from one to the other.

Table 3. Levels of variables in the PCAD model, responses as reported in the literature and their definitions.

PCAD Levels of Variables	Reported responses	Definitions
Behavioural effects (S_2)	Avoidance	Increase in speed directionally away from noise source. Number of animals in area of stressor temporarily decrease i.e. avoid the area when stressor is active. Animal hides.
	Vocalisation	Change in call rate, duration, level etc.
	Vigilance	Change in time spent on being observant
	Resting	Disruption of animals in the state of rest
	Locomotion	Change in speed of travel, in no particular direction
	Orientation	Change of position/direction in response to external stimulus
	Diving	Change in dive rate and duration by marine animals
	Displacement	Target animals permanently avoid areas they previously inhabited.

	Immobilisation	Cessation of all activity usually a startle reaction
	Grooming/Preening	Increase or decrease in rate of grooming or preening
	Rearing	Act carried out primarily by *muridae*, attempting to climb up the side of a cage
	Latency	Hesitancy in carrying out/continuing activity
	Surface time	Length of time spent at the surface of water by marine animals
	Social behaviour	Cessation or change of socializing animals in response to a stimulus
	Ranging	An animal changes the distance it travels to carry out typical activities, or exploring new areas
	Agitation	Showing obvious signs of emotional disturbance
	Aggression	Increase in aggressive behaviour towards conspecifics
	Habitat utilisation	Change in activity habitually carried out in a particular area
	Inter-individual spacing	Distance between individuals of one group
	Mother-infant spatial relationships	Change in distance between mother and offspring

Non behavioural effects (S_{NB})	Acoustic sensitivity	In corporate Auditory Evoked Potentials (AEP) & Auditory brainstem response (ABR) Acoustic startle response (ASR) nervous reaction to sound stimuli, examines permanent or temporary hearing threshold shift, localisation and masking effects
	Hormonal	Change in hormonal levels
	Heart Rate	The number of heartbeats per unit of time, usually expressed as beats per minute.
	Biochemical parameters	Changes in the composition of plasma, saliva or cerebro-spinal fluid (CSF) levels of biochemical substances
	Modification of Outer Hair Cells /Inner hair cells	Noise can result in the death or damage of OHC or IHC of the organ of Corti
	Blood Pressure	Change in blood pressure
	Structural manipulation	Change in tissue and muscles structure
	Respiration & respiratory effects	Change in respiration rate
	Body weight	Change in weight as a response to noise
	Gastrointestinal aggravation	Where the digestive tract is affected by noise
	Body temperature	Change in body temp, e.g. Stress Induced Hyperthermia (SIM) - Increase in deep body temp.
	Learning capabilities	Increase in the capacity to learn due to a noise stimulus
	Immunomodulatory effects	Where the animal’s immune system is affected
	Growth rate	Change in growth rate
	Energetics	Energy transformations

	Rectified diffusion	Leads to the growth of microscopic bubble nuclei in the presence of high-intensity sound.
	Defecation	A response to a stressful situation, rate at which faeces is passed.
Life function immediately affected (S_3)	Survival	Noise disturbance resulting in immediate death of an animal
	Migration	Noise affecting migrating patterns of animals
	Feeding	Direct impacts on the foraging habits of animals
	Breeding	The physical act of reproduction being interrupted
	Nurturing	Noise affecting a parent capacity to look after it's young
	Response to predator	Affects the animals ability to react to a predatory situation
Vital Rates (S_4)	Survival	Auditory stress over time resulting in the death of an animal
	Maturation	Affects an animals ability to physically develop over time
	Reproduction	Affects an animals' capacity to produce young
Population effect (S_5)	Population growth rate	The rate of reproduction within the population
	Population structure	Change in demographics of the population
	Transient dynamics	Age specific population effects
	Sensitivity	The pace at which auditory stress affects a population
	Elasticity	The population's ability to recover after an acute drop in density
	Extinction probability	The likelihood the species will go extinct

Results

Sample sizes

The initial search identified >22,000 published papers, reports and conference papers through searches using the original search keywords (Table 1), though this number includes redundancies between search databases and keywords. The BIOSIS Previews and CAB Abstracts databases returned the majority of the initial hits (Table 4). Once identical papers from the searches were grouped in Endnote® and the refinements outlined above were made, we were left with 630 papers were deemed relevant to the review - from 250 journals and dating from 1969 to 2008.

Table 4. Number of papers found in databases

Database	No. of papers
Biosis Previews and CAB Abstracts	15228
Web of Science	3501
ASFA	2283
Google Scholar	1526*
Total	**22538**

*Search only included conferences, meetings and reports.

Journals and Impact Factors

The twenty journals wherein most of the peer-reviewed papers on effects of sound on animals were found (based on search keywords) accounted for 299 of the 630 papers identified as relevant. These top twenty journals had an average five year Impact Factor of 2.50 (SD=0.551) (ISI Web of Knowledge, Journal Citation Reports, 2003-2008). The five-year journal Impact Factor is the average number of times articles from a given journal published in the past five years have been cited in the Journal Citation Report (JCR) year. It is calculated by dividing the number of citations in the JCR year by the total number of articles published in the five previous years

Animal classes

Of the 630 papers deemed relevant to this review, 17.5% (110) focussed on marine mammals (Table 5).

Table 5. Number of papers found on the effects of auditory stimuli within each animal class

Animal Class	Number of Papers	Proportion of all papers
Mammalia	367	58.25%
Mammalia (marine)	110	17.46%
Aves	70	11.11%
Fish	63	10%
Amphibia	13	2.06%
Reptilia	7	1.11%

Links between the five levels of variables in the PCAD model

Among the main aims of the literature review was to identify papers that report on links between the five levels of variables outlined in the PCAD model. For the purpose of this exercise, we subsequently refer to the five levels of variables in the PCAD model as S_1 (Sound), S_2 (Behavior Change), S_3 (Life Function Immediately Affected), S_4 (Vital Rates) and S_5 (Population Effects), respectively. Furthermore, S_1-S_2 refers to reported links between Sound and Behavior Change, S_1- S_3 refers to reported links between Sound and Life Function Immediately Affected, etc.

Links between noise and non-behavioural responses S_1-S_{NB}.

