Linking short and long-term effects of nature-based tourism on cetaceans

by

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Hvis man på livets store ocean kunne lave bare en lille krusning i den korte tid man er her på jorden, skal man hvis ikke bede om mere.

Kim Schumacher

I dedicate this thesis to my belated grandparents,

Ebba and Tage Jensen,

and to my parents,

Lise and Bjarne Bejder,

whose virtues I can only strive to achieve.

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Abstract

A complex and unresolved problem in wildlife management is detecting whether human activities, which superficially appear to be benign, have cumulative effects that are harmful to wildlife populations. For instance, current understanding of impacts of nature-based tourism on free-ranging cetaceans is far from satisfactory. To ensure the sustainability of the economically-important and rapidly-growing global cetacean-watching industry, there is a pressing need for sound scientific evidence on which to base management.

In a review of the literature pertaining to the evaluation of impacts of nature-based tourism on cetaceans, I identified factors that have limited the utility of this research, and pinpointed factors that allow for effective impact assessment. With this in mind, the Indo-pacific bottlenose dolphin (*Tursiops sp.*) population in Shark Bay, Australia, was identified as a system where all key factors could be incorporated into one impact assessment study.

I designed a multi-faceted study that incorporated experimental vessel approaches to dolphins that had differing histories of exposure to tourism. The long-term nature of the Shark Bay research project (>20 years) allowed for interpretation of short-term responses within a longitudinal perspective by providing information on two fundamental measures of population health, dolphin habitat use and female reproductive success, in response to increased vessel activity over a 14-year period.

Canonical-variate analyses showed that experimental vessel approaches elicited significant changes in patterns of sociality and movement of targeted dolphins at both control and tourism sites. Responses at the control site were stronger, more prevalent, and longer lasting than those at the tourism site. The moderation in the short-term responses at the tourism site was likely not the result of habituation to vessel activity, but could be better explained by a displacement of sensitive individuals during the development of the tourism operations.

Habitat use by individual dolphins was compared between three successive 4.5-year periods in which dolphins were followed by research vessels and no dolphin-watch tour vessels (T0), one tour vessel (T1), and two tour vessels (T2), respectively. In the tourism site from T1 to T2, there was a 1.78 fold increase in the time vessels spent with dolphins, of which 74.9% could be attributed to tour vessels. As the number of tour vessels increased from one to two, there was a statistically significant average decline of 14.9% in numbers of individuals per square kilometer in the tourism site and a non-significant average increase of 8.5% in the control site.

Eighty-four females were identified for whom calf survival was known and ≥ 4 years of reproductive data were available since the onset of tourism in Shark Bay. Each female's long-term exposure to research- and tour vessels was calculated. Female reproductive success was significantly negatively correlated with both tour- and research vessel cumulative exposure.

In the context of these findings, I argue that imprecise usage of the terms habituation, sensitisation and tolerance can lead to misinterpretation of research findings with unintended and potentially dire consequences for wildlife communities. I provide a framework for literal and standardized usage of terminology, and offer an empirical technique for discerning among explanatory mechanisms to detect true habituation and sensitisation responses.

The documented declines raises concerns for the long-term sustainability of the cetacean-watching industry. Although declines within the tourism site may not end in jeopardizing the large, genetically-diverse Shark Bay population, similar effects would be dire for small, closed or isolated cetacean populations. In addition to focusing attention on the potentially detrimental effects of tour vessels on targeted cetaceans, this study recognizes that the cumulative exposure to all vessels types may be a contributing factor to the observed detrimental impacts of vessel activity.

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CHAPTER ONE

EVALUATING IMPACTS OF NATURE-BASED TOURISM ON CETACEANS

Chapter 1 draws on material that also appears in:

Bejder, L. and Samuels, A. (2003). Evaluating impacts of nature-based tourism on cetaceans. *In* Marine Mammals: Fisheries, Tourism and Management Issues (eds N. Gales, M. Hindell and R. Kirkwood), pp. 229-256. CSIRO Publishing, Collingwood.

INTRODUCTION

Public demand for close-up experiences with whales, dolphins and porpoises at sea is at an all time high. Commercial tourist ventures include opportunities for people to observe, swim with, touch, or feed wild cetaceans from shore, sea or air. In 1998, a total of 87 nations and territories offered commercial tourist activities that target wild cetaceans, with more than nine million people participating (Hoyt 2001). Current projections indicate a continued annual growth of well beyond 5% over the next several years (Hoyt 2001).

Is this good news for marine mammals in the wild? Wildlife tourism, including tourism that focuses on free-ranging cetaceans, is generally perceived to be inherently beneficial, and so tends to be considered "ecotourism". Cetacean-focused tourism and ecotourism are both subsets of nature-based tourism, but they are not necessarily overlapping. Nature-based tourism encompasses a variety of ways for people to enjoy nature, whereas, ecotourism additionally requires that there be contributions to the conservation of species or habitats (Goodwin 1996). Strictly defined, ecotourism is environmentally responsible travel that contributes to conservation of biodiversity, sustains the well being of local people, stresses local involvement, includes learning experiences for tourists, involves responsible action on the part of tourists and the tourism industry, and requires the lowest possible consumption of nonrenewable resources (e.g., UNEP 2002). With respect to cetacean-focused tourism, advantages for humans involved are clear. This form of tourism promises considerable economic rewards, as illustrated by recent global revenues in excess of one billion USD per year (Hoyt 2001). Other benefits include local employment opportunities (IFAW 1999) and logistical support for scientific research (Robbins and Mattila 2000). However, for all nature-based tourism, it is open for debate as to whether impacts on animals are truly negligible and whether tourists actually achieve heightened appreciation of the environment that is long lasting (e.g., Manfredo et al. 1995; Goodwin 1996; Ross and Wall 1999; Isaacs 2000). As noted by Berle (1990:6):

"Ecotourism is big business. It can provide foreign exchange and economic reward for the preservation of natural systems and wildlife. But ecotourism also threatens to destroy the resources on which it depends. ...[S]hutterbugs harass wildlife in national parks, hordes of us trample fragile areas. This frenzied activity threatens the viability of natural systems. At times we seem to be loving nature to death."

A one-time meeting with tourists has seldom caused major complications for wild cetaceans. However, the character of cetacean-focused tourism is such that specific communities of animals are repeatedly sought out for prolonged, close-up encounters. In addition, tourists are no longer satisfied with observing wildlife – they crave interaction with wild animals. Thus, there is a potential for serious detrimental consequences for targeted animals, with impacts that are cumulative rather than catastrophic (Duffus and Deardon 1990). For example, repeated disruption to breeding, social, feeding or resting behaviour – and habituation or sensitisation to human activity – can have deleterious effects on reproductive success, health, distribution and ranging patterns, access to preferred habitat, etc. Indeed, a few recent studies have demonstrated harmful outcomes for some subjects of tourism (e.g., Samuels and Bejder 1998, 2004; Mann et al. 2000). These findings are clearly outside the bounds of ecotourism, as rigorously defined. Therefore, as tourists desire more frequent and more intimate encounters with wild cetaceans, there is a pressing need for research that is specifically designed to evaluate the impacts of such activities on the animals.

Unfortunately, assessment techniques, as applied to understanding the impacts of cetacean tourism that focuses on free-ranging cetaceans, are still relatively rudimentary. There are several explanations for the emergent nature of this aspect of cetacean behavioural biology. For wildlife in general, there are a number of obstacles to identifying the impacts of human activity. Often, baseline data are unavailable or unobtainable, thus precluding comparison of animal behaviour under impact situations with behaviour prior to commencement of human activity and/or under undisturbed conditions. In addition, spatial and temporal discontinuities between cause and effect make it difficult to tease apart which observed changes are due to human activity, which are due to ecological factors, and which are due to natural variability. Given the complexity of interactions within ecosystems, difficulties arise in pinpointing those components that contribute to observed impacts (e.g., Vaske et al. 1995). In addition, factors such as species, age, gender, reproductive condition, level of habituation, etc. may influence – either singly or in combination – how individual animals respond to anthropogenic activity. Moreover, although the ultimate goal is to identify long-term responses that have biological significance for the animals, it is the shortterm reactions that are more readily related to a potential source of impact (IFAW 1995). Whether, and in what ways, such short-term responses are linked to long-term consequences has rarely been documented.

With respect to cetaceans, studying impacts of human activity is further confounded by specific methodological obstacles that result from trying to find, follow and observe the behaviour of mobile marine animals at sea. For example, it can be difficult to track continuously and in detail the movements and behaviour of cetaceans in the marine environment because they are out of sight underwater for prolonged periods of time, many species range over large areas, and some are found in groups numbering in the hundreds (e.g., Mann 1999). Furthermore, as a prerequisite for recognising "disturbed" behaviour, a comprehensive catalogue of "normal" behaviour is needed, something that is lacking for nearly all species of cetaceans. In addition, it is relatively recently in comparison with studies of the behaviour of terrestrial animals that hypothesis testing and quantitative behavioural sampling techniques have been widely applied to studies of cetacean behaviour (reviewed in Samuels and Tyack 2000). As a result, many who attempt to study impacts of human activity on cetaceans are:

"... dissatisfied with research into whale [and dolphin] disturbance, both in terms of the overall methodological aspects and the product of the research. Simply stated, the researchers have not obtained answers that satisfy themselves or managers. Difficulties with this kind of research are manifold. Researchers regularly fend off issues of scale, both in time and space, problems in research design, a lack of baseline data for comparative analysis, natural levels of variation..." (IFAW 1995:14).

Dissatisfaction notwithstanding, a considerable body of impact assessment research does exist and this serves as the foundation for present-day management of cetacean-focused tourism. In some locations, management takes the form of legislated, enforced regulations; elsewhere, voluntary guidelines or codes of conduct have been set up (reviewed in Carlson 1998). For example, the finding that dolphins in Porpoise Bay, NZ, avoided tour vessels after lengthy encounters (Bejder et al. 1999) resulted in proposed permit conditions to restrict encounter durations and limit the number of tour operators (H. Kettles, 2001, pers. comm.). In another example, local voluntary guidelines were instituted by tour operators to protect resting dusky dolphins near Kaikoura, NZ (Yin 1999), following the finding that dolphins were disturbed by tourist activities during their normal rest period (Barr and Slooten 1998).

More often than not, however, regulations and guidelines have been based on evidence that is anecdotal, scientific but insufficient, or entirely lacking. In addition, management policies are typically not specific to species, sex, age class, habitat, behaviour, or group composition of the targeted animals (but see, e.g., Constantine (1999) regarding New Zealand's Marine Mammals Protection Act of 1978 prohibiting swimming with cetacean calves or any whale species). Nevertheless, many of the above attributes have been shown to influence cetacean responsiveness to human activity and vessels (e.g., Watkins 1986; Richardson et al. 1995; Constantine 2001; Nowacek et al. 2001a; Williams et al. 2002a; Lusseau 2003a). Shortcomings like these led to the conclusion that "... intense popular demand for swim-with activities [and other cetacean-focused tourist ventures] is pushing the growth of the industry beyond the limits of what current data can justify" (Samuels et al. 2003). In particular, many researchers have noted that interpretation of findings is often limited by methodology (e.g., Constantine and Baker 1997; Barr and Slooten 1998; Yin 1999). While certain factors that confound identification of anthropogenic impacts cannot be eliminated, others may be reduced through studies that are rigorously and meticulously planned. In particular, by building upon the extensive foundation of existing research, research designs can be refined to carry out more in-depth, comprehensive and longitudinal studies. In this way, there will be improved likelihood that any detrimental effects of nature-based tourism on marine animals can be detected, identified and quantified in a timely fashion.

Now is an opportune time to take this step because a number of cetacean biologists are already moving in this direction. To promote this movement, in this chapter, I present a collection of such noteworthy studies and discuss their methodological merits, as a guide for those who wish to embark on research pertaining to cetacean-focused tourism. It is important to clarify at the onset what the boundaries of this chapter are. Specifically, this is not intended as a comprehensive review of the literature pertaining to studies of the impacts of cetacean-focused tourism, nor is it meant as a critique of such research. The chapter is not intended as an inventory of research methods for cetacean studies (see, e.g., Whitehead et al. 2000), nor is it a primer for behavioural sampling techniques (see, e.g., Altmann 1974; Martin and Bateson 1986; Mann 1999). Instead, my goal is to promote, by example, careful research designs for investigating impacts of human activity (tourism and otherwise) on the behaviour of free-ranging cetaceans. Thus, my focus is on well-designed studies of human impacts on cetacean behaviour, and for each case study I present, I emphasize the particular methodological significance. These examples can be used as templates or starting points for planning research to evaluate potential effects of cetacean-focused tourism in the wild.

In compiling this collection, I endeavored to select studies that are specific to cetacean-focused tourism and published in accessible peer-reviewed scientific journals. I departed from these selection criteria only when I was unable to locate appropriate examples of particular methodological attributes from those sources. In such cases, I was compelled to include some excellent examples from the grey literature (several of which are peer-reviewed) and/or from the literature pertaining to anthropogenic impacts on cetaceans unrelated to tourism.

The studies I selected illustrate key components in the planning and execution of effective impact assessment research. In the body of the chapter, I present analyses of research techniques used in the case studies, organised by methodological features. I present and discuss strong attributes of key studies with respect to the selection of study design, analytical design, study subjects, research platforms and response measures (Table 1.1). In an appendix (Appendix 1), I also provide abstracts for each case study, composed by me (not the original authors) with the specific objective of elaborating on the methods used. Because, in the body of the chapter, case studies are dissected and presented piecemeal according to methodological attribute, the appendix serves as a convenient and useful synopsis in which each case study is presented in its entirety.

By putting a spotlight on studies that exemplify rigorous methodologies, I hope to influence the quality of research dedicated to this aspect of cetacean biology, and thereby, to minimise impacts of tourism on the behaviour of free-ranging cetaceans by promoting management that is informed by sound scientific evidence.

Table 1.1. Key components in the planning and execution of effective research to assess effects of human activity on wild cetaceans.

cetaceans.	
Study Design	
1. Cont	trolled experiments
2. Opp	ortunistic observations
3. Histo	orical data
Analytical design	1
1. With	nin impact comparison
	trol vs. impact comparison
	ore/ during/ after comparison
Study subjects	
1. Foci	as on the individual
· · · · · · · · · · · · · · · · · · ·	is on the group
Research platfor	
	i-based
	nmercial tour vessel
	pendent vessel
	erwater
	4a. Visual observations
	4b. Acoustic recordings
5. Aerial	
Measuring respo	
	rt-term measures
	1a. Non-vocal behaviour
	i. Surface, ventilation and dive patterns
	ii. Swim speed, course and orientation
	iii. Group dispersion/ cohesion
	iv. Behavioural states/ activity budgets
	v. Behavioural events
	vi. Ranging patterns and habitat use
	1b. Vocal behaviour
2. Lon	g-term measures
	2a. Habituation and sensitisation
	2b. Ranging patterns and habitat utilisation
	2c. Reproductive success
3. Stre	ss and distress

STUDY DESIGN

In impact assessment studies, it is important to select a study design that is appropriate for the research question, impact situation, and platform. Richter *et al.* (2000) provide an excellent review of study designs used in assessing short-term impacts of boats on cetaceans. Below I discuss controlled experiments, opportunistic observations and analysis of historical data.

Under certain conditions, it is possible to design "controlled experiments" that "minimize the number of plausible alternative hypotheses that are consistent with the data" (Altmann 1974:

229). Controlled experiments require a certain amount of background knowledge about the study animals, study site and potential impact factor(s). When *a priori* knowledge requirements are met, this approach allows for data collection on the same animals under both control and impact exposures while minimising influences of environmental variables, thus facilitating interpretation of responses. More often, however, the special conditions needed for experimental design cannot be met, and then "opportunistic observations" are used. This approach is logistically easier to set up and requires less prior knowledge about dependent and independent variables, attributes that make opportunistic observations especially suitable for pilot studies (Richter *et al.* 2000). A major drawback, however, of opportunistic observations is the potential for violating a fundamental assumption that nothing other than the factor of interest changes between control and impact conditions. Large sample size is therefore needed to tease apart which variable is responsible for observed effects. In contrast, the experimental approach is a more efficient way to obtain adequate sample size because confounding influences are reduced.

Because cetaceans are long lived and there are limits to research time and funding, studies that are explicitly designed to monitor long-term impacts are rare. One method used to circumvent the obstacles to longitudinal data collection is the compilation and analysis of existing "historical data" collected over the long term in the course of studies conducted for other purposes. In some instances, researchers have designed follow-up studies in which data are collected explicitly for comparison with historical records. It is rare that adequate historical records are available from the time prior to the advent of the impact situation, and rarer still that changes in cetacean behaviour or ranging patterns can be directly attributed to increases in human activity. This underscores the importance of collecting pretourism data to provide a foundation for "before and after" comparisons.

Controlled experiments

Ideally, in controlled experiments, each individual animal (or group) provides its own control, *i.e.*, each subject is observed under control and impact situations. For example, Miller *et al.* (2000) used systematic behavioural sampling techniques and a towed calibrated hydrophone array to monitor vocal and non-vocal behaviour of individual singing humpback whales before, during and after exposure to controlled playbacks of low-frequency active sonar. This experimental design was essential to demonstrating variation in responses among individual humpback whales to man-made sounds broadcast underwater. This study also showed that it is possible to measure vocal responses of individual whales in controlled experiments at sea.