One of the most striking and useful outcomes to result from our review is the number of papers that fall outside of the PCAD framework. Specifically, we found 517 papers that demonstrated a link between noise exposure and some non-behavioural effect (see Table 3 for examples of these effects), and of those 517 studies 87 had marine mammals as their subject species (Figure 4). It is important to note that non-behavioural effects are not currently within the PCAD model. However, we would like to fully acknowledge the NRC Panel who produced the PCAD model for their recognition of the importance these non-behavioural effects, but their mandate to focus on behaviour was clear from the start as they were named the '*Committee on Characterizing Biologically Significant Marine Mammal Behavior*'. In outlining the framework for their work, the Committee included physiological effects within the discussion but appropriately returned to their mandate to consider potential population consequences of short-term behavioural responses to noise. Within their report, the Committee did discuss some physiological effects of noise exposure, i.e., hearing loss, resonance effects and rectified diffusion. The non-behavioural effects we encountered certainly included these three but also included approximately 20 others, from changes in hormone levels to immunoregulatory effects (Figure 5). Additionally, 53 of the papers we found that demonstrated non-behavioural effects also reported behavioural effects. Finally, the structure of our search framework did bias our findings toward non-behavioural effects, but this was a conscious decision based on the presence of the recent reviews of the effects of noise on marine mammal behaviour (Nowacek et al 2007, Weilgart 2007). As over 17% of the papers we found that investigated non-behavioural responses to sound had marine mammals as their subjects, we **suggest** that the PCAD model be expanded to include these effects. We will use the term 'S_{NB}' to distinguish this stage from the S_2 used in the PCAD model, henceforth we will distinguish between papers that report results relevant to the 'S_1-S_2' transfer function from those that are relevant to the 'S_1-S_{NB}'.

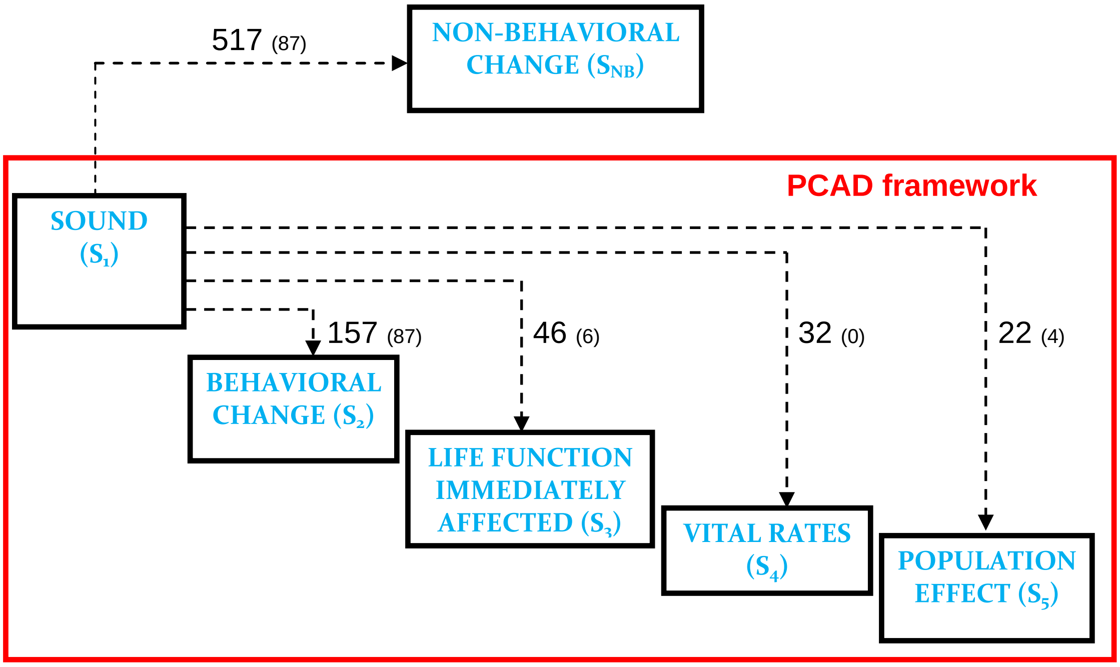

Figure 4. Number of papers reporting effects of sound on various levels of variables within the PCAD framework. Note: majority of effects of sound were reported on "non-behavioural changes" (mostly physiological impacts) which is not included in the current PCAD framework. Number in brackets specifies the number of papers relating to marine mammals

As we see in Figure 5, the non-behavioural effects reported in the papers we found are quite variable. Most of the effects measured are truly physiological (e.g., changes in hormone levels or heart rate), while some are arguably a mix of behaviour and physiology (e.g., defecation rate). Over half of the non-behavioural effects reported were related to auditory sensitivity (which included threshold effects, masking and localization), though there are a considerable number of reports on other physiological effects (Figure 5).

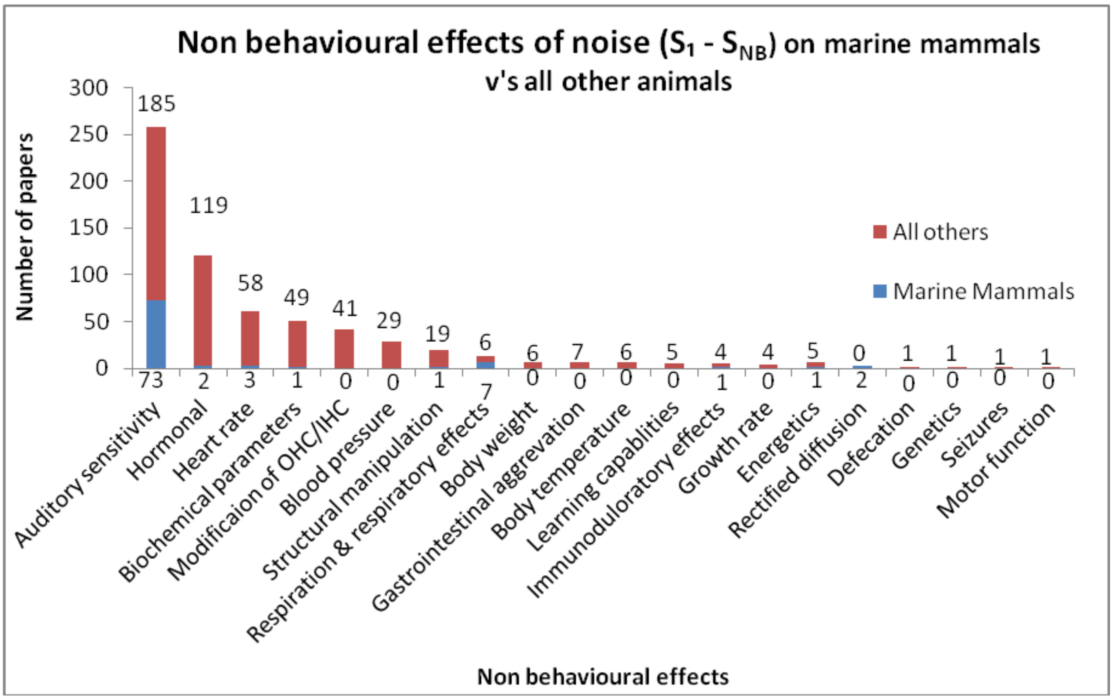

FIGURE 5: Breakdown of non-behavioural effects of noise S_1-S_{NB} (marine mammals vs. others).

In our presentation of the new S_{NB} category, we mentioned that almost 20% of the papers reporting such effects had marine mammals as their subjects. However, upon further investigation, we found that marine mammals occurred in fewer than half of the non-behavioural categories reported in these papers (Figure 5). Furthermore, with the exception of auditory sensitivity, there were very few papers in those represented categories. The existence of any marine mammal papers, however, in categories such as hormonal changes or other biochemical changes is encouraging with respect to our increasing ability to measure such things.

Effects of noise: Behavioural Changes (S_1-S_2):

Despite the structure of our search framework being biased towards non-behavioural effects, the search still returned 157 papers that demonstrated a link between noise exposure and a behavioural effect (Figure 6). Of those, 27% (n=42) had marine mammals as their subject species. The reason for this is likely that impact assessments are often constrained temporally, financially and logistically, and therefore, they typically focus on short-term observable behavioural responses that are more readily obtainable than long-term impact measures. However, it is rarely known whether, and in what ways, short-term behavioural responses translate to longer-term change in reproduction, survival and in turn r population consequences (e.g., Gill et al. 2001; Beale & Monaghan 2004*a*) – and hence the need for the development of the PCAD conceptual model. Furthermore, traditional interpretations of behavioral change in response to disturbance have been questioned recently (e.g., Nisbet 2000; Gill et al. 2001; Beale & Monaghan 2004*b*; Bejder et al. 2006; (Bejder *et al.* 2009, Kellar *et al.* 2009, Nisbet 2000)).

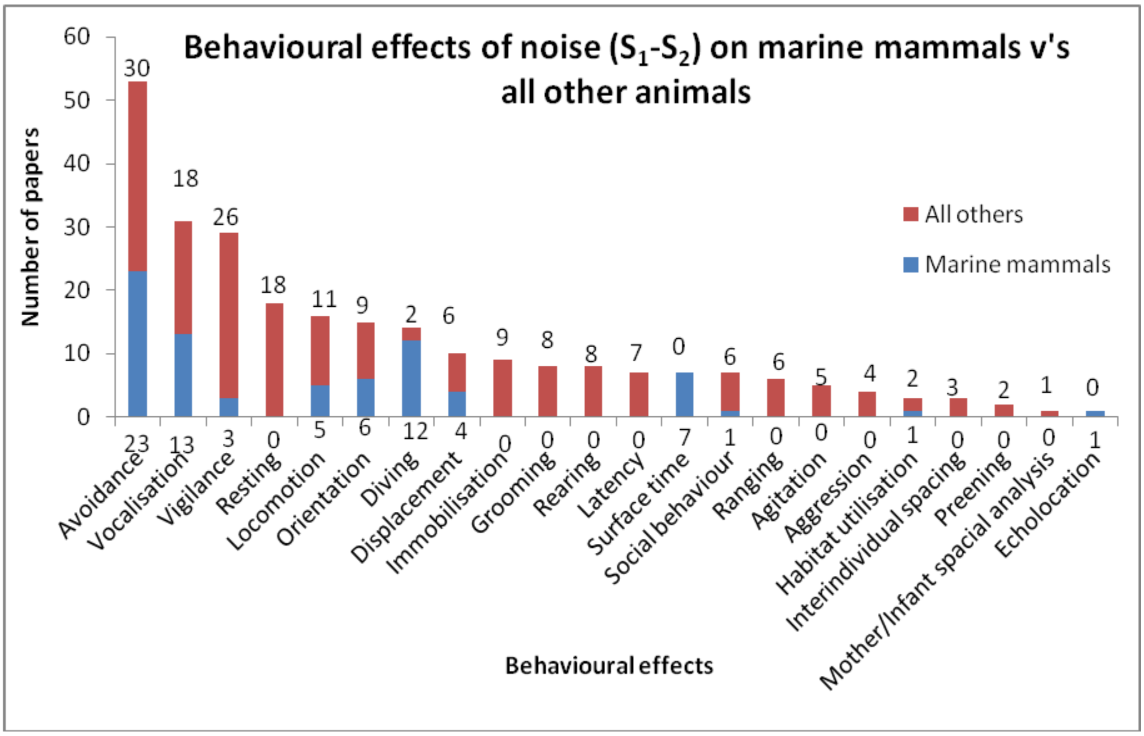

FIGURE 6. Breakdown of behavioural effects of noise on marine mammals vs. others S_1-S_2.

Behavioural responses to sound were reported in twenty-two behavioural categories of which 11 were demonstrated in studies focussing on marine mammals.