In another example, Nowacek *et al.* (2001a) used systematic behavioural sampling techniques and overhead video to monitor the behaviour of individual bottlenose dolphins during controlled approaches of small vessels and thrill craft. In these experiments, vessel type, speed and angle of approach were controlled in order to assess changes in the focal dolphin's travel speed, heading, respiration pattern, and distance to the nearest neighbour. By providing continuous records of both subsurface and surface behaviour, and comparing the same animals under control and impact conditions, this experimental design was effective in quantifying several measures of avoidance and in identifying a class of particularly vulnerable animals.

In some experiments, control subjects are members of the same population as the animals observed under experimental conditions. For example, Goodson and Mayo (1995) recorded dolphin movement patterns and acoustic behaviour while controlling over periods of days the presence and absence of simulated gillnets with acoustic deflectors attached. This design showed the range at which dolphins detected the "nets" and modified their paths to avoid collisions. Similarly, Culik *et al.* (2001) recorded porpoise movements near simulated gillnets while controlling over periods of days the presence and absence of acoustic alarm devices. This design was used to show that the avoidance distance during pinger operation apparently corresponded to the audible range of the acoustic alarm.

Opportunistic observations

Bejder et al. (1999) used theodolite tracking to quantify movement patterns of groups of Hector's dolphins within a bay during opportunistic encounters with commercial dolphin watch vessels. This method was effective in demonstrating increased group cohesion when vessels were present, and an initial attraction to vessels followed by avoidance when vessel exposure was prolonged. In a second example, Nowacek et al. (2001a) complemented the controlled experiments described above with systematic observations of the surface behaviour of individual dolphins during opportunistic approaches of passing vessels. These opportunistic observations provided the majority of data used to analyse changes in respiration rate in response to boat approaches. In addition, Richter et al. (2001) combined land-based theodolite tracking and boat-based acoustic recordings to document changes in sperm whale vocal and non-vocal behaviour during opportunistic encounters with whale watch vessels. This study design demonstrated individual variation in behaviour of sperm whales and that resident whales off Kaikoura, New Zealand, may be more tolerant to vessels than transient whales.

There are many other examples. In fact, the majority of impact assessment studies come under the category of opportunistic observations (reviewed in Richter *et al.* 2000).

Historical data

Watkins (1986) reviewed historical, anecdotal records to assess changes in whale responses to vessels over a 25-year period. Because this time period encompassed the absence, initiation and growth of commercial whale watch activities, this method was useful in revealing changes in whale behaviour associated with tourism that were gradual, both positive and negative, and species-specific. Laist *et al.* (2001) also used historical records and stranding databases to investigate collisions between ships and whales. Analysis of historical records revealed that fatal ship strikes first occurred in the 1800s when ships attained speeds of 13-15 kn, and the frequency increased during the 1950s-1970s as the number and speed of ships increased. Analysis of stranding records led to the recommendation that reducing ship speed to less than 14 kn in critical areas may be effective in minimising fatal collisions.

Analyses of long-term databases and comprehensive literature reviews might also be included in this category. For example, Mann *et al.* (2000) analysed data collected over a 10-year period to compare the reproductive success of food provisioned vs wild feeding bottlenose dolphins. In this study, use of long-term data was essential to reveal detrimental consequences of food provisioning on a small sample of individual animals. In another example, Richter *et al.* (2000) looked at a selection of studies that evaluated effects of vessels on cetaceans, focusing on choice of research platform, analytical design and statistical methods. In addition, Samuels *et al.* (2000) conducted a detailed review of the literature pertaining to swimming with wild cetaceans, the findings of which have been used to inform US policy (updated and summarised in Samuels *et al.*, 2003).

ANALYTICAL DESIGN

Study designs described above are further partitioned into what Richter *et al.* (2000) termed "analytical designs". Richter *et al.* (2000) discussed several analytical designs typical in vessel impact assessment studies, including "control/impact" and "before/during/after" (BDA) comparisons. Below, I expand on these categories and also consider the value of studies in which there are no control data.

Within impact comparison

In many studies, researchers look at cetacean behaviour only in the presence of a potential impact situation, then make a judgement as to whether observed behaviours constitute "positive" or "negative" responses. Interpreting the findings of such studies can be problematic when there are no adequate baseline ("undisturbed") behavioural data for comparison (unfortunately true for many aspects of cetacean behavioural biology). However, in some situations, this design is used of necessity when it is not possible to obtain data on "undisturbed" animals, for example, in locations where the level of human activity is very high (e.g., dusky dolphins and dolphin tour boats in Kaikoura, NZ (Barr and Slooten 1998)) or in cases where the research platform itself is potentially disturbing (e.g., observations of dolphin behaviour conducted from dolphin watch vessels (Constantine 2001)).

The "impact only" design has been used effectively to look at changes in behavioural response over the course of encounters or over the long term, and to compare responses under gradations of the impact situation. As an example, in opportunistic observations of swim-with-dolphin attempts from the vantage of commercial tour vessels, Constantine (2001, Constantine and Baker 1997) used a scan sampling technique to systematically record dolphin behaviour at specified time intervals within a specified distance, thus providing a record of changes in dolphin behaviour over the course of encounters. These data were later translated into categories to indicate the "success" of an encounter, *i.e.*, "interaction" (at least one dolphin within 5m of at least one swimmer for at least 15 sec); "neutral" (no apparent change in dolphin behaviour); and "avoidance" (dolphins changed direction of travel and/or moved away from swimmers). In addition, Constantine (2001; Constantine and Baker 1997) used this design to compare dolphin responses to gradations of swim-with attempts, *i.e.*, swimmer placement strategies such as "in path", "line abreast", and "around boat". Finally, Constantine (2001) used this design to compare dolphin responses to swim-with attempts over a several-year period, providing evidence that avoidance to swimmers increased over the long term.

Bejder *et al.* (1999) also used this design to evaluate dolphin behaviour over the course of encounters, demonstrating that dolphins were initially attracted to the tour vessel but subsequently avoided the vessel when encounters lasted >70 min. Allen and Read (2000) provide another example in which this design was used to evaluate dolphin behaviour under gradations of the impact situation, *i.e.*, temporal and spatial differences in vessel density. In addition, Lesage *et al.*

(1999) compared beluga vocal behaviour under two conditions of an impact situation: *i.e.*, a small motorboat moving rapidly and erratically vs. a large ferry moving slowly and predictably.

Control vs. impact comparison

In the simplest of experiments, the goal is to vary one condition (independent variable) in order to measure the effects on outcome measure(s) (dependent variable) (e.g., Martin and Bateson 1986). One way to accomplish this is to compare a treatment group with a control group, members of control and treatment groups presumably being similar in all respects except the experimental treatment. For example, by conducting focal follows of dolphins in the same region that do and do not tolerate human swimmers nearby, Samuels and Bejder (1998, 2004) were able to demonstrate dramatic differences in the behaviour of habituated vs. unhabituated dolphins. In another example, Mann et al. (2000) compared long-term reproductive records for food provisioned vs. wild-feeding dolphins within the same population, thus demonstrating lower survivorship of calves of provisioned females.

However, to minimise effects of individual variation, the same animals are observed under both experimental and control conditions, thus serving as their own controls. Williams *et al.* (2002a) conducted controlled experiments in which the movements of individual killer whales were tracked by theodolite first under control conditions (no boats present), followed by experimental vessel approaches. Similarly, Nowacek *et al.* (2001a) recorded respiration patterns of individual dolphins during boat-based focal follows and compared inter-breath intervals during conditions of control (no boats present) vs. treatment (closest approach of vessel).

A variation of this design consists of looking at the behaviour of the same animals in the presence and absence of an impact situation. For example, by recording the vocal behaviour of individual sperm whales in the presence and absence of whale watch vessels, Richter *et al.* (2001) demonstrated that transient whales showed an increase in time elapsed from fluke-out to first click when whale watch vessels were nearby; in contrast, presence of whale watch vessels did not appear to affect vocal behaviour of resident whales. In addition, Mann and Smuts (1999) conducted focal follows of food provisioned dolphin mothers and calves, within and away from the provisioning area. To evaluate effects of human activity on maternal behaviour, the behaviour of provisioned dolphins within the provisioning area was compared to the behaviour of provisioned and wild-feeding dolphins away from the provisioning area.

Janik and Thompson (1996) used both variations of this design to look at changes in dolphin surfacing patterns in response to boat traffic. By comparing the total number of dolphin surfacings during the minute preceding and following a vessel approach, they used the dolphin group as its own control, and showed that the number of surfacings significantly declined following the approach of the dolphin watch vessel. No such pattern was apparent in a second set of control data comprised of randomly-selected 2-min periods when no boats were present.

Before/ during/ after comparison

The BDA design (also known as "preexposure", "exposure" and "postexposure") is most commonly, but not exclusively, used in experimental studies. Pre- and post-exposure conditions are sometimes both considered controls; however, residual effects of the treatment may be apparent in the post-exposure period. In one example, Miller *et al.* (2000) used individual humpback whales as their own controls by recording songs of individual whales during focal follows and comparing song duration before, during and after experimental playbacks of low-frequency active (LFA) sonar. They found that whales sang significantly longer songs during exposure to LFA sonar. Lesage *et al.* (1999) also used a BDA design to demonstrate changes in the vocal behaviour of groups of beluga whales over the course of controlled vessel approaches. Culik *et al.* (2001) used a variation of the BDA design in which conditions changed over successive days. They compared porpoise responses to: (1) an artificial non-lethal gillnet with no acoustic pinger (5 days), (2) the same net with a continuously operating pinger (5 days), and (3) the same net after removal of the pinger (2 days). This design was essential to show that it was the pinger not the net that porpoises were avoiding.

The BDA design is comparable to a category of experimental designs referred to as "BACI" (Before-After-Control-Impact) designs in that they both monitor impact variables over time in response to stimuli. However, in contrast to BDA studies, BACI experiments monitor impact variables over time at both control and impact *sites* (Underwood 1991, 1992, 1993, 1994; Stewart-Oaten *et al.* 1986), whereas BDA experiments typically monitor impact variables over time *within* the same site.

STUDY SUBJECTS

For cetaceans, the level at which impact can be assessed is largely determined by characteristics of the species of interest, the research question, and the research platform. With respect to behavioural sampling, researchers typically select among such levels of focus as long-term cohesive group, ephemeral group, or individual, using measures based on these samples to extrapolate to community- or population-level impacts. In studies of the behaviour of terrestrial animals, the individual has long been regarded as the appropriate unit of analysis, both from theoretical and methodological viewpoints (e.g., Altmann 1974; Williams 1966). It is the case in cetacean research, however, that for certain species and circumstances, there are significant logistical obstacles to following and observing the behaviour of a single animal, e.g., wideranging species in which individuals cannot be readily identified, group size is typically large, and/or dive times are long (e.g., Mann 1999). Nevertheless, even when conditions indicate that an individual focus is appropriate and feasible, and conversely, that a group-level focus would introduce significant bias, studies of cetaceans seldom emphasise the behaviour of individual whales and dolphins (e.g., Mann 1999; but see Whitehead 2004). This ill-advised preference for group-level analyses has historical origins (reviewed in Samuels and Tyack 2000), but fortunately for cetacean behavioural biology, recent efforts are advancing the field towards approaches that are more objective, quantitative and precise. Several references provide guidance as to the suitability of an individual- vs. group-level focus in cetacean behavioural research (e.g., Altmann 1974; Mann 1999; Whitehead 2004).

It should be mentioned that on occasion, the source rather than the recipient of potential disturbance, may be selected as the focus of an impact assessment. For example, due to logistical constraints on observing individual dolphins from land, Colborn (1999) selected human swimmers and tour vessels as the focal subjects in a study of dolphin-focused tourism in Florida, USA. Au and Green (2000) provide another example in which the focus is on the source of potential disturbance: they measured underwater acoustic characteristics of five types of whale watch vessels to evaluate potential impacts of vessel noise on the auditory system of humpback whales near Maui, Hawaii, USA.

Focus on the individual

A focus on individual animals is the preferred method for obtaining unbiased records of behaviour. When pseudo-replication can be avoided by treating the individual as the unit of analysis, such an emphasis provides the basis for quantitative measures of frequencies of behavioural events, duration of behavioural states, time budgets, etc. – all of which provide the bases for direct comparisons between disturbance conditions, among other things. Data obtained with a focus on the individual can be used to determine which animals, and what proportion of a local community, are more likely to interact with, be detrimentally affected by, and/or avoid human activity. Conducted over time, such studies provide valuable information about the short-term, seasonal, and long-term impacts of cetacean-focused tourism on the lives of individual cetaceans, on animals of different gender, age class, activity state, or reproductive condition, and on cetacean communities.

Several recent impact assessment studies have employed a focal-animal sampling scheme (defined in Altmann 1974) in which a single animal is the subject of each observation session. For each focal subject, systematic records are made as to that animal's behaviour, including habitat selection and foraging behaviour (Allen and Read 2000), vocal behaviour (Miller et al. 2000; Richter et al. 2001), respiration patterns (Nowacek et al. 2001a), interactions with human swimmers (Samuels and Bejder 1998, 2004), and movement patterns (Williams et al. 2002a). A few of these studies were based upon longitudinal research that provided substantial demographic, reproductive and behavioural background on individual subjects. Thus, by tracking via theodolite individual killer whales from the well-studied population near Vancouver, Canada, Williams et al. (2002a) were able to determine sex-specific differences in movement patterns and in responses to boat traffic. Similarly, boat-based follows of individual dolphins from the well-studied Sarasota, Florida, USA, population enabled Nowacek et al. (2001a) to identify the particular vulnerability of inexperienced mothers to vessel traffic. In addition, by focusing on the vocal behaviour of individually-identified sperm whales, Richter et al. (2001) were able to show that transient, but not resident, whales responded to whale watch vessels.

Although background information was unavailable in other study populations, an individual focus was essential to the findings that food provisioning by humans may pose serious risks for dolphins of the juvenile age class (Samuels and Bejder 1998, 2004), that there were different levels of habituation to humans among dolphins living in the same region (Samuels and Bejder 1998, 2004), and that not all male humpback whales responded in the same way to underwater man-made noise (Miller *et al.* 2000). Although Constantine (2001) primarily used a group-level behavioural sampling method (see below), by recording the age class of individual dolphins that approached humans in the water, she determined that juveniles were significantly more likely than adults to interact with human swimmers.

Of particular note are a handful of studies on large whales that challenge conventional wisdom that focal-individual follows are feasible only for coastal delphinids. Miller *et al.* (2000) and Richter *et al.* (2001) provide examples in which the focus was on the behaviour of individual humpback whales and sperm whales, respectively (see also, *e.g.*, southern right whale mother-calf pairs: Taber and Thomas 1982; minke whales: Dorsey 1983; fin whales: Stone *et al.* 1992; Biassoni 1996).

An individual focus is also important in assessing the impact of human activity on the local community or sub-population. By identifying individual animals via photo-identification in order to determine the number of dolphins within the Bay of Islands, NZ, Constantine (2001) was able to estimate the number of swims attempted with the "average" dolphin on an annual basis. Similarly, Samuels and Bejder (1998, 2004) conducted a behavioural assessment of each animal identified by photo-identification in order to estimate a minimum number of dolphins habituated to human activity and food provisioning in Panama City, Florida, USA.

Focus on the group

Although cetologists have often cited Altmann (1974) to justify their use of group-level observations in behavioural studies, Altmann was quite clear in her landmark paper that such an emphasis is appropriate only under a stringent set of circumstances, criteria that are rarely met in cetacean research or elsewhere. A group focus is typically not an appropriate unit for behavioural sampling because an observer cannot continuously monitor all the behaviour of all individuals within a group of animals (Altmann 1974). Thus, in behavioural studies of cetaceans, situations in which a focus on the group is acceptable will be the exception, not the rule (but see Whitehead 2004). Below I discuss several recent impact assessment studies in which a group focus was correctly employed.

Altmann (1974) endorsed focal sub-group sampling for pairs of animals, particularly for pairs comprised of a mother and young infant who tend to move together as a single unit. Accordingly, in their study of food-provisioned dolphins, Mann and Smuts (1999) followed mother-and-calf pairs, recording both maternal and calf behaviour. In focal sub-group sampling, a decision rule is needed as to which individual the observer will follow if the pair splits up (*i.e.*, the calf in Mann and Smuts (1999)).

In some cases, rigorous behavioural sampling rules can offset drawbacks to a group-level focus. For example, in studying dolphin responses to swim-with attempts from the vantage of tour vessels, Constantine (2001) compensated for lack of manoeuvrability of the research platform by developing careful criteria to systematically record group behaviour: *i.e.*, at the initiation of a swim attempt a scan sample (defined in Altmann 1974) was conducted in which the behaviour of each dolphin within a specified distance of the tour vessel was recorded. Thus, dolphin responses to swim attempts were recorded within 5 sec of the first swimmer's entry into the water. In another example, Lesage *et al.* (1999) compared the total number of vocalisations recorded from each group of belugas before, during and after an experimental boat approach. They set such high standards for ensuring that all vocalisations of the group could be detected that only six of 77 experiments were approved for analysis.