S_1 to all other levels of variables in the PCAD model

Next, we found a group of papers demonstrating links between noise exposure 'S_1' and some later stage of the PCAD model. Figure 7 shows the breakdown of papers showing links between noise exposure and life functions, e.g., feeding and breeding. Also, for each life function, we show the number of these papers involving marine mammals. Figure 8 shows the papers linking S_1 with vital rates, e.g., survival. The PCAD model actually includes a 'stage specific' category in this phase, but upon reviewing the papers we decided that it was most appropriate to assign each paper to a specific vital rate. We could not discern a means of accurately segregating what was a purely stage-specific effect; instead we felt that each effect could be assigned to a vital rate. For example acoustic exposure to pregnant female mice (Arck et. al. 1995) affect the survivorship of the offspring, and we assigned this paper to 'survival' though it could be argued that this was an effect on the foetal stage. Interestingly in this S_1-S_4 category, there were no papers dealing with marine mammals. Finally, we found 22 papers reporting direct links between acoustic exposure and a population level effect (Figure 9), and 4 of those papers involved marine mammals specifically affecting population growth rate.

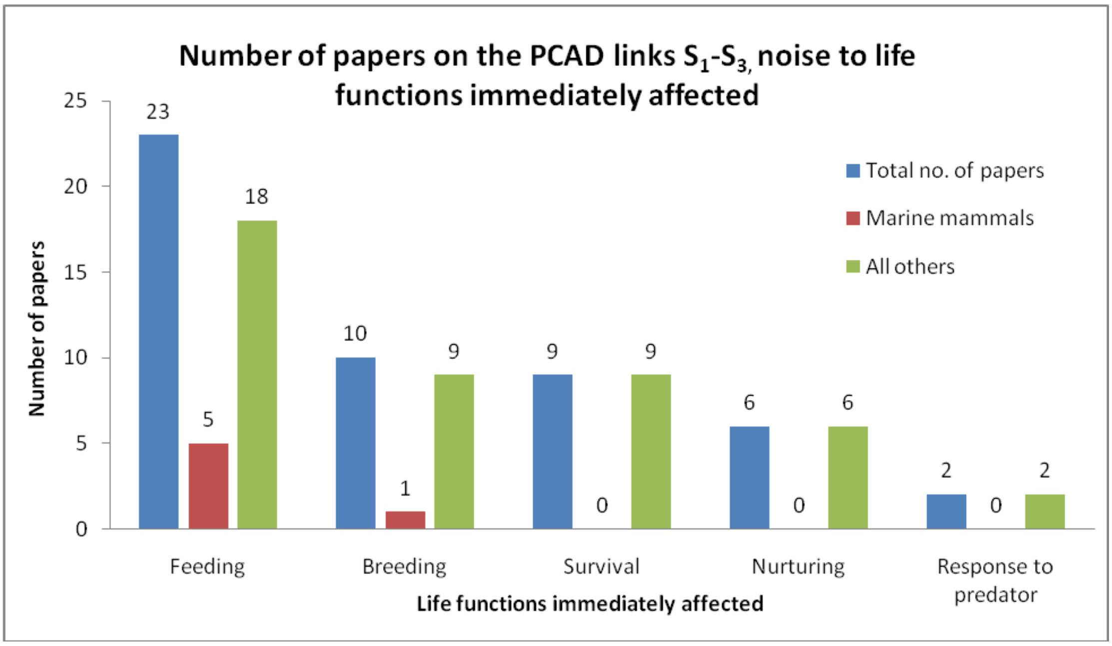

Figure 7. Papers reporting effects linking noise exposure with life functions, showing the total number of papers and then how many involve marine mammals.

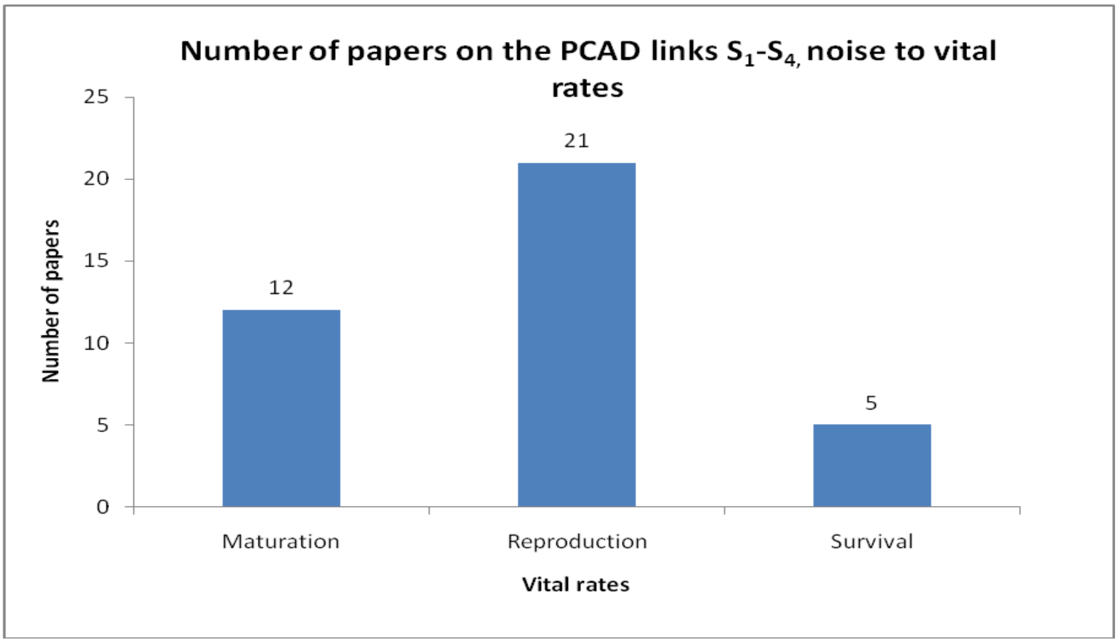

Figure 8. Papers reporting links affected between noise exposure and vital rates, note the absence of marine mammal papers.