Under certain conditions, group sampling can be effectively used to record all occurrences of a conspicuous behaviour. For example, in a comparison of the behaviour of dolphins that do and do not interact with humans, Samuels and Bejder (1998, 2004) conducted follows of individual dolphins (see above) as well as follows of focal groups of dolphins that were cohesive for the duration of the follow. They noted that sampling of group behaviour was adequate to continuously monitor whether any group members had interactions with humans. In another example, Janik and Thompson (1996) investigated effects of vessel traffic on dolphin behaviour by videotaping surfacings within a circumscribed area and comparing the total number of surfacings occurring during ± 1 min of a vessel approach. They were careful to note that, since group size estimates were not exact, it was not appropriate to calculate individual rates or infer individual behaviour; rather, they interpreted the decrease in the number of surfacings after the vessel approach to indicate that at least some of the dolphins were diving for longer periods and/or moving away from the vessel.

RESEARCH PLATFORMS

There are five types of research platforms typically used in assessing impacts of nature tourism on cetaceans: observations are conducted from (1) land, (2) commercial tour vessels, (3) independent research vessels, (4) underwater, and (5) an aerial view. The underwater category includes both (4a) visual observations and (4b) acoustic recordings, from an in-water vantage. The choice of an observation platform greatly influences the design of the study, how data are collected, and which response measures can be observed and recorded, reliably and without bias. A mismatch of platform and observational methods is a common design error, usually resulting in unrecognised

biases in data collection and/or over-generalisation of findings. Even when access to the platform of choice is limited by research budgets, geographic features, and/or characteristics of the species of interest, it is important to select methods and impact measures that are appropriate to the platform used.

The resolution of behavioural data that can be obtained from a single type of research platform is often inadequate to fully assess impacts. To take advantage of the strengths of each platform type, and accommodate their respective weaknesses, it may be useful to collect multiple datasets from different vantage points. Such a strategy will result in complementary datasets in which the biases or gaps within data collected from one platform may be offset by the attributes of those collected from another platform. In addition, simultaneous data collection from multiple platforms can be used to identify the ways in which data collection methods and research platforms affect conclusions about anthropogenic disturbances on cetaceans.

Land-based research platform

Land-based platforms are valuable for studying coastal groups of cetaceans, having the advantage that remote observers on land are unlikely to have any impact whatsoever on cetaceans in nearby waters. Disadvantages include restricted viewing of animals – *i.e.*, only when they are within range of the land platform – and limited viewing of their behaviour. However, an elevated land platform is a good vantage point for getting a "big picture" perspective, which is useful, for example, to track the speed and direction of movements of animals, vessels, or human swimmers within a circumscribed area, or to measure group cohesion and spread. A land platform is typically an appropriate choice for following movements and activities of *groups* of cetaceans, and may be the best option for small, coastal species that travel rapidly within large groups. A land platform may also be suitable for observing the movements of individuals (or small groups), particularly of large, solitary, slow-moving species. A land platform is sometimes used to record conspicuous surface displays, but is usually too remote to obtain accurate details about behaviour.

As an example, Culik et al. (2001) used a land-based research platform to study responses of harbour porpoises to an artificial gillnet with and without acoustic pingers. Close proximity of preferred porpoise habitat to cliffs along the shore enabled Culik et al. (2001) to use theodolite tracking from land to record movements of small groups of porpoises travelling along the coastline. They found that use of a pinger resulted in avoidance of the experimental net at distances that corresponded to the audible range of the acoustic alarm. In this study, a land

platform was essential to record porpoise behaviour that was undisturbed by the presence of researchers, to conduct controlled experiments in which only one variable was modified, and to obtain an overview of porpoise movements within ±1 km of the experimental net.

Bejder *et al.* (1999) used a land platform to conduct concurrent behavioural sampling and theodolite tracking in order to record responses of Hector's dolphins to the presence and absence of vessels. The combination of techniques provided simultaneous information about the movement pattern, behavioural state, and dispersion of dolphin groups. For example, by recording group dispersion at 5-min intervals, Bejder *et al.* (1999) showed that dolphins formed groups that were significantly more compact in the presence of a vessel. In addition to benefits listed above for Culik *et al.* (2001), in the Bejder *et al.* (1999) study, an elevated land platform was an excellent perspective from which to assess the dispersion and cohesion of dolphin groups.

Janik and Thompson (1996) filmed from a pier to look at surfacing patterns of bottlenose dolphin groups in response to boat traffic. A narrow channel frequented by dolphins, boats, and tour vessels provided an opportunity for comprehensive surveillance of all occurrences of a specified behaviour within a circumscribed area. The measure "surfacing", a behavioural event readily counted from video, was used to compare total number of surfacings within ± 1 min of a vessel approach. Janik and Thompson (1996) showed that overall the number of surfacings significantly decreased after the dolphin watch vessel approached the animals, indicating that dolphins made longer dives and/or left the region.

Williams *et al.* (2002a) provide a good example in which the behaviour and movements of individually-identified killer whales were tracked by theodolite from a shore station. In another example, as a result of unusual circumstances in which dolphins visit a beach on a near-daily basis to be fed, Mann and Kemps (2003) were able to obtain from shore detailed records of the behaviour of individually-identified dolphins. In a similar situation in which tourist activities were facilitated by food provisioning, shore-based observations provided details about the interactions between humans and bottlenose dolphins (Colborn 1999). Other examples include land-based theodolite tracking to document responses to acoustic alarms (*e.g.*, Goodson and Mayo 1995) and vessels (*e.g.*, Baker and Herman 1989; Stone *et al.* 1992; Barr and Slooten 1998).

Commercial tour vessel as research platform

Commercial tour vessels are often used as platforms for studying various aspects of cetacean biology (reviewed in Robbins 2000; Robbins and Matilla 2000). However, using a tour vessel as a platform to measure impacts of the selfsame vessel places a number of limitations on which behavioural sampling methods are appropriate, what kinds of data can be reliably collected, and how those data are interpreted. First, the observer is restricted to what can be seen when the tour vessel is in close proximity to cetaceans. Thus, it is possible to detect only those avoidance responses that occur near to the vessel, only those animals that are tolerant of vessel proximity, and only those behaviours that occur in the presence, but not the absence, of the vessel. In addition, the researcher rarely has control over which cetaceans are observed or identified, how much time is spent in proximity to the animals, and how the vessel is manoeuvred around the animals, constraints that preclude many types of behavioural sampling methods.

Despite these caveats, there are several benefits to using commercial tour vessels as a research platform, the most significant being that this is a relatively inexpensive way to gain regular and frequent access to the animals, and to obtain a large sample of observations of tourist-cetacean interactions. From tour vessels, it is sometimes possible to record systematically vessel approach strategies and swimmer placement types, and it may be possible to record on an *ad libitum* basis (defined in Altmann 1974) behavioural details of in-water interactions between swimmers and cetaceans. During close encounters, observers onboard tour vessels can sometimes identify the individual identities or age classes of animals that interact with tourists or the tour boat. An additional advantage is that researchers onboard tour vessels often impart accurate knowledge about cetaceans, marine life, and the ocean to tour operators and tourists, thereby influencing movements of tour vessels around cetaceans and the quality of educational programmes.

Constantine (2001, Constantine and Baker 1997) used commercial tour vessels as a research platform to good effect in studying commercial swim-with-dolphin operations. In the initial study, Constantine and Baker (1997) demonstrated species-specific differences in behavioural responses to tour vessels such that groups of common dolphins were significantly more likely than bottlenose dolphins to change their behaviour as the tour vessel/research platform approached from 400m to 100m. For both species, socialising was the activity most likely to change; whereas, feeding and resting were least likely to be affected for bottlenose and common dolphins, respectively. Using tour vessels as a platform also enabled Constantine and Baker (1997) to assess responses of dolphin groups to specific swimmer placement types: *i.e.*, the "line abreast" strategy

resulted in lowest rates of avoidance but also low rates of swim success; in contrast, "in path" resulted in highest rates of avoidance.

Constantine (2001) compared behavioural data that she collected from commercial tour vessels during two field seasons – 1994-95 vs 1997-98 – to show increased avoidance over time by groups of bottlenose dolphins to commercial swim-with tours. Using tour vessels as the research platform enabled Constantine (2001) to re-evaluate responses of dolphin groups to swimmer placement methods, with greatest avoidance occurring when swimmers were placed in the dolphins' path of travel. Observations from tour vessels also enabled Constantine (2001) to document what proportion of dolphin groups, and which age class, were likely to interact with swimmers: *i.e.*, when swim attempts were successful, on average only 19% of dolphins were involved, and members of the juvenile age class were most likely to interact with swimmers. Observations made from tour vessels, combined with a photo-identification effort from an independent research vessel, and logbooks from commercial tour operators, were used to estimate the exposure of dolphins in this region to swim attempts.

Other examples in which commercial tour vessels were used as the research platform include ongoing studies of swimmer interactions with dwarf minke whales in the Great Barrier Reef Marine Park, Queensland, Australia (Arnold and Birtles 1998, 1999; Birtles *et al.* 2001). Ransom (1998) used commercial tour vessels as the research platform in a different way: she compiled records collected onboard tour vessels to show an increase in the duration of swim encounters over a 5-year period.

Independent vessel as research platform

Use of an independent vessel as the research platform provides a number of controls over research design, including the ability to select and repeatedly follow specific individual animals, to confirm in real time the identity of animals under observation, and to designate the duration of follows. In addition, use of an independent research vessel facilitates the application of several analytical designs, *e.g.*, the researcher can plan to make observations in the presence and absence of disturbance, or before, during and after impact situations. Use of an independent vessel as the research platform is likely to be the best way to obtain information about the details of behaviour and/or behavioural responses of individual cetaceans. The primary drawback to using an independent research vessel is the potential for disturbance to the animals being studied by the research vessel itself. When the vessel is handled consistently in a manner intended to lessen

disturbance, effects of the research vessel are likely to be minimised and constant. Impacts of an independent research vessel may be further reduced by using a "quiet" vessel, e.g., a vessel under sail (e.g., Corkeron 1995). However, use of an independent vessel will confound interpretation of the data if the combined presence of tour and research vessels results in cumulative effects on cetacean behaviour, or when the behaviour of the research vessel is altered over the course of observations, e.g., when there are changes in vessel type, speed, engine noise, proximity, and/or approach angle relative to animals.

Samuels and Bejder (1998, 2004) used an independent vessel as the research platform in studying bottlenose dolphins that have habitual interactions with humans in the water. By using an independent research vessel, Samuels and Bejder (1998, 2004) were able to select specific dolphins for observing and to assess impacts of human interaction from the perspective of individual animals. Specifically, use of an independent research vessel made it possible to observe dolphins that did and did not have interactions with humans within the same region, to conduct repeated focal follows of individually-identified dolphins, and to quantify and record the details of the focal dolphins' interactions with humans. Based on repeated follows of individuals, Samuels and Bejder (1998, 2004) calculated that human interaction put one specific juvenile dolphin at risk once every 12 min, including being fed by humans at least once per 59 min. In this study, dolphins were so often surrounded by tourist vessels, to the exclusion of the research vessel, that it is unlikely the presence of a research vessel had a significant effect on the behaviour of focal dolphins.

Nowacek et al. (2001a) used an independent research vessel to study behavioural responses of individual bottlenose dolphins during vessel approaches. In particular, use of the independent vessel enabled Nowacek et al. (2001a) to conduct controlled approaches by experimental vessels at predetermined times during focal follows of individually-identified dolphins. In these experiments, the independent research vessel provided a platform for an innovative method for measuring a difficult-to-see disturbance response: the research vessel towed a tethered blimp mounted with an overhead video system (Nowacek et al. 2001b) which enabled Nowacek et al. (2001a) to quantify subsurface behavioural response such as changes in inter-animal distance, heading, and swimming speed. Nowacek et al. (2001a) explicitly tested for, but did not detect, an effect of the research vessel on dolphin behaviour; however, they acknowledged that due to the presence of the research vessel, their experimental design actually tested the impact of multiple vessels in proximity to focal dolphins.

Other examples include Mann and Smuts (1999) who used an independent research vessel to conduct repeated focal follows of individually-identified food provisioned bottlenose dolphins when those dolphins were away from the provisioning area. In addition, Miller *et al.* (2000) and Allen and Read (2001) both used an independent research vessel to conduct focal follows of humpback whales and bottlenose dolphins, respectively, in order to evaluate impacts of anthropogenic disturbances on individual animals.

Underwater research platform

Visual observations from underwater

Cetacean biologists are commonly asked by nonscientists whether their research is conducted by getting in the water with the animals. However, underwater observations are rarely effective for studying cetaceans and are the exception rather than the rule. The in-water platform has been used to study the behaviour of spotted and bottlenose dolphins that are habituated to human swimmers (e.g., Herzing 1996; Dudzinski 1998). However, in-water visual observations are seldom useful for studying impacts of tourist activity because the factors that can preclude unbiased observations of behaviour from an independent vessel are all-the-more likely to come into play when people enter the water with unhabituated cetaceans. First and foremost, a person in the water near enough to view behaviour constitutes a potential impact. In addition, a swimmer in such close proximity is usually accompanied by a vessel, therefore, impacts may be compounded. Moreover, an underwater observer, with a narrow range of view and limited mobility, is typically limited to fleeting glimpses of those animals that tolerate humans in the water and that come close enough to be seen. As a result of these limitations, in-water observations of human interactions with cetaceans are typically anecdotal, but may be useful to identify the gender (Glockner-Ferrari and Ferrari 1990), identity (Arnold and Birtles 1999) of individual animals, or details of behavioural events (Arnold and Birtles 1999).

Acoustic recordings of underwater sound

An underwater research platform is used to make acoustic recordings of underwater sound. Because cetaceans rely on sound for communication, navigation, finding prey, and detecting predators, there are many studies that evaluate how underwater man-made sound affects cetacean behaviour (e.g., reviewed in Richardson et al. 1995). In addition, a few recent studies look at effects of potential anthropogenic disturbances – acoustic or otherwise – using cetacean

vocalisations as the response measure. Collection of acoustic data is often associated with other research platform types and therefore subject to the attributes of that particular platform, *e.g.*, acoustic recordings may be made via hydrophones deployed from an independent research vessel or from a land-based research platform. In addition, acoustic recordings are sometimes made from tags temporarily attached to animals or via remote recordings from sonobuoys.

From sonobouys or hydrophones mounted at fixed locations, acoustic recordings can be made with minimal disturbance to study animals. However, studies in which acoustic monitoring is conducted from fixed locations are time consuming because obtaining an adequate sample size is dependent upon movement of study animals into areas where transducers are deployed. In addition, these remote recording systems rarely permit identification of individual animals (but see: Janik et al. 2000). In contrast, studies in which acoustic recordings are made from a manoeuvrable platform such as an independent research vessel are typically more efficient in obtaining an adequate sample size (e.g., Richter et al. 2000) and may permit identification of individual animals (e.g., Miller and Tyack 1998). In these cases, confounding factors may be introduced due to the physical and/or acoustic presence of the vessel.

As an example, Miller *et al.* (2000) used a calibrated hydrophone array, towed from an independent research vessel, to monitor the vocal behaviour of individual singing humpback whales while simultaneously monitoring the surface behaviour of each whale. In this experiment, the independent research vessel was a constant presence from which concurrent behavioural and acoustic observations were made before, during and after exposure to controlled playbacks of LFA sonar.

In very few studies of cetacean acoustics has it been possible to establish the identity and/or exact number of animals responsible for recorded vocalisations. Therefore, interpreting the measure, "change in vocal behaviour", for a group of animals in response to anthropogenic disturbance can be problematic. For example, some individuals may *increase* vocal activity in response to stimuli, whereas other individuals in the same group or region may *decrease* vocal activity, such that all individuals alter their vocal behaviour but the overall net change at the group level is zero. Lesage *et al.* (1999) provide an example in which group vocal behaviour was carefully recorded and quantified. They recorded vocalisations of groups of beluga whales via hydrophones mounted on the sea floor, and by selecting only those experiments in which they could be sure of recording all

emitted vocalisations, they were able to look at changes in vocal behaviour in response to controlled vessel approaches.

Aerial research platform

Aerial research platforms, e.g., airplanes, helicopters and blimps, have occasionally been used to study reactions of cetaceans to anthropogenic impacts (e.g., Au and Perryman 1982). As is the case with elevated land-based observations, an aerial vantage can provide a "birds-eye view" of group cohesion and large-scale animal movements in response to human activity. Aerial platforms share some of the negative aspects of elevated land-based platforms, e.g., restricted viewing of animals and behaviour due to the remoteness and relative lack of manoeuvrability and stability of most aerial platforms. Unlike elevated land-based observations, however, observations from air are likely to have physical and/or acoustic impacts on cetaceans in nearby waters. And, in contrast to on-the-water research platforms that can be handled in a consistent and predictable manner around study animals, most types of aerial platforms are likely to be less predictable and more irregular sources of acoustic and physical disturbance.

As an example, Au and Perryman (1982) used a helicopter as one of their research platforms to quantify long-range movement patterns of spotted, striped and spinner dolphins in reaction to controlled vessel approaches in the eastern Pacific. Specifically, the helicopter was used to spot dolphins and direct the approach of a large ship from a large distance (>10 km). During the approach, the helicopter hovered over the dolphins, providing a continuous marker of the dolphins' location. Dolphin movements in response to the approaching ship were measured from ship to helicopter using the ship's radar. In this study, use of an aerial platform was essential for documenting evasive responses of dolphins to an approaching vessel over a large distance, reactions not easily quantified solely from land- or vessel-based platforms.

Nowacek *et al.* (2001a) also took advantage of an aerial platform to evaluate anthropogenic disturbance on cetacean behaviour. Specifically, from an independent research vessel, they towed a blimp mounted with an overhead video system (Nowacek *et al.* 2001b) which enabled them to record subsurface behaviour of individual dolphins in response to controlled vessel approaches. Retrospective analyses of video records provided information about the orientation and speed (via fluke stroke counts) of each focal dolphin in response to vessel traffic, showing that dolphins changed orientation away from the path of approaching vessels, and increased swimming speed

more often during vessel approaches than during control periods. Nowacek *et al.* (2001a) suggested that the overhead video system enabled them to detect quick and subtle reactions that would likely have gone unnoticed in observations from other observational platforms.

MEASURING RESPONSES

Impacts of nature-based tourism on cetaceans are rarely as evident as the mortalities brought about by such human activities as whaling and fisheries by-catch. Seldom has tourism been shown to be directly responsible for fatalities, although there are scattered reports of commercial whale watch vessels colliding with humpback, fin and minke whales (e.g., M. Weinrich 2001, pers. comm.). Instead, as noted above, exposure to nature tourism is more likely to have cumulative rather than catastrophic effects (e.g., Duffus and Deardon 1990). Harmful impacts are unlikely to result from single encounters with vessels or human swimmers, however, tourism focusing on free-ranging cetaceans typically targets specific individuals or subgroups for repeated, close, prolonged and persistent encounters. As a continual and undeniable presence, such tourist activities have the potential to result in chronic stress and/or repeated disruptions to maternal care, breeding, feeding and resting which, in turn, may bring about decreased reproductive success, loss of physical condition, altered habitat use, or even mortalities.

"Ultimately, it would be valuable to estimate the direct energetic 'cost' of human disturbance to whales. This cost could then be compared with the whales' overall energy budget to determine the potential loss in long-term reproductive success as a result of disturbance. In other words, how much energy is expended or lost, as a result of disturbance that might otherwise be devoted to reproduction?" (Baker and Herman 1989:40). At present, however, there are few, if any, studies in which baseline and disturbed behaviour are quantified such that behavioural responses can be translated to energetic costs and long-term impacts.

Typically, researchers look at vocal and non-vocal behaviour to evaluate potential effects of nature-based tourism on cetaceans. Immediate behavioural responses are more readily related to potential sources of impact than are long-term or cumulative impacts. Careful selection of biologically-relevant behavioural measures is crucial, but decisions are often tempered by such logistical concerns as characteristics of the species, extent of species-specific background behavioural information, geographic location of animals in question, nature of the potential

disturbance, selection of research platform and sampling methods, available technology, and constraints on researcher time and finances.

Interpretation of response measures in relation to disturbance can be tricky. In order to identify certain behaviours as responses, it is first necessary to be able to describe and quantify "normal" undisturbed behaviour. In addition, absence of behavioural response to potential disturbance can be due to a variety of factors: sometimes, lack of response truly signifies that no effect has occurred; alternatively, it may indicate that targeted animals have become habituated to the stimulus. Unfortunately, an apparent lack of response can also result from imperfect or inadequate monitoring techniques. For example, monitoring schemes that focus on reactions of groups to stimuli are likely to be biased towards detecting the behaviour of more conspicuous individuals, to the detriment of documenting effects on other individuals. Moreover, responses that are physiological with no visible sign will not be readily detectable in free-ranging animals. As exemplified by several of the studies highlighted here, simultaneous recording of multiple response measures appears to optimise the likelihood of response detection.

In the sections that follow, I use examples from the case studies to illustrate short-term behavioural measures, both vocal and non-vocal, and long-term measures that have been used to evaluate impacts of human disturbance on cetaceans. In addition, I address the measurability of "stress" and "distress".

Short-term measures

Non-vocal behaviour

I know of no quantitative studies that directly relate short-term behavioural responses to energetic costs and long-term impacts. Instead, short-term changes in behaviour are typically used as a measurable, quantifiable, best-guess proxy for long-term costs. For non-vocal behaviour, responses presumed, but not necessarily demonstrated, to be indicative of long-term impacts of human disturbance include changes in (i) surfacing, ventilation and dive patterns; (ii) swim speed, course and orientation; (iii) group dispersion; (iv) behavioural states/activity budgets; (v) behavioural event frequencies; and (vi) ranging pattern and habitat use.

i) Surfacing, ventilation and dive patterns

Changes in surfacing, ventilation and dive patterns are commonly used as indicators of disturbance. These measures may be indicative of avoidance reactions; indeed, some researchers

have claimed these as the most sensitive indicators of whale responses to vessels (Baker and Herman 1989). Benefits include that these measures are readily quantifiable and can be recorded from a variety of research platforms. As with most behavioural data, these measures are most informative when recorded for individual animals; group-level rates (e.g., total number of blows divided by number of animals in the group per time unit) are unlikely to be very meaningful due to age, sex, and individual differences in behaviour.

Nowacek *et al.* (2001a) used the measure, inter-breath interval, to compare the behaviour of individual dolphins during experimental and opportunistic vessel approaches. Focal animals had longer inter-breath intervals during vessel approaches than during control periods. In particular, females without calves and inexperienced mothers had significantly different inter-breath intervals from experienced mothers, with experienced mothers having the longest intervals of any dolphin class during vessel approaches. In this study, inter-breath interval was used to represent vulnerability to vessel strikes: longer inter-breath intervals during vessel approaches correspond to less time at the surface when boats are nearby, which was presumed to correspond to a lower probability of being struck.

In another example, Stone *et al.* (1992) recorded from land all occurrences of breaths taken by individual fin whales in conjunction with theodolite tracking of their movements in the presence and absence of whale watch vessels. Results revealed significantly reduced dive durations, surface durations, and number of blows per surfacing sequence for individual whales when whale watch vessels were nearby. However, the authors felt that observed differences were not of sufficient magnitude to warrant a practical definition of "harassment". In particular, they deemed that the definition for "control" periods – no vessels within 450m of the focal whale – was unlikely to be compatible with whale perceptions of vessel presence, since other studies have shown that cetaceans may respond to acoustic stimuli at distances of up to 10s of kilometres (*e.g.*, Au and Perryman 1982; Richardson *et al.* 1985; Baker and Herman 1989).

Janik and Thompson (1996) recorded dolphin surfacings within a circumscribed area within ± 1 min of a vessel approach. Cognisant of the problems associated with calculating group-level rates, they used the total number of surfacings as their measure. They found a decrease in the total number of surfacings following vessel approaches (particularly approaches of the dolphin watch vessel), which they interpreted to mean that at least some of the dolphins either dived for longer periods and/or moved away after the boat approached them.

ii) Swim speed, course and orientation

Many researchers have looked at short-term changes in swimming speed, course of travel, and orientation relative to potential sources of disturbance as measures of the impacts of anthropogenic activity on cetaceans. These parameters are most accurately recorded using a theodolite stationed on an elevated vantage point on land which provides an overview and precise measurements of the locations of study animals and sources of disturbance. Swim speed, course and orientation appear to be useful measures of short-term avoidance reactions to human activity. These measures are typically recorded immediately *before* and/or *during* interactions between study animals and sources of potential impact. In this way, spatial and temporal discontinuities between cause and effect can be isolated.

Bejder *et al.* (1999) used land-based theodolite tracking to determine orientation of Hector's dolphin groups relative to vessel movement. In this study, orientation was used as a measure of attraction and avoidance. Of particular interest was the question: Does dolphin orientation with respect to the tour vessel vary with time during the encounter? Dolphins tended to orient towards vessels significantly more often than expected during initial stages of the encounter but less frequently than expected as the encounter duration increased beyond 70 min, which was presumed to indicate an initial attraction followed by avoidance. These findings led to pending proposals for permit conditions to restrict the duration of encounters (H. Kettles 2001, pers. comm.).

Williams *et al.* (2002a) also used land-based theodolite tracking to record swim speeds and "directness" of travel for individual killer whales under conditions of no vessels, experimental vessel approaches, and opportunistic vessel approaches. By following individually-identified animals of known age class and gender, they were able to document the potential for sex-specific responses to vessel traffic, including that, overall, male whales swam significantly faster than females, and female whales responded to vessel approaches by swimming faster and increasing the angle of successive dives.

iii) Group dispersion/ cohesion

Dispersion or cohesion of cetacean groups is often considered to be a useful measure of disturbance under the presumption that cetaceans will bunch together in situations of surprise, threat or danger (Johnson and Norris 1986). Various measures of group cohesiveness have been

recorded from several platforms, and can often be directly related to potential sources of disturbance.

From an elevated land platform providing an overview of groups of Hector's dolphins, Bejder *et al.* (1999) scored relative group dispersion on a scale from 1, tightly bunched together (dolphins within 0-2 body lengths of each other), to 4, spread out (dolphins generally >10 body lengths apart). Based on this assessment, they showed that dolphin groups were significantly more compact in the presence of dolphin watch vessels than when no vessels were present. Similar responses to approaching vessels have been reported in other species (*e.g.*, *Stenella* sp.: Au and Perryman 1982).

Nowacek *et al.* (2001a) used a different measure of group dispersion. The overhead video system afforded a "big picture" view around the focal animal from which inter-animal distance was estimated based on the distance from the focal to the nearest neighbour. These data showed that dolphins decreased the distance to the nearest neighbour, *i.e.*, increased group cohesion, during controlled approaches by vessels relative to control periods.

iv) Behavioural states/ activity budgets

Repeated disruptions due to human activity and/or habituation to human activity are likely to affect behavioural activity budgets, *i.e.*, how much time animals spend foraging, resting, socialising with conspecifics, etc. Over the long term, it is presumed that altered activity budgets would result in decreased reproductive success, loss of physical condition, or even mortality. Thus, many researchers record behavioural states to look at short-term changes induced by anthropogenic activity and/or to compare activity budgets.

Mann and Smuts (1999) recorded specific activities to compare the behaviour of mother dolphins and their calves within and away from a provisioning-and-human-interaction area. In this study the activity, "echelon swim" with the mother, was recorded continuously during focal follows of individual calves. Time spent in echelon swim with the mother was used as an indicator of maternal care, as the calf may derive energetic benefits from swimming in contact with, or in the slipstream of, the mother. Mann and Smuts (1999) found that, although echelon swimming was common away from the provisioning area for both provisioned and wild-feeding dolphins, the proportion of time calves spent in echelon swim was significantly reduced within the provisioning area. In a follow-up study, Mann and Kemps (2003) observed provisioned dolphins within and

away from the provisioning area, recording continuously the activity, swimming in "infant position". Time spent in infant position was used as another indicator of maternal care, as swimming beneath the mother's ventrum is likely to correspond directly to opportunities for nursing. They found that nursing opportunities, *i.e.*, time spent in infant position, were significantly reduced when mothers and calves were in the provisioning area.

In another example, Samuels and Bejder (1998, 2004) conducted focal follows of individuals and small groups to compare behaviour of dolphins living in the same region that did and did not have interactions with humans. Dolphin activity (or for groups, "predominant group activity" (Mann 1999)) was recorded at specified intervals. In addition to standard activity categories, *i.e.*, travel, forage, rest, socialise with conspecifics, a "human interaction" activity state was included to encompass a suite of human-focused behavioural events (see "Behavioural events", below). Samuels and Bejder (1998, 2004) minimised biases associated with sampling the behaviour of cetacean groups (see "Study subjects", above) because they were able to monitor continuously whether any group members had interactions with humans. They found that some dolphins in this region, categorised as "habituated", engaged in human-interaction activity during 77% of observation time, whereas other dolphins, categorised as "unhabituated", never engaged in human-interaction activity.

Constantine and Baker (1997) used the measure, change in predominant group activity, as an indicator of disturbance during approaches by swim-with-dolphin vessels. From their tour vessel research platform, predominant group activity was assessed upon first sighting of a dolphin group and reassessed when the tour vessel was within 100m. Thirty-two percent of vessel approaches to bottlenose dolphins resulted in a change in group activity with feeding being the activity least likely to be disrupted and socialising most likely; 52% of approaches to common dolphins resulted in behavioural change with resting least likely and socialising most likely to change.

v) Behavioural events

Presence/ absence and frequency of specific behavioural events may be useful indicators of disturbance, and indeed, many researchers record some subset of discrete behaviours. However, with the exception of "blows" (see "Surface, ventilation and dive patterns", above), there are few examples in which behavioural events have been used to assess disturbance. In part, this is because little is known for cetaceans about the functions of many behavioural events. In order to identify changes in behaviour or "abnormal" behaviour as responses to disturbance, there must be

familiarity with what is "normal" behaviour or baseline levels. In most instances for most cetaceans, that is not known, in part because the preferred group-level focus is not sensitive to individual or age/sex class variations in behaviour. In addition, only a few behavioural sampling techniques provide unbiased records of behavioural events. For example, focal-individual follows are appropriate for quantifying, or making detailed observations of, social behaviour; group scan sampling is appropriate for recording frequencies of such conspicuous behaviours as aerial displays.

The study by Samuels and Bejder (1998, 2004) provides several examples of measuring behavioural events as indicators of disturbance. In the course of focal follows from an independent research vessel, Samuels and Bejder (1998, 2004) recorded specified behavioural interactions ("behavioural events") between dolphins and humans in order to classify individual dolphins as habituated or unhabituated to human activity (see "Behavioural states", above). Thus, the behavioural state of being habituated was defined by the presence of certain behavioural events. Human-interaction behaviours indicative of habituation included: remain close by vessels or humans, leap up or lunge at vessel, beg from humans, accept food from humans. In addition, behavioural events were also recorded to identify human-dolphin interactions that pose a risk for dolphins or humans, including: physical contact between dolphin and human, dolphin in close proximity to a vessel or deployed fishing gear, humans feeding or offering objects to dolphin. Based on systematic records of these behavioural events, Samuels and Bejder (1998, 2004) calculated that human interaction put one juvenile dolphin at risk once every 12 min.

Barr and Slooten (1998) recorded aerial behaviours of dolphins in the presence and absence of boats. At specified intervals, they conducted scans of the focal group from a clifftop vantage point and recorded the number of "clean leaps" and "slaps" as indicators of disturbance or agitation. They found that aerial behaviour substantially increased when boats were present, especially after midday during the dolphins' presumed rest period.

vi) Ranging patterns and habitat use

Human disturbance may also result in short-term changes in ranging patterns and habitat use, which if repeated or chronic, are likely to have harmful long-term effects. For example, if preferred habitats are rendered less desirable through human presence, animals may be denied access to areas critical for breeding, foraging or resting. Disturbance may also result in redistribution of animals within a population, such that less tolerant individuals or members of

certain age, sex or reproductive classes become sensitised and displaced to less optimal areas where food resources are less abundant or predators are more prevalent. Thus, several researchers have looked at effects of human activity on cetacean ranging patterns and habitat use.

For example, Allen and Read (2000) followed individual dolphins to assess potential effects of vessel traffic on habitat selection. They found that habitat selection by foraging dolphins differed between two time periods that varied in vessel density. Specifically at one site, foraging dolphins showed significant preferences for certain habitats during low vessel activity, but habitat preferences were not apparent during periods of high vessel activity. They suggested that dolphins shift habitat use either to avoid directly areas of high vessel traffic or in response to vessel traffic.

Samuels and Bejder (1998, 2004) documented differences in the ranging patterns of habituated and unhabituated dolphins living in the same region. Focal follows of dolphins revealed that habituated dolphins remained within a <1nm² area where they engaged in interactions with humans (including food provisioning); whereas, in follows of comparable duration, unhabituated dolphins traveled distances of several nautical miles, moving through the area frequented by habituated dolphins without stopping or showing any interest in humans.

Vocal behaviour

Because cetaceans rely on sound for navigation, communication with conspecifics, and locating predators and prey, it is often assumed that short-term changes in vocal behaviour may be related to energetic costs and long-term impacts. Studies monitoring vocal behaviour may provide insights as to whether communication, navigation and/or predator/prey detection are compromised by anthropogenic disturbance, either by altering vocal patterns or by acoustic masking, *i.e.*, reducing the ability to detect conspecific calls and other underwater sounds. As with non-vocal behaviour, there are no quantitative studies that demonstrate conclusively links between short- and long-term measures; however, short-term vocal responses to disturbance often may be reasonable and measurable approximations of long-term impacts. Vocal responses that are presumed, but not necessarily demonstrated, to be indicative of long-term impacts of human disturbance include changes in vocal repertoire, cessation of vocalisations, and changes in the frequency or duration of specific vocalisations. Changes in attributes of vocalisations is the measure most commonly used.

The logistical hurdles to following and systematically recording the non-vocal behaviour of a single animal (see "Study subjects", above) are all-the-more evident when it comes to recording the vocal behaviour of individual cetaceans (e.g., reviewed in Whitehead et al. 2000). There are few visual cues to assist human observers in identifying which animal within a group is making which sound. In addition, recordings of vocalisations made from vessels may be obscured by ship noise. Moreover, vocal repertoires are not completely known for many species, nor are vocalisations typically described using standardised classification systems.