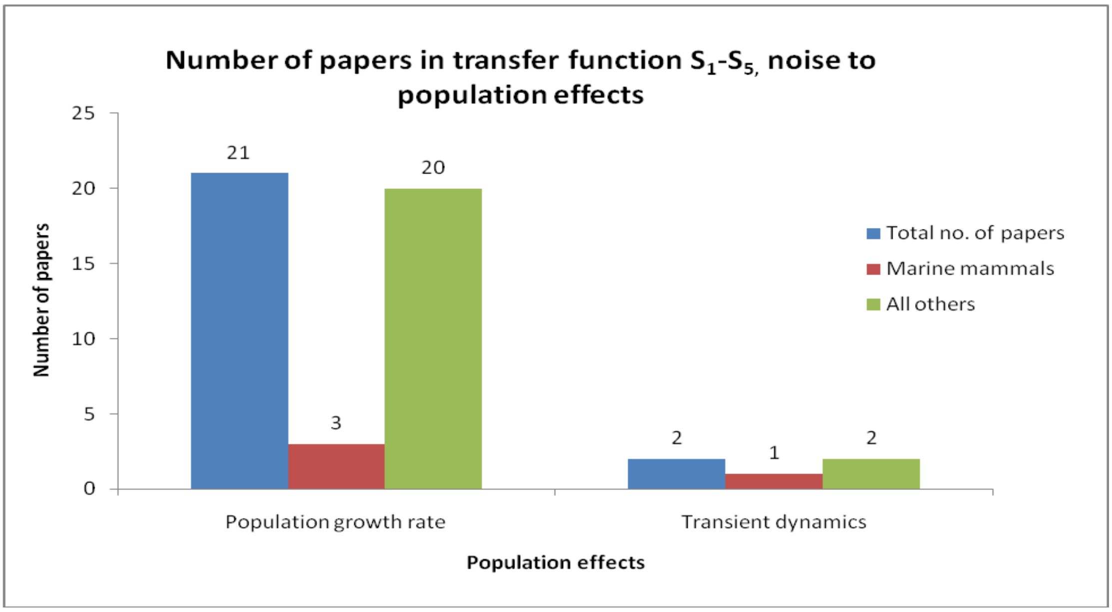

Figure 9. Papers reporting links between noise exposure and population level effects, with total number of papers and the breakdown of those involving marine mammals.

Many papers reported finding effects of noise exposure linking S_1 with more than one stage of the PCAD model, e.g., finding both behavioural effects as well as an effect on a vital rate, which we would categorize as 'S_1- S_2' and 'S_1- S_4'. Figure 10 breaks out all these papers, showing all the links between the various stages. We further divided these papers to show the multiple effects as they relate to 'S_{NB}', the non-behavioural effects. Interestingly, 41% of these papers overall reported both behavioural and non-behavioural effects (Figure 10). The existence of these cases having both behavioural as well as non-behavioural effects begs the question as to how these effects may be linked. Remage-Healey et al (2006) found that toadfish exposed to broadband pulses similar to dolphin echolocation both decreased their calling rate (i.e., a behavioural response) and had increased levels of a stress hormone (i.e., a non-behavioural, physiological response). As Remage-Healey et al (2006) discuss, previous experiments investigating toadfish territoriality demonstrated that it was changes in hormone levels that precipitated changes in calling rates.

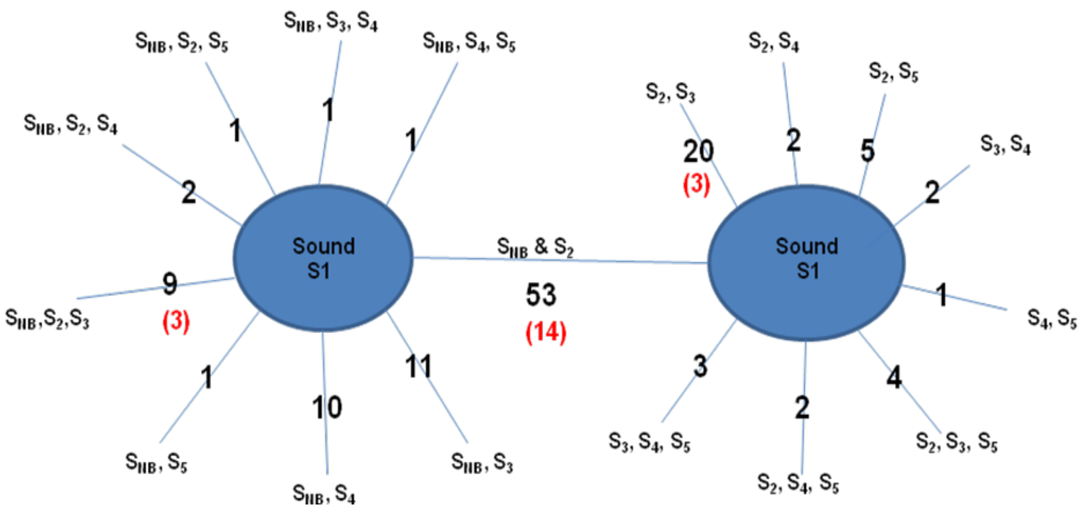

Figure 10. Number of papers reporting effects on multiple transfer functions. The left-hand side of the figure shows the papers reporting links between S_1, S_{NB} and a then variety of other combinations. The right-hand side shows only those papers that fall within the original PCAD framework and report links between multiple stages. The line connecting the two 'S_1' bubbles shows the papers reporting both a behavioural as well as a non-behavioural effects. The red numbers indicate the subset of papers that included marine mammals.

Marine mammals which are estimated to have similar sensitivity to sound

The NRC (2005) report correctly stated that it is unrealistic to obtain data for the PCAD model for each marine mammal species. Thus, the report endorsed previous research recommendations from NRC (2000) to work towards general models that were representative of pinnipeds, baleen whales and odontocetes with differing hearing sensitivity. High-priority research recommendations identified the need to group representative species and carry out models for the following seven categories:

- Sperm whales (not to include other physterids)
- Baleen whales
- Beaked whales
- Pygmy whales, dwarf sperm whales and porpoises
- Delphinids
- Phocids (true seals) and walruses
- Otariids (eared seals and sea lions)

Our search results were further broken down to explore the number of papers that reported on effects of noise on marine mammals based on the categories indentified by the NRC. We also added an eighth category, sirenia, for the sake of comparison.