Due to the technical difficulties associated with identifying vocalising individuals, researchers often record vocal behaviour of groups of cetaceans in studies evaluating potential disturbance. This approach is fraught with many of the same biases associated with group-level analyses of non-vocal behaviour (see "Study subjects" and "Non-vocal behaviour", above). In particular, apparent changes in group vocal behaviour may be due to one, a subset, or all animals in a group; therefore, group-level analyses may well obscure actual responses. In a few studies, however, special care has been taken in the handling and interpretation of recordings of group vocal behaviour.

For example, Lesage *et al.* (1999) recorded vocalisations of groups of beluga whales during experimental vessel approaches in order to study effects of vessel noise on whale vocal behaviour. Vocalisations were classified using a systematic scheme, and exceptional care was taken to include only those experiments in which all calls could be counted, *i.e.*, an unbiased sample of vocalisations. Only six of 77 experiments satisfied the criteria for suitable recording quality and were used in acoustic analyses. Numbers of calls were compared between preexposure, exposure and postexposure conditions. Despite a small sample of high-quality experiments, results showed that experimental vessels induced changes in calling rates, longer call durations, an upward shift in the frequency range, and a tendency to emit calls repetitively, with responses to the larger and slower of two experimental vessels being more persistent. Lesage *et al.* (1999) suggested that the observed vocal responses to vessel noise appeared to be strategies to compensate for acoustic masking and increase signal detectability.

Despite the logistical obstacles listed above, several researchers have successfully recorded the vocalisations of single animals by taking advantage of technological advances and the particular characteristics of the species of concern. For example, recent techniques such as beamforming and two-dimensional hydrophone arrays have enabled researchers to make simultaneous acoustic

and behavioural records for individual free-ranging cetaceans (e.g., Miller and Tyack 1998; Janik et al. 2000; Janik 2000a,b).

In an example related to impact assessment, the solitary nature of sperm whales near Kaikoura, NZ, enabled Richter et~al.~(2001) to use directional hydrophones to track individuals underwater, and thereby, to monitor effects of whale watch vessels on the vocal behaviour of individual whales. Strictly speaking, in this study they evaluated additional effects of a whale watch vessel on a whale that was already being followed by a research vessel. A response measure was calculated for individual whales -i.e., time elapsed from fluke-out to first click - and this measure was compared in the presence and absence of whale watch vessels. Coupled with sighting histories for individual whales based on photo-identification, Richter et~al.~(2001) demonstrated that for "transient" whales, time to first click increased by nearly 50% in the presence of whale watch vessels; whereas, effects on "resident" whales were not detected.

In another example, Miller et al. (2000) made continuous recordings of the songs of individual humpback whales using a towed, calibrated hydrophone array, in order to study effects of experimental sound playbacks on individual whales. As in Richter et al. (2001), this study evaluated the additional effects of anthropogenic sound on a whale that was already being followed by a research vessel. By recording song before, during and after experimental playbacks of LFA sonar, Miller et al. (2000) demonstrated a variety of individual responses to sound playbacks: some whales responded to sound playback by ceasing to sing, other whales responded by increasing the duration of songs, and still others gave no apparent response. Miller et al. (2000) suggested that those humpbacks that sang longer songs during sonar transmission did so in order to compensate for acoustic interference. As humpback song is thought to be a sexual display, alteration of song in response to man-made noise may have detrimental effects on reproduction.

Long-term measures

The title of this section is something of a misnomer since the entire chapter is about measuring the long-term impacts of cetacean-focused tourism. The short-term measures described above are actually surrogates -i.e., more readily measurable estimates - for the long-term impacts that have biological relevance. Ideally, in impact assessment research, one goal is to link such short-term reactions with long-term effects on the animals. In particular, it is important to know: Do the short-term responses elicited by human activity translate into long-term impacts on behavioural

repertoire, reproduction, physical condition, distribution, habitat use, etc, and in what ways do these changes influence survival and population size? In practice, it has rarely been possible to demonstrate conclusively the biological significance of short-term behavioural change in response to anthropogenic activity. As one example, when male humpback whales sing longer songs (a sexual display) during exposure to man-made sound (Miller *et al.* 2000), it might be reasonable to assume that there would be some cost to whale reproduction, but obtaining the data needed to confirm this supposition is easier said than done.

For one, difficulties arise in distinguishing impacts of human activity from long-term change resulting from ecological factors. Spatial and temporal discontinuities between cause and effect can result in spurious correlations that erroneously point a finger at human activity as instigator. Further complications are highlighted by time-series modeling to assess trends in demographic parameters for right whales (Branao *et al.* 2000) and by power analyses to investigate trends in population size and effectiveness of monitoring programs for bottlenose dolphins (Wilson *et al.* 1999) – both studies show that nearly a decade of data is needed to detect impacts at the population level. In addition, the present climate for the funding of cetacean behavioural studies is not supportive of the baseline research needed to identify what is "normal" behaviour for cetaceans of various species, age/sex classes, reproductive classes, etc, nor of the longitudinal research needed to quantify long-term change in response to human activity.

With respect to assessing impacts of cetacean-focused tourism, studies that explicitly set out to measure long-term effects are few. In some instances, follow-up studies have been designed for comparison with existing pretourism datasets but interpretation of these findings may be complicated by other factors (e.g., Brown 2000; Forest 2001). In several cases, historical data collected for other purposes have been analysed to investigate possible correlation between tourism and long-term change in behaviour (e.g., Watkins 1986; Ransom 1998) and reproductive success (e.g., Mann et al. 2000), but again, to conclusively link tourism with the observed trends may be difficult. In only one instance of which I am aware was longitudinal monitoring of the impacts of cetacean-focused tourism an explicit part of the research design (Constantine and Baker 1997; Constantine 2001).

Habituation and sensitisation

Habituation is defined as a gradual weakening of the behavioural response to a recurring stimulus that provides no apparent reward or punishment (Thorpe 1963; Allaby 1999). In field studies of

animal behaviour, habituation of animal subjects may be desirable when researchers want to study behaviour that is relatively unaffected by their own presence (e.g., Goodall 1986; Tutin and Fernandez 1991; Johns 1996). Some cetaceans that are repeatedly targeted by tourist activities may be similarly inclined towards habituation. This is a concern, however, when the reduction in the animals' natural wariness to human activity results in heightened vulnerability to vessel strikes, entanglement and vandalism (e.g., Samuels and Bejder 1998, 2004; Spradlin et al. 1998, 2001; Stone et al. 2000).

Sensitisation is defined as an increased likelihood that repeated exposure to a particular and significant stimulus will produce a response in an animal (Richardson *et al.* 1995; Allaby 1999). Constantine (2001: 690) noted that: "[without] any apparent incentive to interact with humans, marine mammals are less likely to tolerate a situation they perceive as threatening". Thus, some animals may become sensitised to stimuli over time, with repeated or chronic exposure resulting in a higher frequency or intensity of avoidance reactions.

Quantification of the habituation or sensitisation status of individual cetaceans targeted by tourism should be one priority for impact assessment studies. As an example, Samuels and Bejder (1998, 2004) identified certain dolphin behaviours to be indicative of habitual interaction with humans, and they classified individual dolphins as "habituated" to human interaction or not based on the presence or absence of these behaviours in each animal's repertoire. In another study, Constantine (2001) documented sensitisation by comparing responses of dolphins to swim-with-dolphin tourism over a period of several years. Sensitisation was indicated by findings that the percentage of successful swim attempts decreased over time with a concomitant increase in swim attempts avoided by dolphins (Constantine 2001). Watkins (1986) inferred from historical records changes in the habituation and sensitisation of different whale species to whale watch tourism: specifically, avoidance responses by humpback whales at the onset of cetacean-focused tourism were replaced with "positive" curious responses following years of exposure to whale watch tourism; conversely, the initially positive responses by minke whales changed to avoidance.

In addition to identifying habituation or sensitisation status, it is important to document what costs, if any, are incurred by such changes in wariness to human activity. In one example, based on focal follows of habituated and unhabituated dolphins, Samuels and Bejder (1998, 2004) were able to quantify the rate at which a specific juvenile dolphin was put at risk as a result of human-dolphin interaction, *i.e.*, once every 12 min. In another example, Samuels *et al.* (2000)

documented a high occurrence of mortality among "lone sociable" habituated dolphins – those dolphins that eschew companionship of conspecifics and seek out humans and human activity. Based on a review of the literature pertaining to swimming with wild cetaceans, Samuels *et al.* (2000) identified 28 lone sociable dolphins whose lives were well documented. Of these, at least four were killed by humans, and five others disappeared under "mysterious circumstances", *i.e.*, around the time of human-dolphin conflict. Other lone sociable dolphins repeatedly incurred serious injuries and seemed destined for a fatal accident as a result of their habituation to humans. It was noted that although lone sociable dolphins are the ones who typically make first contact with humans, habituation is usually a gradual process achieved through considerable effort on the part of humans, an effort that ultimately puts these dolphins at risk of injury or death.

Ranging patterns and habitat utilisation

Long-term displacement of cetaceans from preferred areas has been correlated with human activity in several instances. For example, spinner dolphin groups in Hawaii favour a particular bay for daytime rest and socialising (Norris and Dohl 1980). Forest (2001) documented a reduction in usage of the bay from pretourism frequencies, and speculated that dolphins may enter the bay less often due to increasing levels of dolphin-focused tourism. Forest (2001) suggested that the bay had become "less suitable" due to increased human activity, but noted that other explanations are also possible, *e.g.*, changes in population structure or ecology of the area. Other examples of habitat abandonment that may be related to human activity include reduced usage of Guerrero Negro Lagoon in Baja California by grey whales and Glacier Bay, Alaska, by humpback whales in apparent response to vessel disturbance (Gard 1974, Bryant *et al.* 1984, Dean *et al.* 1985). In all three examples, researchers were unable to confirm definitively that human activity was the cause of the observed change, which highlights the problems with inferring causation from correlation.

Reproductive success

A long-term research project dedicated to studying the behaviour and social organisation of bottlenose dolphins in Australia provided useful data for investigating effects of tourism on a subset of dolphins in this population. Analysis of ten years of demographic data revealed long-term detrimental consequences on the reproductive success of individual bottlenose dolphins fed by humans at a tourist resort (Mann *et al.* 2000). Specifically, provisioned female dolphins were found to have significantly lower calf survivorship than wild-feeding females in the same bay.

Stress and distress

"Stress" has been defined as "the biological response elicited when an individual perceives a threat [stressor] to its homeostasis. When a stress response truly threatens the animal's well-being, then the animal experiences 'distress'" (Moberg 2000:1). The term "distress" has been used to "indicate specifically that the stressor may cause harm or decrease the welfare and (or) fitness of the organism" (Lay 2000:249). Animal research shows that chronic stress, severe acute stress, and/or distress can contribute to reduced fitness, reproductive disorders, disease, and mortality (e.g., Ridgway 1972; Moberg 1985; Sapolsky 1987; Dierauf 1990; Apaninus 1998; von Holst 1998; Sweeney 1990; Waples and Gales 2002). Thus, one goal in assessing the impacts of human disturbance on wildlife is to determine whether or not, and to what extent, human activity may be stressful for targeted animals.

Unfortunately, there is limited knowledge as to how stress and distress are expressed. There are few quantitative studies that correlate physiological and behavioural measures, and there are many uncertainties and discrepancies associated with interpreting physiological measures. In addition, little is known about how short-term responses to disturbance may be linked to stress or distress. Another confounding factor is that a stress response is not necessarily harmful unless it results in distress, *e.g.*, temporary changes in heart rate or blood pressure may or may not have significant impacts on an animal's welfare. Biological costs of stress are likely to be minimal when animals have adequate compensatory biological reserves. However, when costs exceed reserves – for example, under conditions of chronic, severe, prolonged and/or cumulative stressors – stress may have significant impacts on fitness, reproduction or mortality.

To identify biological indicators of animal distress, Moberg (1985, 1987, 2000) proposed a conceptual model in which the stress response is comprised of up to four components: behavioural, endocrine, immunological and/or autonomic nervous system. Ideally, measures of these four defence mechanisms could serve as indicators of stress and distress; however, no measure by itself has proven adequate to the task, in part because responses may be disturbance-or animal-specific (Moberg 2000). Further complicating the utility of these defence mechanisms as indicators of stress is that "positive" and "negative" stressors can elicit comparable responses (e.g., in stallions, similar cortisol levels were recorded during conditions of mating and confinement (Colborn et al. 1991)). To overcome obstacles in identifying stress and distress in animals, it may be advisable to monitor several potential indicators simultaneously and over the long term. For example, concurrent, longitudinal monitoring of behavioural and physiological

measures may help pinpoint situations of stress by providing complementary evidence and baseline data for comparison (e.g., Waples and Gales 2002).

For cetaceans, links have been suggested between specific anthropogenic activities and stress or distress (e.g., Frohoff 2000), but these relationships have rarely, if ever, been substantiated. Although techniques have been developed for minimally-invasive collection of physiological stress measures in field studies of terrestrial mammals (e.g., Sapolsky 1992), to my knowledge, such measurements have not been collected for free-ranging cetaceans. There are several possible reasons for this. First, physiological measures are difficult to obtain from marine animals at sea. In addition, collecting physiological samples typically requires darting, biopsies or temporary restraint, techniques that may be inherently stressful themselves. Indeed, several studies of wild dolphins show that temporary capture for biological sampling can elicit temporary physiological stress responses (e.g., Thomson and Geraci 1986; Aubin et al.1996; but see: Ortiz and Worthy 2000). With respect to behavioural measures, although functions have been proposed for specific behavioural events, there are few, if any, quantitative studies demonstrating that certain behaviours are expressions of stress and distress.

Thus, in the absence of appropriate examples from field research on cetaceans, I highlight several studies of animals in captive settings. The examples provided below illustrate potentially useful techniques derived from studies of cetaceans in captivity, settings where minimally-invasive biological sampling and detailed behavioural observations can be more easily accomplished.

Waples and Gales (2002) provide an example in which quantitative behavioural indices were correlated with physiological measures of stress for captive dolphins. The success of this study was due to ongoing collection of quantitative behavioural, clinical and physiological data for individual dolphins for months prior to one case of illness and two cases of mortality. Specifically, Waples and Gales (2002) documented changes in social dynamics and association patterns within the captive group that correlated with physiological measures of stress and poor physical condition. They concluded that stress resulting from social instability contributed to documented illness and mortalities.

In another example, Miksis *et al.* (2001) recorded cardiac responses of captive dolphins to sound playbacks of pool noise, familiar signature whistles, and agonistic jaw claps. By training dolphins to permit the temporary attachment of a suction-cup hydrophone, Miksis *et al.* (2001) were able to

continuously monitor cardiac activity before and after playback sessions, using "change in heart rate" as their response measure. They documented an initial acceleration in heart rate after playback of all three acoustic stimuli, particularly in response to jaw claps. Heart rate subsequently continued to increase after playbacks of signature whistles and jaw claps, but returned to normal after playbacks of pool noise.

In a third example, Samuels and Spradlin (1995) conducted detailed behavioural observations of individual dolphins during captive swim-with-dolphin programs and during the dolphins' "free" time. For certain swim programs in which dolphins and human swimmers were not controlled by trainers, they found that dolphins responded submissively to human swimmers. Samuels and Spradlin (1995) suggested – and there is ample evidence from studies of terrestrial animals – that behavioural expression of submission may be a marker for physiological response. Although physiological measures were not available to corroborate this claim, the study identifies specific behaviours that are demonstrated expressions of subordination (Samuels and Gifford 1997) and may be useful indicators of stress.

CONCLUSIONS

Current understanding of the impacts of tourism on free-ranging cetaceans is far from satisfactory. This is partly attributable to a scarcity of studies that incorporate the longitudinal perspective vital both for studying such long-lived creatures and for evaluating impacts that are likely to be cumulative rather than immediate. In addition, current methods in behavioural research have not been fully applied to this endeavour, with the result that detection and interpretation of possible impacts are impaired. Nevertheless, many studies investigating effects of tourism have demonstrated that these activities often elicit short-term changes in the behaviour of targeted cetaceans. Results of longitudinal monitoring are only starting to emerge, but, again, available information points towards detrimental effects on those animals that are the focus of tourist activity. Existing studies provide an important first step in assessing potential long-term impacts of cetacean-focused tourism; however, present knowledge of the biological significance of observed short-term effects is rudimentary, as are the methodologies used to evaluate such. It is clear that more refined, in depth, and longitudinal investigations are needed.

I identified several explanations for the limited nature of research to evaluate impacts of cetaceanfocused tourism. In part, these limitations can be attributed to problems inherent to all impact assessment studies (aquatic and terrestrial), and in part, to the logistical difficulties specific to cetacean behavioural research. In particular, studies of cetacean-focused tourism tend to be handicapped by an incomplete understanding of "normal" undisturbed behaviour, and a lack of baseline data for comparative analysis. In addition, it is only recently that cetacean behavioural biologists have taken full advantage of the quantitative techniques developed for studying the behaviour of terrestrial animals. As one example, contrary to a long-established focus on the individual in behavioural studies of terrestrial animals, the majority of impact assessment studies of cetacean-focused tourism have concentrated on measuring the behaviour and responses of groups of animals. Because a group-level approach will sometimes promote unwanted bias and incomplete information, there is a pressing need to complement existing work with additional studies emphasising behaviour at the level of the individual. Such a focus provides the framework for precise quantification of behavioural responses to human activity, facilitates detection of interindividual behavioural differences in attraction or vulnerability to tourism, and provides for comparison of behaviour of the same animals in the presence and absence of human activity. An individual focus maintained over the long term would provide valuable information about shortand long-term impacts of tourism on individuals, local communities, and populations.

As a result of these methodological shortcomings, and the subsequent inconclusiveness of current research efforts, both the scientific community and wildlife managers have voiced their discontent with the inadequacies in the knowledge base regarding impacts of nature-based tourism on cetaceans (e.g., IFAW 1995). However, as exemplified by the studies that I selected to highlight in this chapter, such deficiencies can be ameliorated by research designs that are meticulously and rigorously planned and executed, thereby promoting optimal environment for impact detection. These noteworthy case studies serve as helpful guides for future research whose goal is the assessment of impacts of cetacean-focused tourism.

Analysis of these case studies shows that their effectiveness can be attributed to a multi-faceted approach, including one or more of the following research design features: 1) collecting data from multiple research platforms, 2) utilising appropriate behavioural sampling techniques, 3) monitoring several response measures simultaneously, 4) supplementing opportunistic observations with controlled experiments, 5) analysing existing, historical data, and 6) taking advantage of innovative technologies. As an example, Nowacek *et al.* (2001a) incorporated all of these attributes to look at the responses of individual bottlenose dolphins to vessel approaches. In this study, opportunistic observations of the approaches of passing vessels, made from an

independent research vessel, were complemented by controlled vessel approaches, monitored from a newly-developed overhead video system. Focal-animal sampling in the context of this multi-faceted methodology made it possible to document differences in both surface and subsurface reactions to vessels by individually-identified dolphins, each of whose history, age, gender, and reproductive condition were well known. As a result, Nowacek *et al.* (2001a) were able to identify a class of individuals that were particularly at risk. This example shows that, taken together, complementary methods can be used to identify and overcome the shortcomings of solitary techniques. The attributes of this case study, and others highlighted in the present chapter, show that power and efficacy are enhanced in studies that employ a multi-pronged approach. Such research designs facilitate cross-validation of findings and restrict biases and confounding factors, thus maximising the likelihood of detecting and defining impacts, if any exist.

The Nowacek *et al.* (2001a) study also illustrates ways in which future impact assessment studies may benefit from recent developments in cetacean biology. Some useful techniques for impact assessment were developed in captive settings, including quantitative fine-scale monitoring of behaviour (*e.g.*, Samuels and Spradlin 1995), physiological measures (*e.g.*, Miksis *et al.* 2001), or preferably, concurrent behavioural and physiological measures (*e.g.*, Waples and Gales 2002). A number of recent field techniques provide ways to simultaneously monitor the behaviour and acoustics of individual animals at sea (*e.g.*, Miller and Tyack 1998; Janik *et al.* 2000; Janik 2000a,b), including underwater movements of large whales recorded from a temporary tag attachment (Johnson and Tyack 2003), sub-surface behaviour of dolphins recorded from an overhead video system (Nowacek *et al.* 2001b), and behaviour and acoustics of large whales during controlled experiments (Miller *et al.* 2000). Some new field techniques also permit measurement of physiological responses from unrestrained cetaceans at sea, including measures of cardiac activity (*e.g.*, Johnson and Tyack 2003) and body condition (*e.g.*, Moore *et al.* 2001).

The scale of the cetacean-focused tourism industry, and its continued growth worldwide, call for expansion and refinement of the ways in which potential impacts are monitored. In the present chapter, I highlight several exemplary case studies that can help to point the way for future research. I encourage colleagues to continue to build on the creative traditions within the field of cetacean biology, as well as to seek inspiration from other fields of research. I hope that the points made in this chapter will help to elevate and refine understanding of the impacts of nature-based tourism on cetaceans, and thereby, minimise any such impacts by promoting sound scientific evidence as the basis for informed management policies.

OBJECTIVES

As a result of methodological shortcomings, and the subsequent inconclusiveness of current research efforts, both the scientific community and wildlife managers have voiced their discontent with the inadequacies in the knowledge base regarding impacts of nature-based tourism on cetaceans. This introductory chapter argues that, to ensure the sustainability of the cetacean-watching industry, by minimising impacts on targeted animals, there is a pressing need for an evaluation and improvement of current methodologies and research designs to assess whale- and dolphin-watching impacts and for development of adequate measures that will identify the effects of vessel activity. By reviewing the literature pertaining to impacts of human activity on cetaceans, the objectives of the introductory chapter were to:

- illustrate key components in the planning and execution of effective impact assessment research;
- promote, by example, careful research designs for investigating impacts of tourism on free-ranging cetaceans.

From the knowledge gained through this exercise, I identified the cetacean population with optimal power for impact detection. Specifically, I used the population of cetaceans whose behaviour has been documented in greatest detail; where data are available both before and during vessel-based dolphin-watch tourism and at two tourism levels; and where there exist identifiable subsets of the population with very different levels of encounter with tour vessels. The objectives were to:

- identify short-term effects of vessel-based tourism targeting Indo-Pacific bottlenose dolphins (*Tursiops sp*) in Shark Bay, Western Australia, by conducting experimental vessel approaches to groups of dolphins within a tourism region and an adjacent control site where virtually no vessel activity occurred (Chapter 2);
- identify long-term effects of vessel-based tourism on habitat use and females reproductive success of individuals from this same population (Chapter 3).

In the context of these findings, I show that short-term findings interpreted in absence of a longitudinal perspective can be misunderstood (Chapters 2 and 3). Furthermore, I argue that imprecise usage of the terms, habituation, sensitisation and tolerance, can lead to

misinterpretation of research findings with unintended and potentially dire consequences for wildlife communities. The objectives of Chapter 4 were to:

- provide a framework for literal and standardized usage of this terminology;
- present an empirical technique for discerning among explanatory mechanisms to detect true habituation and sensitisation responses.

With respect specifically to the Shark Bay dolphin population my objectives were to:

- develop recommendations, pertaining to vessel activity specifically in Shark Bay, to minimise impacts on targeted animals that, in turn, will help ensure the sustainability of the local industry (Chapters 5).
- develop recommendations for designing impact assessment studies elsewhere where longterm data are unavailable (Chapter 2 and 3);
- develop management recommendations for cetacean tourism at locations where impact assessment is lacking and long-term data are unavailable (Chapter 2 and 3).

CHAPTER TWO

AN EXPERIMENTAL APPROACH TO STUDYING MOVEMENT- AND SOCIALITY RESPONSES OF INDO-PACIFIC BOTTLENOSE DOLPHINS (TURSIOPS SP.) TO VESSEL-BASED TOURISM

INTRODUCTION

Tourism that focuses on whales and dolphins in the wild provides members of the public worldwide with many types of opportunities to learn about, observe, swim with, or feed marine mammals. This popular form of nature-based tourism is a growing industry that, as of 1998, involved more than US\$ 1 billion and nine million people per year (Hoyt 2001). Given the character of this activity such that specific communities of animals are repeatedly sought out for prolonged, close-up encounters, there is a potential for detrimental consequences for targeted animals, in particular, for resident animals with small, coastal home ranges. In these cases, impacts, if any, are likely to be cumulative rather than catastrophic, and therefore, difficult to detect in long-lived, slowly reproducing species such as cetaceans (Duffus and Deardon 1990; Corkeron 2004) because impact assessments are typically constrained, fiscally and logistically, to focus on short-term behavioural responses (e.g., Baker and Herman 1989; Corkeron 1995; Bejder et al. 2001; Nowacek et al. 2001a; Williams et al. 2002a; Lusseau 2003a; Constantine et al. 2004; Samuels and Beider 2004). In most cases, however, the biological relevance of behavioural change in response to repeated disturbance has yet to be determined, nor is it known whether, and in what ways, short-term responses translate into long-term effects on reproduction, physical condition, distribution, and habitat use, etc, and how those changes may affect survival and population size. As one example, when male humpback whales (Megaptera novaeangliae) sing longer songs (a sexual display) during exposure to anthropogenic sound (Miller et al. 2000), it might be reasonable to assume that there may be a cost of altered sexual display to whale reproduction, but obtaining confirmatory evidence is very difficult to achieve.

Methodological shortcomings are partly to blame for difficulties in determining the significance of short-term responses to whale watch tourism (Bejder and Samuels 2003; Chapter 1). Baseline data are often unavailable or unobtainable, thereby precluding comparison of behaviour under an impact situation with behaviour prior to, or in absence of, disturbance. Spatial and temporal discontinuities between cause and effect make it difficult to tease apart which observed changes are due to human activity, and which are due to ecological factors or natural variability. Given the complexity of interactions within ecosystems, difficulties arise in pinpointing those components that contribute to observed impacts (e.g., Vaske et al. 1995; Gill et al. 2001). In addition, factors such as species (e.g., Gutzwiller et al. 1998), age (e.g., Stalmaster and Newman 1978; Constantine 2001; Müllner et al. 2004), sex (e.g., Williams et al. 2002a; Lusseau 2003a), condition (e.g., Culik and Wilson 1995; Nellemann et al. 2000; Parent and Weatherhead 2000; Beale and Monaghan 2004a), and prior experience (e.g., Burger and Gochfeld 1999) may

influence – either singly or in combination – how individual animals respond to anthropogenic activity. Studying impacts of human activity on cetaceans is further confounded by specific methodological obstacles that stem from trying to find, follow and observe the behaviour of mobile marine animals at sea. For example, it is a challenge to track, continuously and in detail, the movements and behaviour of cetaceans in the marine environment because many species are out of sight underwater for prolonged periods, range over large areas, and/or are found in groups numbering in the hundreds (e.g., Mann 1999).

Given the many factors that can influence the occurrence and form of response, and the difficulties in determining whether responses are biologically significant, it is not surprising that interpretation of findings is not entirely straightforward. As a result, both the scientific community and wildlife managers have voiced their discontent with the inadequacies in the knowledge base regarding impacts of nature-based tourism on cetaceans (IFAW, 1995:14).

It is possible, however, to overcome some of these methodological obstacles by employing a multi-faceted approach to assessing the impacts of human activity on cetaceans (Bejder and Samuels 2003, Chapter 1). Analysis of noteworthy studies identified the following research attributes as key components in effective impact assessment research: 1) using multiple types of research platform, 2) applying appropriate behavioural sampling techniques, 3) monitoring multiple response measures simultaneously, 4) supplementing opportunistic observations with controlled experiments, 5) taking advantage of historical data, when available, and 6) making use of innovative technologies (Bejder and Samuels 2003; Chapter 1).

Following this analysis (Bejder and Samuels 2003; Chapter 1), I designed a multi-faceted study to incorporate all of the above attributes into studying impacts of boat-based tourism that targets Indo-pacific bottlenose dolphins (*Tursiops sp.*) in Shark Bay, Australia. Specifically, I carried out experimental vessel approaches to groups of dolphins in two adjacent study sites where dolphins have had different histories of exposure to vessel activity. Multiple behavioural response measures were monitored from land-based observation platforms before, during and after each experimental approach. Individual dolphins involved in experiments were photographically identified and information about their age and sex was obtained from long-term records of the Shark Bay dolphin research project. Here, I present the behavioural responses of individually identified dolphins to experimental vessel approaches. These short-term responses to vessel

activity are further interpreted within the longitudinal perspective provided by long-term research on Shark Bay dolphins (Chapter 3).

METHODS

Field methods

Long-term research program and field site

The long-term nature of research on resident Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia (~ 25°45' S, 113°44' E; Fig. 2.1), provided favorable conditions for assessing effects of vessel-based tourism on targeted animals. Since 1984, approximately 800 individual dolphins have been identified and dolphin behaviour has been studied through photo-identification and focal follow techniques (e.g., Connor and Smolker 1985; Smolker et al. 1992; Connor et al. 1992; Connor et al. 1992; Connor and Smolker 1995; Connor et al. 1999; Mann et al. 2000). Based on the long-term research, individually specific demographic and behavioural information was available for the dolphins targeted in experiments. For example, for the majority of dolphins, birth-date or age class was known, and gender was determined either through direct observation of genital slits and/or mammaries, long-term association with a dependent calf, and/or genetic samples (Krützen et al. 2003, 2004a-b). In addition, for many dolphins, age at weaning or onset of reproduction was also known.

The present study was conducted in the eastern gulf of Shark Bay near Monkey Mia (Fig. 2.1a-b). Shark Bay was listed as a World Heritage Area in 1991 on the basis of its unique natural attributes (www.sharkbay.org). The bay is bisected by the Peron Peninsula, ~1800km² landmass, with the resort of Monkey Mia on the peninsula's eastern shore. Monkey Mia receives over 100,000 visitors annually, of which 69% come primarily to see dolphins (Reark Research 1995). Due to the remote location and limited infrastructure, tourist access to the eastern gulf is limited to Monkey Mia, thus there is little boating activity at distances greater than approximately 8 km from the resort.

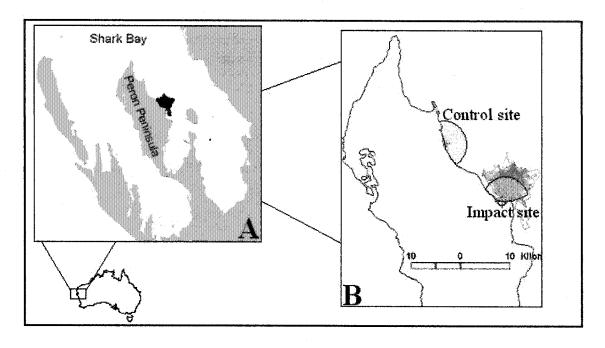


Figure 2.1. Study site. A: Shark Bay and Peron Peninsula. B: Control and impact sites - impact site defined by automatic GPS downloads during 372 tour vessel trips (black dots). Semi-circles signify the areas within which dolphin groups could be reliably tracked from the elevated land-based platforms.

Two commercial dolphin-watch tour vessels (hereon referred to as "tour vessels") have been in operation in the waters immediately adjacent to Monkey Mia since 1993 and 1998, respectively. Since the arrival of the second operator in 1998, a combined total of eight trips have been offered every day, with each operator running two tours in the morning and two in the afternoon. All tours are 2.5 hours duration with the exception of the first morning tour, which lasts for one hour. All tours target dolphins, in addition the first afternoon tour which targets dugongs as well.

Overall study design and experimental procedure

Potential effects of vessel activity on dolphins were studied in controlled experiments during the austral autumn/winter of 2000-2003 (4 field seasons, 21 months of effort). Dolphin behaviour was recorded before, during and after (BDA – see Bejder and Samuels 2003, Chapter 1) experimental vessel approaches in order to evaluate short-term, non-vocal, behavioural responses to nearby vessel activity. Data were collected at two sites: 1) "impact" site where dolphins have been targeted by vessel-based tourism since 1993; and 2) "control" site where dolphins were naïve to vessel-based tourism and seldom experienced any vessel activity. The impact site was defined as the waters in which tour vessels typically operated, as measured by automatic Global Positioning System (GPS) downloading of tracks from tour vessel trips (Fig. 2.1b). Experiments were conducted at one site at a time, and experimental procedures and data collection methods were

identical at each site. The study design provided for comparison of group-level dolphin behavioural responses to vessel activity, based on BDA experimental segments within and between control and impact sites.

Three types of data collection platforms were used: shore-based theodolite stations, tour vessels, and an independent research vessel. Theodolite tracking data and behavioural observations were recorded at each of the two shore sites, one each at the impact and control sites; GPS tracking data were recorded on each of the two tour vessels. An independent vessel, or "approach vessel", made experimental approaches to dolphin groups, during which identities of individual dolphins were documented. The approach vessel was a 4.3m aluminium runabout equipped with a 25 hp four-stroke outboard engine.

The subject of each experiment was a dolphin group. A focal "group" was considered to consist of one or more animals and spatially defined by a 50m chain rule: if individual A was within 50m of individual B and B was within 50m of C, then A and C were considered to belong to the same group regardless of the distance between A and C (modified from Smolker *et al.* 1992). At the beginning of each experiment, a focal group was selected on the basis of its proximity to the theodolite station (within ~4 km) and the absence of any vessels, tour or otherwise, within 300m. When several groups met these criteria (in 8 of 78 experiments), the focal group was selected by alternating between smallest and largest groups.

The BDA design was used to document from the shore station the movement and behaviour of the focal group during three 15-min periods: before (B), during (D) and after (A) an experimental approach. After selecting the focal group, baseline data were recorded during the 15-min B period. At the end of the B period, shore-based observers used VHF radio to direct operators of the approach vessel (waiting at >300m from the focal group) to come within 50m of the focal group. The "approach" was defined to begin when the vessel was within 50m of the nearest dolphin in the focal group. During the approach (15-min D period), the vessel maintained a distance of approximately 10-50m from the focal group, and mimicked the behaviour typical of tour vessels as described in the operators' license conditions. Specifically, tour operators are restricted to a 15-min limit to be "in contact with" (*i.e.*, within 50m of) a given dolphin group, and they are not permitted to "cut off the path of", "box-in", "herd", or "chase" dolphins, nor "restrict" the dolphins' normal behaviour group (Western Australian Wildlife Conservation Notice 1998 (Close Season for Marine Mammals); Western Australian Wildlife Conservation

Regulations 1970, Regulation 15 Marine Mammal Interaction License). The experimental approach (D period) was defined to end when the vessel moved beyond 50m of the nearest dolphin within the focal group. The approach vessel continued to move to >300m from the focal group, and the 15-min A period began when no vessels, including the approach vessel, were within 300m of the focal group. Thus, one complete experiment consisted of three data collection periods (BDA) for a minimum duration of 45 min.