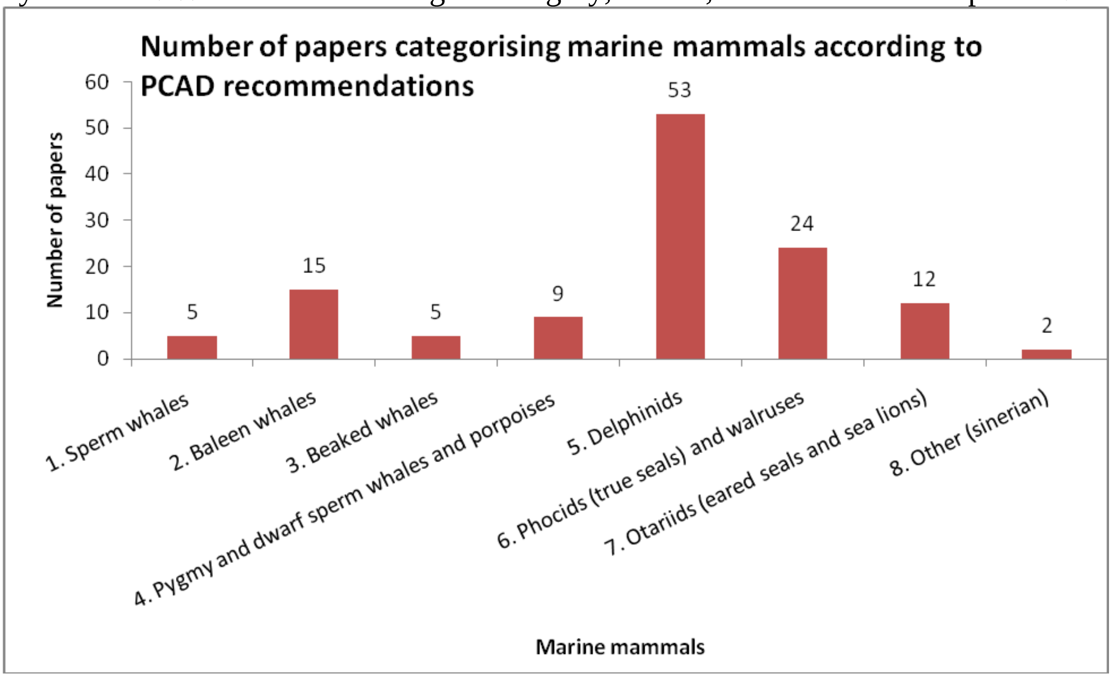

Figure 11. Number of papers reporting effects of noise on marine mammals which are estimated to have similar sensitivity to sound (NRC 2005).

Based on our key words, we found a total of 110 papers that reported effects of noise on marine mammals of which forty eight percent (n=53) were studies on delphinids and 22% (n =24) were on phocids (Figure 11). Beaked whales, likely to be most sensitive to mid frequency acoustic signals than other marine mammals, accounted for 4.5% (n=5) of papers.

We found 97 and 45 papers that demonstrated a link between noise exposure and non-behavioural (S_1-S_{NB}) and behavioural effects (S_1-S_2), respectively, among the marine mammal categories (Figure 12). Seventy two papers reporting links between noise and non-behavioural effects within the eight marine mammal categories focussed on auditory sensitivity. Of the 53 papers reporting non-behavioural effects of noise on delphinids, 42 were based on effects on auditory sensitivity, and 35 of these papers were carried out through captive studies. While auditory sensitivity effects are the most reported, it is encouraging to see studies evaluating effects of noise on responses in hormonal excretion, heart rate and respiration. Further promising signs in this area are recent advances in development of techniques using blow samples (Hogg at al., 2009), faecal samples (Rolland 2005) and blubber tissue (Keller et al., 2009) to explore hormone concentrations in free ranging cetaceans.

There were no studies on cetaceans that reported effects of noise on life functions (S_3), vital rates (S_4) or population effects (S_5). There was only one study on marine mammals that reported effects of noise beyond the "life functions" stage (S_3) in the PCAD model, however this was speculative. As Bejder et al (2006) demonstrated, it is possible to link sub-lethal effects on marine mammals to population level consequences, although this paper did not investigate acoustic exposure.

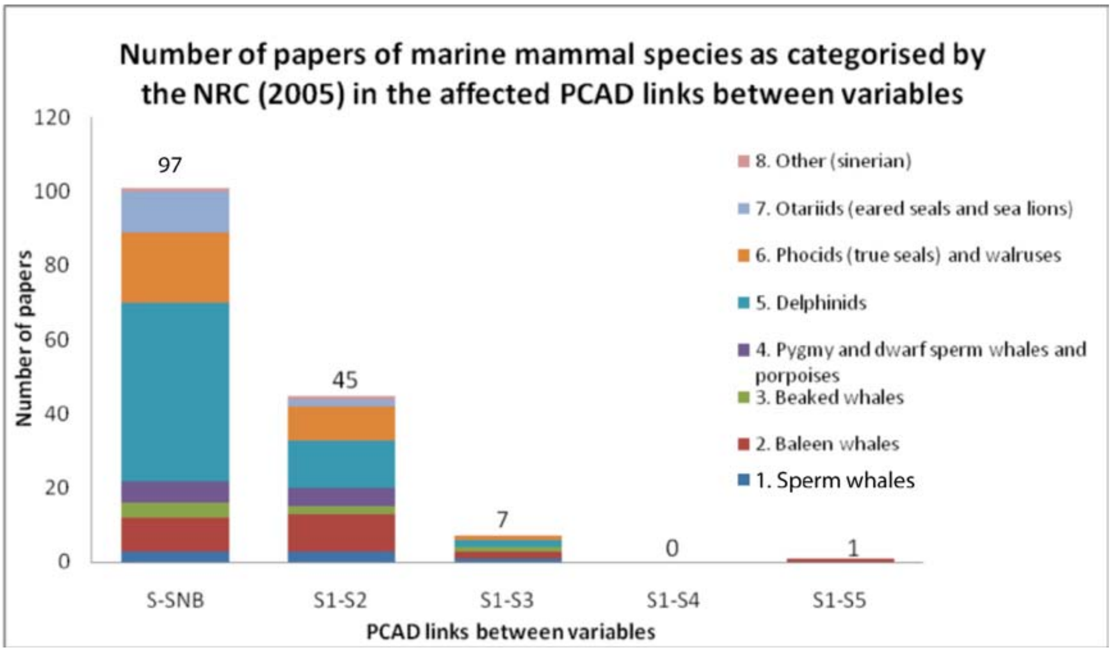

Figure 12. Papers reporting links between noise exposure (S_1) and non-behavioural effects (S_{NB}), behavioural effects (S_2), effects on life functions (S_3), effects on vital rates (S_4) and population effects (S_5) on marine mammals which are estimated to have similar sensitivity to sound (NRC 2005).