To provide clearly defined BDA periods, data collected during transitions -i.e., as the approach vessel moved between 300 and 50m of the focal group - were excluded from analyses. Experiments were terminated prematurely when the identity or behaviour of a focal dolphin group could no longer be determined with certainty (e.g., poor visibility, dolphins moved out of range, etc.), or when a vessel moved to within 300m of the focal group during the B or A periods. For cases in which a focal group was observed >15min during B and/or A periods, only data collected during the 15 min leading up to and following the D period were used. Thus, analyses were based on experiments that encompassed, at the minimum, both B and D periods; 63% of experiments analyzed also included the A periods.

A pilot study was conducted in the initial field season (2000) in order to become familiar with the theodolite, to assure consistency in tracking, and to develop and refine rigorous sampling protocols. Thus, field effort in 2000 (n = 34 days, 182 hrs) was treated as a training period and the corresponding data were not included in analyses.

Data collection

i. Data collected from tour vessels: Defining impact and control sites

Movements of the two tour vessels were recorded at 75-sec intervals via automatic GPS downloading during a combined total of 372 trips in 2000, 2002 and 2003 (n=188, 84, 100, respectively, per year of study; 177 and 195 trips per commercial dolphin watch vessel, respectively). GPS tracks obtained during the 2000 pilot season served as the basis for defining the impact site by documenting the location and routes of the two tour vessels; data collected in 2002-03 confirmed that the area of tour vessel activity did not change over the study period (Fig. 2.1b).

Once the impact site was defined, a control site with similar topography characteristics was chosen approximately 17km away from the impact site, such that there was no tour vessel activity

and negligible recreational vessel activity. In addition, the distance between sites minimized the potential for overlap among individual dolphins between the two sites (see Characteristics of Study Population", in Results section).

ii. Data collected from shore stations: behaviour and movement patterns of focal dolphin groups

The shore team consisted of a theodolite operator, who recorded successive positions of targets (*i.e.*, focal dolphin group, approach vessel), and a computer operator, who downloaded positions and recorded information on dolphin group size, behaviour and group spacing. Both team members functioned as dolphin spotters and behavioural observers.

A dolphin group was observed continuously throughout each experiment using focal-group sampling (Altmann 1974). Concurrent theodolite tracking and behavioural sampling provided simultaneous information about the movement pattern, behaviour, and inter-individual spacing of the focal group throughout each BDA period of the experiment. Behaviours and sampling schemes were selected to meet the rigorous requirements for a group-level focus (Altmann 1974, Mann 1999). In addition, theodolite tracking of the approach vessel was conducted during the D period of the experiment to provide information about vessel position throughout the interaction.

a. Theodolite tracking: Response variables related to movement patterns

Positions of focal dolphin groups and approach vessels were recorded from an elevated vantage point at each site (29.33 and 29.12 m above sea level at impact and control sites, respectively) using a Leitz DT5 digital theodolite (x30 telescope). The theodolite was used to simultaneously measure horizontal and vertical angles to a target (dolphin group, vessel). Each theodolite was connected to a laptop computer that ran a data acquisition program entitled "Pythagoras" (Gailey and Ortega-Ortiz 2002). This software downloaded angles to targets (measured from a reference point of known latitude and longitude), associated each record with the exact time of acquisition, and converted readings into rectangular (x,y), latitude and longitude, coordinates for the object ("fixes"), taking into account the instrument's position and height above sea level (including tidal fluctuations). Theodolite readings for dolphin groups were always taken at the estimated center of the group. In the B and A periods when no vessels were within 300m of the focal group, fixes were taken approximately 60-second intervals. During vessel interactions (D period), fixes were taken approximately every 30 seconds, alternating between the focal group and approach vessel.

The precision of a theodolite fix is proportional to the instrument's elevation above sea level and inversely proportional to distance to the target. For example, a 10cm inaccuracy in the instrument's height-above-sea-level measurement at a 30m-elevated station will provide measurement accuracy to within 9m for targets at 2500m away; however, measurement accuracy improves to within 2m for targets at 500m (Würsig *et al.* 1991). As the sites' had nearly equal elevations, between-site differences in the precision of position calculations were assumed to be negligible.

Pythagoras software used theodolite fixes to calculate movement variables. Two consecutive theodolite fixes of a focal dolphin group defined a "leg" of movement. On average, 15 theodolite fixes of the focal group were obtained within each of the 15-min BDA periods, resulting in approximately 14 legs per period. For each experiment, four movement variables were calculated for each BDA period: average speed, standard deviation of speed, distance traveled and average change in direction (Table 2.1).

Table 2.1. Definitions of response variables calculated for each BDA period.

Response variables related to		Response variables related to	
MOVEMENT		SOCIALITY	
Average speed	Average of speeds (m/s) measured over all legs	Number of fission events	Number of times one or more animals moved to >50m of focal group
SD of speed	Standard deviation of differences in speed between consecutive legs	Number of fusion events	Number of times one or more animals moved within 50m of focal group
Distance traveled	Sum of distances (m) of all legs	Group spacing	Modal inter-individual spacing within focal group (spacing categories defined in Table 2.2)
Avg. change in direction	Average change in direction of movement between consecutive legs (0-180 degrees)	Group size	Total number of dolphins within focal group, assessed at onset of experimental period

Standard deviation (SD) of speed is a measure of the consistency in the speed of travel. For example, a low SD would indicate constancy in speed. Average change in direction is a measure of consistency in direction of travel, with a low value indicating constancy in the direction of movement.

Although the objective was to take theodolite fixes of a given target at approximately 60-sec intervals, the ability to take a fix on dolphin groups was dependent on the dolphins coming to the surface. Therefore, actual fixes were not evenly spaced in time. Moreover, fix rates varied between BDA periods within each experiment, with B and A periods typically having a lower fix rate than D periods. This created a consistent positive bias in path resolution during interactions with the approach vessel (D period), likely due to the relative ease in spotting dolphins (and hence, acquiring a fix) when the vessel was nearby. To eliminate this bias, fix rates were compared between BDA periods for each experiment to identify the period having the lowest fix rate. Based on the assumption that the focal group traveled in a straight line and at a constant speed between two consecutive fixes, the entire BDA track for that experiment was interpolated at the lowest fix rate. This resulted in interpolated fixes at evenly-spaced intervals throughout the entire experiment, allowing for comparison of movement variables between BDA conditions.

b. Systematic behavioural sampling: response variables related to sociality patterns

Specified behavioural data were recorded, and linked by time to theodolite tracking data, during shore-based follows of focal dolphin groups. Four social response variables were calculated for each BDA period: number of fission events, number of fusion events, group spacing and group size (Table 2.1). Sampling schemes (defined in Altmann 1974) included: "continuous" (*i.e.*, "alloccurrence") sampling of fission/fusion events; and "scan" sampling of inter-individual spacing at 10-min intervals. In addition, group size was estimated at the onset of each BDA period.

Fission-fusion events: All occurrences were recorded of fissions (group splits) and fusions (joins) involving the focal group. A "fission" was defined to occur when one or more members of the focal group moved beyond the 50m criterion that defined a dolphin group. Conversely, a fusion was defined to occur when non-focal dolphin(s) came within 50m of the focal group. When a fission occurred, the follow was continued by focusing on one of the two resultant subgroups, by alternately selecting the smaller and larger subgroup.

Group spacing: Inter-individual spacing within a focal group was assessed at 10-min intervals. Group spacing was evaluated on a relative scale based on modal distances between nearest neighbors within the focal group (Table 2.2).

Table 2.2. Relative scale of group spacing response variable.

Category	Modal distance of inter-individual spacing within focal dolphin group		
0	< 0.3 meters		
1	> 0.3 but < 2 meters		
2	2-5 meters		
3	5-10-meters		
4	10-50-meters		
5	group size = 1 animal, <i>i.e.</i> spacing not applicable		

iii. Data collected from the approach vessel: Individual dolphin identities

During experimental approaches (D period), observers onboard the approach vessel documented the individual identities of all dolphins in the focal group using standard photo-identification techniques (Würsig and Jefferson 1990), and recorded the timing and identities of individuals that left or joined the focal group. When fissions occurred during B or A periods, the shore team monitored movements of the splinter subgroup until observers on the approach vessel were free to approach and identify individual dolphins. Identities and background information for individual dolphins targeted in experiments were obtained by comparing dorsal fin photos with the long-term identification catalogue.

Statistical methods

For purposes of statistical analyses, it was assumed that each focal group was an independent unit. For each experiment, movement and behavioural variables compared behaviour between BDA periods and between control and impact sites. Although some individuals (18 and 11 individuals at the impact and control site, respectively) were present in more than one focal group, the composition of all focal groups varied, *i.e.*, a focal group of a given composition was not involved in more than one experiment. Thus, each focal group can reasonably be considered independent of the others, and representative of dolphins inhabiting the two study areas. Multivariate analyses (canonical variate analyses and multivariate analysis of variance tests) were used to summarise the data, identify patterns of responses, and reduce the number of hypothesis tests performed, thus minimizing the problem of multiple comparisons (Manly 1994).

RESULTS

Sample sizes for analysis

Experimental vessel approaches to focal dolphin groups were carried out at the impact site in 2001 and 2002 (68 days, 336 hrs, and 12 days, 53 hrs, respectively). Experimental approaches were conducted at the control site in 2002 (20 days, 120 hrs).

A total of 78 experiments were used to investigate differences in movement and behaviour of focal groups in comparisons among BDA periods and control vs. impact sites (Table 2.3). Experiments analyzed were those in which movement and behavioural response variables were obtained reliably through, at a minimum, the B and D periods. Exploratory analyses revealed that there was no statistical difference between experiments where information during only BD periods was obtained compared to experiments where information on BDA periods was obtained (t-test, p = 0.65). Thus, BD and BDA experiments were combined for further analyses.

Table 2.3. Sample sizes for experiments.

Experimental Periods	Site	
	Impact	Control
BD	13	16
BDA	36	13
Total	49	29
Total # B, D, A periods	49, 49, 36	29, 29, 13

Characteristics of the study population

Up to 118 dolphins were targeted in experimental approaches. The majority could be identified as individuals; however, it was not always feasible to photo-identify all individuals in the focal group when group changes occurred during the experiment. A total of 93 dolphins could be identified as individuals (*i.e.*, 41 and 52 at impact and control sites, respectively); 6-25 dolphins were not identified (4-11 and 2-14, respectively). The number of unidentified dolphins was presented as a range because it was not always possible to establish whether the same individuals had been observed more than once. Given the extensive identification catalogue for individual dolphins in Shark Bay, unidentified animals were likely to be known individuals whose identifies had not been confirmed.

Based on photo-identification of dolphins involved in experiments, a complete segregation of individuals was documented between the two experimental sites. That is, none of the individual dolphins involved in experiments at the control site was involved in experiments at the impact site, and vice versa. This finding validated the selection of control and impact sites.

Based on longitudinal records for the study population, dolphins involved in experiments could be classified by sex and as belonging to one of three age classes: "calf" (dependent on mother); "juvenile" (from weaning to reproductive maturity); and "adult" (all males >15 years old; all

females that were reproductive and/or >13 years old). This classification scheme revealed no statistical difference between control and impact sites in experimental subjects that were male vs. female (Fisher's exact test p = 0.647), or belonging to the three age categories (p = 0.462).

Group size estimates revealed no significant differences in sizes of groups that were targeted in experiments at the control vs. impact sites. Specifically, group size per BDA period did not differ between sites (p = 0.84; 0.68 and 0.84, for BDA, respectively), with average group size at control and impact sites, respectively, being: for B: 3.9 vs. 3.4; for D: 4.0 vs. 3.3; and for A: 4.5 vs. 3.4.

Thus, although there was complete segregation of individual dolphins between the control and impact sites, there were no significant differences in the age structure, sex ratio or group size between sites. By minimizing the number of plausible alternative and confounding explanatory factors, these factors enhance the probability that the documented differences in response between sites were due to differences in the history of exposure of animals to vessel activity.

Descriptive statistics for experiments

Summary statistics (mean and standard deviation) were calculated for each response variable for each BDA period at each site (Table 2.4). Summary statistics were based upon 134 and 71 BDA periods at impact and control sites, respectively (sample sizes from Table 2.3), with the exception of the response variable, group spacing. BDA periods with a group size of one dolphin were eliminated from analyses of group spacing, resulting in 99 periods at the impact site (38 B, 34 D, 27 A), and 64 at the control site (25 B, 26 D, 13 A).

Table 2.4. Summary statistics for experiments (mean and (SD)).

	IMPACT SITE		CONTROL SITE					
	В	D	A	В	D	A	Units	
Avg. speed	2.70	2.64	2.76	2.91	2.92	3.12	Km/hr	
	(0.90)	(1.0)	(1.03)	(0.88)	(0.98)	(0.91)	KIII/III	
SD of speed	1.21	1.77	1.38	1.15	1.62	1.64	Km/hr	
	(0.63)	(2.17)	(0.71)	(0.57)	(1.47)	(1.12)	KIII/III	
Distance traveled	0.68	0.70	0.71	0.67	0.74	0.80	Km	
	(0.23)	(0.30)	(0.26)	(0.26)	(0.26)	(0.26)	KIII	
Avg. change in	34.20	42.46	37.76	29.74	39.02	36.65	0-180 degrees	
direction	(19.43)	(23.32)	(19.55)	(23.70)	(22.23)	(16.69)	0-180 degrees	
No. of fission	0.41	0.45	0.25	0.10	0.69	0.31	Count of splits	
events	(0.57)	(0.58)	(0.44)	(0.31)	(0.71)	(0.59)	Count of spins	
No. of fusion	0.43	0.57	0.17	0.28	0.55	0.31	Count of joins	
events	(0.61)	(0.68)	(0.38)	(0.46)	(0.74)	(0.62)	Count of Joins	
Group spacing	1.82	1.21	1.63	2.40	1.58	1.92	Relative scale 0-5	
	(1.21)	(0.59)	(1.18)	(1.08)	(0.86)	(0.98)	(Table 2.2)	

Overall differences between sites and among experimental periods

A 2-way repeated measures multivariate analysis of variance (R-MANOVA) was carried out to investigate how the two predictor variables – site (control vs. impact; the between effect) and experimental period (BDA; the within effect) – simultaneously related to the response variables listed in Tables 2.1 and 2.4. Due to missing response variables and incomplete experiments (i.e., no "After" observations for some experiments), a mixed-model approach to the repeated measures analysis was carried out. All response variables were normally distributed within BDA periods, with the exception of numbers of fissions and fusions. A square-root transformation was used to normalize fission/fusion data.

The analysis indicated that, with both sites combined and all response variables considered, there was a significant differences between BDA periods ($F_{2,123} = 4.27$; p = 0.01), and a significant difference when the interaction BDA*site was considered ($F_{2,123} = 3.64$; p = 0.02). There was no statistically significant difference when sited between sites when considered alone ($F_{1,76} = 1.92$; p = 0.17)

Differences between experimental periods

To explore those differences in more detail, a canonical variate (CV) analysis was conducted to identify which response variables were most useful in discriminating between BDA experimental

periods. CV scores were calculated for each response variable and BDA period, with data from both sites combined.

Table 2.5. Eigenvalues and canonical loadings for first (CV1) and second (CV2) canonical variates.

	CV1	CV2
Eigenvalue	0.259	0.061
Distance traveled	0.051	1.804
Avg. speed	-0.064	-1.280
SD of speed	-0.372	-0.655
Avg. change in direction	-0.342	0.615
No. of fission events	-0.365	-0.204
No. of fusion events	-0.398	-0.628
Group spacing	0.725	-0.299

The first canonical variate (CV1) described the greatest variability between the means of all variables between the three periods. Eigenvalues indicated that the CV1 described the majority, by far, of differences, and therefore, was the best discriminator among BDA experimental periods (Table 2.5). As a result, only CV1 was subjected to further appraisal. High numeric canonical loadings indicated that the greatest influences on CV1 were group spacing, numbers of fissions and fusions, SD of speed, and average change in direction. Thus, CV1 related to "sociality" (*i.e.*, group spacing and fission/fusion events) and "movement consistency" (*i.e.*, changes in speed and direction of movement).

For both sites combined, CV1 values were generally lower during experimental approaches (D period) when compared to B or A periods (Fig. 2.2). In other words, during approaches, more fissions and fusions occurred, groups were more compact, and swimming speed and direction were more erratic. This is illustrated in Fig. 2.2, in which the majority of CV1 points to the left (*i.e.*, more negative) on the plot were taken during approaches (D period).

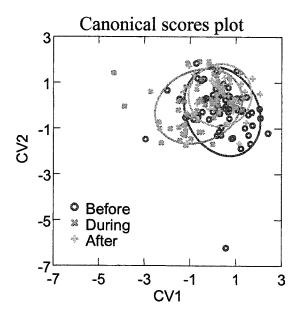


Figure 2.2. Canonical scores, for both sites combined, stratified by B, D, and A experimental conditions. Despite that only CV1 was significant, CV2 (y-axis) is included on this figure to ease the visual representation of changes in the CV1 during experimental during experimental conditions.