Discussion

We have provided a comprehensive review of the literature pertaining to the PCAD model as it relates to noise as a stressor for mammals, birds, reptiles and fish.

Specifically, we have identified all of the peer-reviewed literature that can increase our understanding of the links that may exist between the 5 stages or groups of variables described in the PCAD model. To investigate links between any given stages we have identified and catalogued all of the available literature; the NRC report refers to these links as ‘transfer functions’, though it limits these to the transitions between successive stages only. Our review found that there exists a significant literature that can be used to describe links between, for example, S_1 and S_3 or S_1 and S_4, though very little of this literature involved studies of marine mammals. We hope that by identifying these sources, we have provided some information useful for the continued development of the PCAD model from a conceptual framework towards a predictive model useful for management of marine mammals and their exposure to noise.

As we have discussed, our review considered only those papers where noise was used as a stressor, though we cast this net broadly to include any auditory exposure as an experimental stimulus. We did investigate all links between this exposure and the four downstream stages of the PCAD model (i.e., behavioural change, life function, vital rate, and population consequences), and furthermore we investigated these links for all mammals, birds, fish, reptiles and amphibians. As such, our review did not address the interactions between the downstream stages of the PCAD model, e.g., links between fecundity and population growth – this would have required a much larger and far more complex review. We do not mean to imply that these links are not important for marine mammal research, and indeed investigation of them can and should be either within or without of the framework of acoustic exposure.

Given the recent reviews and discussions of the behavioural responses of marine mammals to noise, we purposefully biased our searches towards non-behavioural responses, although we did search on many behaviourally specific terms (Table 1). Not surprisingly then, we found a great deal of literature reporting on links between noise exposure and non-behavioural responses (i.e., S_1-S_{NB}). The NRC Committee certainly recognized the importance of non-behavioural responses, most of which are physiological, but their mandate was to investigate the biological significance of behavioural responses. Indeed we found a rich literature exploring links between acoustic exposure and non-behavioural responses, though only a fraction of these involved marine mammals and anything other than auditory sensitivity. Therefore, we **recommend** that the PCAD model be expanded to include direct physiological responses to noise, specifically that a link be established between S_1 and our category ‘S_{NB}’.

The NRC Committee identified the paucity of experiments investigating non-behavioural effects of noise exposure, and our review confirmed that even as of 2009 there are few such studies beyond those investigating auditory sensitivity. Effects on the auditory system are clearly important to understand, but we argue that there should be an **expansion of research** into studies investigating other immediate, non-behavioural effects, e.g., heart rate, hormonal changes. Furthermore, the extent of studies found that reported both behavioural and non-behavioural responses (Figure 9) suggests that such studies with marine mammals are likely to be fruitful in revealing potential effects of noise exposure. Such studies can readily be conducted with captive animals, and as discussed in the case of toadfish calling and hormone changes, finding robust links between behavioural indicators of physiological changes could be useful in deepening our understanding of the effects of noise exposure. Our review can be used to pinpoint where physiological studies have added to the understanding of consequences of sound exposure on terrestrial as well as marine animals.

In our literature search, we explicitly looked for papers that could have informed any of the transfer functions in the PCAD model, i.e., we did not limit our searches to sequential transfer functions. The papers we found that related to each of the transfer functions are reported in our work, so any links that lack references are indeed holes in the literature, at least with respect to the taxanomic groups we explored.

For studies investigating so-called multiple effects (e.g., 'S_1- S_{NB}' and 'S_1- S_5' in Figure 9), it will be important although challenging to investigate the links between demonstrated behavioural effects and other effects, e.g., physiological changes. The toadfish example discussed above, shows that physiological changes can mediate a behavioural change, calling rates in this case. Most studies of marine mammals, however, are restricted to monitoring short-term, observable, behavioural responses rather than, for example, physiological responses that typically have no visible, external indicator and are thus not readily detectable in free-ranging animals. This emphasis on one modality of response effectively limits the scope of conclusions that can be drawn from the investigation. The most effective course of action in impact studies would be to complement behavioural assessment with monitoring of physical condition and of physiological measures such as heart rate, body temperature and/or hormonal levels. The value of this approach has been affirmed by studies in which behavioural and physiological responses were monitored simultaneously. Disconcertingly, these studies have indicated that changes in behaviour do not always provide a sufficiently sensitive or timely indicator of a response to a stimulus, or indeed the effects of disturbance if considered in isolation (Beale & Monaghan 2004a,b). For example, several studies have indicated that physiological evidence of a response could be detected in animals even when they exhibited little or no behavioural reaction or sign of disturbance (Moen et al. 1982, Culik et al. 1990, Wilson et al. 1991, Nimon et al. 1995, Regel & Putz 1997, Ratz & Thompson 1999, Müllner et al. 2004). So we see that animals may respond in one modality but not in another, may respond consistently in two or more modalities, or, as in the case of the toadfish, a response in one modality may cause a response in another. If robust links can be established between observable behavioural changes and some physiological change, then marine mammal scientists could use the behavioural change as a proxy for measuring these other changes. Investigation of such links is certainly more tractable in captive studies, and our results certainly confirm the gap in physiological studies of marine mammals in general and more specifically in this mode of measuring multi-modal responses.

Within the PCAD framework we found a significant number of papers that reported on links between S_1 and all of the successive stages (Figure 4), though the reader is reminded that many of these did not involve marine mammals, particularly for those reporting on S_3, S_4 and S_5. Furthermore, even considering all taxa, more than half of the papers we found reported on links between noise exposure and a behavioural response. Furthermore, with each successive stage in the PCAD model we found fewer and fewer papers reporting on the link to noise exposure. However, as the NRC Committee recognized, it is the connection of the path from acoustic disturbance to population level consequences that is the ultimate goal of the entire exercise. So, while we found a decreasing number of papers, those we found could be quite useful in at least framing research on marine mammals.

In conclusion, we have catalogued a significant number of research reports that either directly or by way of other taxa will hopefully inform and promote the process of turning the conceptual PCAD model into a predictive one useful for scientifically based management of marine mammals and their exposure to noise. We believe we have strong support for advocating the inclusion of non-behavioural responses into the PCAD framework, particularly in light of the amount of research reporting both behavioural and non-behavioural responses to acoustic exposures. Including physiological responses to acoustic exposure in particular, e.g., hormone levels, will be important both as they relate to behavioural responses as well as their relationship to downstream effects of changes in the other, downstream stages of the PCAD model. While research with marine mammals has filled some gaps since the development of the PCAD model, e.g., temporary threshold shifts (Kastak et al 2005), many gaps still exist. We hope that our work in identifying literature from other taxa can help to inform both an update of the PCAD model as well as identifying research priorities for marine mammal research.

References

ARCK, P. C., F. S. MERALI, J. MANUEL, G. CHAOUAT and D. A. CLARK. 1995. Stress-triggered abortion: Inhibition of protective suppression and promotion of tumor necrosis factor-alpha (TNF-alpha) release as a mechanism triggering resorptions in mice. *American Journal of Reproductive Immunology* **33:** 74-80.

BEALE, C. M. and P. MONAGHAN. 2004a. Behavioural responses to human disturbance: a matter of choice? *Animal Behaviour* **68:** 1065-1069.

BEALE, C. M. and P. MONAGHAN. 2004b. Human disturbance: people as predation-free predators? *Ecology* **41:** 335-343.

BEJDER, L., A. SAMUELS, H. WHITEHEAD, H. FINN and S. ALLEN. 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series*.

BEJDER, L., A. SAMUELS, H. WHITEHEAD and N. GALES. 2006a. Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. *Animal Behaviour* **72:** 1149-1158.

BEJDER, L., A. M. Y. SAMUELS, H. WHITEHEAD, N. GALES, J. MANN, R. CONNOR, M. HEITHAUS, J. WATSON-CAPPS, C. FLAHERTY and M. KRUTZEN. 2006b. Decline in Relative Abundance of Bottlenose Dolphins Exposed to Long-Term Disturbance. *Conservation Biology* **20:** 1791.

CULIK, B., D. ADELUNG and A. J. WOAKES. 1990. The effect of disturbance on the heart-rate and behaviour of Adelie Pinguins Pygoscelis adelie during the breeding season. *Antarctic ecosystems, ecological change and conservation***:** 177-182.

GILL, J. A., K. NORRIS and W. J. SUTHERLAND. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation* **97:** 265-268.

HOGG, C. J., T. L. ROGERS, A. SHORTER, K. BARTON, P. J. O. MILLER and D. NOWACEK. 2009. Determination of steroid hormones in whale blow: It is possible. *Marine Mammal Science* **25:** 605-618.

KASTAK, D., B. L. SOUTHALL, R. J. SCHUSTERMAN and C. R. KASTAK. 2005. Underwater temporary threshold shift in pinnipeds: Effects of noise level and duration. *The Journal of the Acoustical Society of America* **118:** 3154.

KELLAR, N. M., M. L. TREGO, C. I. MARKS, S. J. CHIVERS, K. DANIL and F. I. ARCHER. 2009. Blubber testosterone: A potential marker of male reproductive status in short-beaked common dolphins. *Marine Mammal Science* **25:** 507-522.

LUSSEAU, D. and L. BEJDER. 2007. The long-term consequences of short-term responses to disturbance: Experiences from whalewatching impact assessment. *International Journal of Comparative Psychology* **20:** 228-236.

LUSSEAU, D., L. SLOOTEN and R. J. C. CURREY. 2006. Unsustainable dolphin-watching tourism in Fiordland, New Zealand. *Tourism in Marine Environments* **3:** 173-178.

MOEN, A. N., S. WHITTEMORE and B. BUXTON. 1982. EFFECTS OF DISTURBANCE BY SNOWMOBILES ON HEART-RATE OF CAPTIVE WHITE-TAILED DEER. *New York Fish and Game Journal* **29:** 176-183.

MÜLLNER, A., K. EDUARD LINSENMAIR and M. WIKELSKI. 2004. Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (Opisthocomus hoazin). *Biological Conservation* **118:** 549-558.

NIMON, A. J., R. C. SCHROTER and B. STONEHOUSE. 1995. HEART-RATE OF DISTURBED PENGUINS. *Nature* **374:** 415-415.

NISBET, I. C. T. 2000. Disturbance, habituation, and management of waterbird colonies. *Waterbirds* **23:** 312-332.

NOWACEK, D. P., L. H. THORNE, D. W. JOHNSTON and P. L. TYACK. 2007. Responses of cetaceans to anthropogenic noise. *Mammal Review* **37:** 81-115.

RATZ, H. and C. THOMPSON. 1999. Who is watching whom? Checks for impacts of tourists on Yellow-eyed Penguins Megadyptes antipodes. *Marine Ornithology* **27:** 205-210.

REGEL, J. and K. PÜTZ. 1997. Effect of human disturbance on body temperature and energy expenditure in penguins. *Polar Biology* **18:** 246-253.

REMAGE-HEALEY, L., D. P. NOWACEK and A. H. BASS. 2006. Dolphin foraging sounds suppress calling and elevate stress hormone levels in a prey species, the Gulf toadfish. *Journal of Experimental Biology* **209:** 4444-4451.

ROLLAND, R. M., K. E. HUNT, S. D. KRAUS and S. K. WASSER. 2005. Assessing reproductive status of right whales (Eubalaena glacialis) using fecal hormone metabolites. *General and comparative endocrinology* **142:** 308-317.

SOUTHALL, B. L., A. E. BOWLES, W. T. ELLISON, J. J. FINNERAN, R. L. GENTRY, C. R. GREENE JR, D. KASTAK, D. R. KETTEN, J. H. MILLER and P. E. NACHTIGALL. 2009. Marine mammal noise exposure criteria: Initial scientific recommendations. *The Journal of the Acoustical Society of America* **125:** 2517.

WEILGART, L. S. 2007. The impacts of anthropogenic ocean noise on cetaceans and implications for management. *Canadian Journal of Zoology* **85:** 1091-1116.

WILSON, R. P., B. CULIK, R. DANFELD and D. ADELUNG. 1991. People in Antarctica—how much do Adélie Penguins Pygoscelis adeliae care? *Polar Biology* **11:** 363-370.