Changes in response variables within experiments

To evaluate possible differences in response variables within experiments, CV scores were also calculated for each experimental period for each experiment with both sites combined. In this analysis, each focal dolphin group provided its own control, thereby minimizing any environmental, temporal or site influences, and facilitating interpretation of observed responses. Note that not all experiments were comprised of all three BDA periods, nor were all response variables obtained for each period. When values were missing, the period was not included in this analysis.

Figures 2.3a-c illustrated the direction of change in CV1 and CV2 over the course of each experiment. [Again, only CV1 was significant and subject to further appraisal. CV2 was depicted on the y-axis for ease of visual representation.] Visual inspection indicated that as an experiment progressed from the B to D period, CV1 tended to shift from larger to smaller values (Fig. 2.3a), indicating that, compared with the baseline (B) period, focal groups during approaches (D period) typically engaged in more fissions and fusions, were more compact, and traveled at speeds and headings that were more erratic. CV1 tended to shift towards higher values from D to A (Fig. 2.3b), indicating that after departure of the approach vessel, focal groups were typically less compact, engaged in fewer fissions and fusions, and traveled at more constant speeds and in more

consistent directions. There was no obvious pattern when comparing B and A periods (Fig. 2.3c), indicating that, when both sites were combined in the analysis, focal groups tended to resume baseline (B period) levels of sociality and movement consistency after the experimental vessel departed (A period).

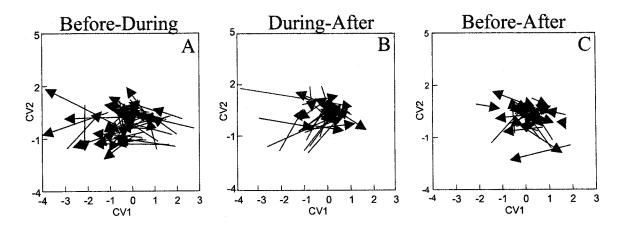
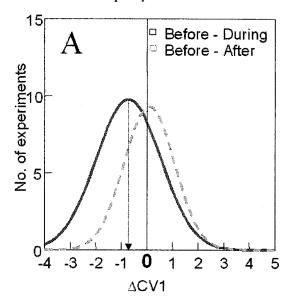


Figure 2.3. Canonical scores (CV1, CV2) representing preceding and succeeding periods (B,D, and A) within an experiment are linked. The arrowhead represents the last obtained canonical score during a given segment (B to A; D to A; B to A) within an experiment.

Differences in response variables between sites

Differences in CV1 scores (Δ CV1) were calculated for B to D, D to A, and B to A for each experiment in order to compare dolphin responses between the impact and control sites. In these calculations, negative values (*i.e.*, Δ CV1<0) represented a shift between experimental periods towards greater instability in group composition (*i.e.*, more fission and fusion events), greater group cohesion (*i.e.*, more compact group spacing), and more erratic swim speeds and headings. Smoothed frequency distributions depicting Δ CV1 for each experiment showed that the majority of B-to-D values were negative (Fig. 2.4a-b, Table 2.6), thus, during experimental approaches (D period), focal dolphin groups became more compact, engaged in more changes in group membership, and swam at more erratic speeds and headings than during the baseline (B) period.



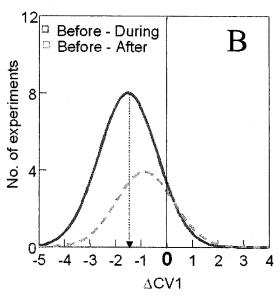


Figure 2.4. Smoothed frequency distributions depicting Δ CV1 for each experiment. Differences in CV1 values for Before to During, During to After, and Before to After conditions for each experiment at each site (A and B impact and control site, respectively). The x-axis depicts the change in the CV1 value when going from one experimental condition to the next within an experiment. The y-axis represents the frequency of experiments with a given change in CV1.

Further examination of this result showed that the effect was more prevalent at the control site. That is, a B-to-D calculation of Δ CV1 < 0 was demonstrated in 95.6% of experiments at the control site, but in only 74.2% of experiments at the impact site (Table 2.6). Thus, although focal dolphin groups did respond to experimental approaches at both sites (Fig. 2.4a-b, Table 2.6), B-to-D shifts that were characterized by Δ CV1 < 0 were more prevalent at the control site.

Table 2.6. Percentage of experiments in which Δ CV1 < 0. Sample size indicated in parentheses.

	B-to-D	D-to-A	B-to-A
Control site	95.6% (23)	23.1% (13)	81.8% (11)
Impact site	74.2% (31)	14.4% (23)	48.0% (23)

Additional inspection of B-to-D Δ CV1 calculations revealed that responses of focal dolphin groups were significantly stronger at the control site as well. This was evidenced by the lower (more negative) average Δ CV1 value for experiments at the control site (-1.53) as compared with those at the impact site (-0.70) (p = 0.022; df = 49). This result was depicted graphically by the

more negatively-shifted peak in the B-to-D curve in Fig. 2.4a (control site) when compared with Fig. 2.4b (impact site).

B-to-A Δ CV1 calculations indicated that responses to experimental approaches were also longer lasting at the control site (Fig. 2.4a-b, Table 2.6). That is, the B-to-A Δ CV1 curve for the control site peaked at <0 (Fig. 2.4a), indicating that, for dolphins at the control site, sociality and movement consistency remained altered and did not resemble pre-approach (B period) levels for up to 15 min after the approach vessel had departed (A period). In contrast, the B-to-A Δ CV1 curve for the impact site peaked at 0 (Fig. 2.4b), indicating that dolphins at the impact site did resume pre-approach (B period) levels of sociality and movement consistency during the A period.

Thus, although experimental vessel approaches elicited changes in sociality and movement consistency at both the impact and control sites, these behavioural changes were stronger, more prevalent, and longer lasting in groups at the control site where dolphins were naïve to vessel activity.

DISCUSSION

Experimental vessel approaches elicited significant changes in the behaviour of targeted groups of bottlenose dolphins, in comparison with their behaviour before and after approaches. Behavioural change was based on response variables related to group sociality and consistency of movement. With respect to sociality, focal groups during approaches were more compact and had higher rates of change in group membership. With respect to movement consistency, focal groups during approaches had more erratic speeds and directions of travel. These responses were documented at both the control (virtually no vessel activity) and impact (regular tour vessel activity) sites. However, responses of dolphin groups at the control site were more dramatic than those at the impact site: specifically, responses of control site dolphins were stronger, more prevalent, and longer lasting than those at the impact site. In addition, dolphin groups at the control site did not resume pre-approach levels of behaviour during the 15-min period after the experimental vessel departed, whereas, groups at the impact site did.

Variability in response to disturbance has been linked to various characteristics of targeted dolphins (e.g., sex: Williams et al. 2002a; Lusseau 2003a; age: Constantine 2001; group size:

Constantine *et al.* 2004). This did not appear to be the case in the present study. I found no statistically significant differences in the sex ratio, age structure, or group size of dolphins between sites; therefore, site-specific differences in behavioural response were more likely due to differences in exposure to vessel activity by dolphins residing in each area.

Effects of vessel activity on sociality: group cohesion and stability of membership

Dolphins at both sites formed more compact groups in response to experimental vessel approaches. Increased group cohesion has been documented as a response to human disturbance by terrestrial mammals (e.g., mountain goats, *Oreamnos americanus*: Foster and Rahs 1983; pronghorns, *Antilocapra Americana*: Berger et al. 1983), and as a response to predation threats by schooling fish (e.g., Pitcher and Parrish 1993). Similarly, for cetaceans, increased group cohesion has been documented in the presence of vessels (e.g., Au and Perryman 1982; Blane and Jaakson 1994; Denardo 1998; Bejder et al. 1999; Nowacek et al. 2001a), and in contexts of presumed surprise, threat or danger (e.g., Whitehead and Glass 1985; Norris et al. 1994). For cetaceans, increased cohesion has been suggested as a mechanism to enhance rapid response to danger, perhaps by improving the ability of group members to track each other's movements (e.g., Johnson and Norris 1986; Norris and Schilt 1988).

Dolphin groups at both sites had heightened rates of fission and fusion in response to experimental vessel approaches. Similar instability of group membership in response to human disturbance has been reported for terrestrial mammals (e.g., mountain goats: Foster and Rahs 1983, Côté 1996; Sulawesi black macaques, *Macaca nigra*: Kinnaird and O'Brian 1996). For some terrestrial and avian species, human disturbance has resulted in separation of mothers from their young and increased predation on unprotected offspring (e.g., Dall sheep, *Ovis dalli dalli:* Nette et al. 1984; Eider ducks, *Somateria millissima:* Keller 1991; mountain goats: Côté and Beaudoin 1997; numerous species of water birds: Carney and Syderman 1999).

Effects of human disturbance on group membership have not been previously described for a cetacean species. Disruption of grouping behaviour by vessel activity, no matter how short term, may have far-reaching repercussions for socially complex species like bottlenose dolphins that exhibit long-term, individually-specific bonds (e.g., Smolker et al. 1992; Connor et al. 1992, 1999; Owen et al. 2002). For example, Lusseau and Newman (2004) recently showed the vulnerability of a population of bottlenose dolphins in Doubtful Sound, New Zealand, to removal of key individuals. Even though coastal bottlenose dolphins are characterized as having a fission-

fusion society (Wells et al. 1987; Smolker et al. 1992), intensification of the rate of change in group membership may diminish the ability of individuals to rely upon long-term social networks. Social interdependence may be especially important in reducing vulnerability to shark predation, which has been proposed as a primary determinant in the evolution of cetacean grouping behaviour (e.g., Norris and Dohl 1980; Wells et al. 1980; Norris et al. 1994). Although random aggregations of individuals can effectively carry out such anti-predator tactics as detection and confusion (e.g., Krebs and Davies 1993), an actively cooperative defense may depend on coordination among individuals with established social ties (e.g., Mann and Barnett 1999). Thus, for Shark Bay dolphins - whose risk of predation by sharks is exceptionally high (Heithaus 2001) - frequent group fissions in response to vessels may relegate dolphins to smaller subgroups and/or split up mutually reliant associates, inducing a concomitant escalation to their predation risk.

Habituation versus Tolerance

Although dolphins responded significantly to experimental vessel approaches at both sites, behavioural responses at the control site were stronger, more prevalent, and longer lasting. Can the more moderate responses at the impact site be attributed to the dolphins' habituation to regular human activity in a region where boat-based tourism is prevalent? Not necessarily.

Behavioural habituation is defined as a reduction in response over time as an individual learns that there are neither adverse nor beneficial consequences to occurrence of the stimulus (Thorpe 1963). Despite this definition of habituation as a process, the term has come into colloquial usage to categorize moderation in wildlife response to human disturbance, and thus, has often been applied inaccurately to any instance of moderated response (Nisbet 2000). In many such cases, however, the moderate responses described were increased tolerance levels rather than habituation (Nisbet 2000). In contrast to habituation, tolerance is defined as "the intensity of disturbance that an individual... tolerates without responding in a defined way" (Nisbet 2000:315). A tolerance level can be measured instantaneously and is more readily demonstrated than the longer term process of habituation (Chapter 4). Therefore, confirmation that habituation has occurred would necessarily require longitudinal, sequential measurements of responses of individuals to controlled stimuli (Nisbet 2000), a rigorous assessment technique that has rarely been employed (but see, e.g., Tutin and Fernandez 1991; Johns 1996). Because habituation may evoke a beneficial connotation for some wildlife professionals, incorrect usage can lead to flawed conservation plans and unintended consequences for wildlife (Chapter 4).

With respect to the present study, without having measured the gradual waning of responses of individual dolphins over time, the finding that dolphin groups at the impact site responded more moderately does not, in and of itself, document that those animals were habituated to vessel approaches. Instead, results indicated that, at the time of the study, dolphins residing within the impact site had *higher tolerance* levels to vessel activity than did dolphins at the control site.

The distinction between habituation and tolerance is important because there are various ways in which differences in tolerance levels can arise, several of which resemble habituation responses. Specifically, in Chapter 4 I present four explanatory mechanisms for habituation-like responses: learning, physiology, selection and ecology. Of these, only learning results in true behavioural habituation, with its potentially neutral or beneficial outcomes for wildlife. Other mechanisms are likely to have detrimental consequences. For example, reduced responsiveness to a given stimulus may be documented in cases in which: repeated or prolonged exposure results in physiological impairment (physiological mechanism); animals respond to an ecological factor other than the given stimulus (ecological mechanism); or the more responsive individuals have already been removed (selection mechanism), e.g., through death, spatial displacement, or decreased reproductive success (e.g., Griffiths and van Schaik 1993; Lott and McCoy 1995; Fowler 1999; Nellemann et al. 2000).

In the present study, documented differences in tolerance levels provide a snapshot of the responses of dolphins residing in two adjacent regions at one point in time. These findings, in and of themselves, do not allow us to distinguish between alternative explanatory mechanisms that include both behavioural habituation and selection.

Enhanced interpretation within a longitudinal perspective

The long-term nature of research in Shark Bay, with monitoring of individually known dolphins over many years, provided a context within which I was better able to interpret these short-term behavioural responses. In the longer term study, by comparing the numbers of individual dolphins per km² over three successive four and a half-year periods as vessel-based tourism increased, I documented a significant reduction in the number of individuals within the impact site and a simultaneous but not statistically significant increase within an adjacent control site (Chapter 3). Moreover, I demonstrated that, since the advent of vessel-based dolphin tourism, the reproductive success of individual females in Shark Bay was significantly negatively correlated with exposure to vessel activity (Chapter 3). Taken in the context of these longer term findings, one can now

choose between the alternative explanations proposed above for the short-term behavioural responses. Specifically, documentation of spatial displacement and reduced reproductive success in association with increased vessel activity suggests that the observed moderation in short-term response to vessel disturbance by dolphins at the impact site was not the result of habituation to vessel activity, but was more likely the result of selection producing an absence of sensitive individuals. Thus, in this case, documentation of a moderated response to disturbance likely resulted, at least partially, from a biased sample in which one subset of the study population had already departed and/or was omitted from the assessment (see also: Griffiths and van Schaik 1993; Fowler 1999).

Conclusions and management implications

Dolphins at both sites responded to experimental vessel approaches, both in terms of movement patterns and aspects of group sociality. Despite the importance of social factors for some species, social relations have rarely been considered in studying impacts of anthropogenic disturbance (but see, e.g., pygmy marmosets, *Cebuella pygmaea*: de la Torre 2000; Cuban rock iguanas, *Cyclura nubile*: Lacy and Martins 2003). I suggest that repeated disruption of social networks, however brief, may contribute to social instability, inadequate maternal care and increased predation. Thus, I propose that social factors be integral to assessing impacts of anthropogenic activity on socially complex species of wildlife.

Although dolphins at the control site responded more strongly, it is striking that resident dolphins at the impact site still showed significant signs of behavioural change in response to vessel activity, despite having been the focus of 10 and 20+ years of vessel-based tourism and research, respectively. Taken out of context, the more moderate responses at the impact site could be misconstrued to mean that those dolphins had become habituated to vessel activity. I was fortunate to be able to call upon an extensive, long-term database for individual dolphins in Shark Bay, and thereby, interpret the short-term responses within a longitudinal perspective (Chapter 3), and to determine that moderation in response at the impact site was not an indication that vessel activity there has had no impact.

In few other cases, however, are there comparable long-term data sets that permit short-term responses of cetaceans to tourism to be evaluated over broad time scales (but see Constantine 2001). This is cause for concern on several counts. First, cetacean watch tourism is a growth industry, operating in 492 communities worldwide by 1998 (Hoyt 2001). In addition, cetaceans in

many locales are subjected to tourist pressures that are many-fold greater than that found in Shark Bay (e.g., killer whales in British Columbia, Canada: Williams et al. 2002a; Foote et al. 2004; bottlenose dolphins in Bay of Islands and Fjordland, New Zealand: Constantine et al. 2004; Lusseau 2004a; bottlenose dolphins in Port Stephens, Australia: Allen 2001; spinner dolphins in Hawaii, USA: Forest 2001). Moreover, it has been demonstrated that decades of investigation are needed to detect impacts at the population level for long-lived, slowly reproducing species like cetaceans (Wilson et al. 1999; Thompson et al. 2000), or to link short-term behavioural responses to long-term processes (this study). Unfortunately, logistical and fiscal constraints typically limit studies of cetacean watch tourism to brief, onetime assessments, which provide only partial answers to the questions of how these activities may affect targeted cetaceans. For the sake of the vast majority of targeted cetacean populations for which there are no longitudinal or before/after data sets, it is important to think ahead about how best to monitor and manage these situations.

Findings of the present study took on greater significance in light of the extensive background data acquired over 20+ years of research effort in Shark Bay. Although it would be desirable to have high levels of research effort at all sites where cetacean tourism occurs, this is an unrealistic expectation. As a proxy for continuous, longitudinal monitoring at sites where this is not feasible, I recommend the development of long range strategic plans, one feature of which would be focused impact assessments of brief duration carried out at specified intervals over a span of tens of years. Repeated assessments of short duration conducted over such an extended period will provide much of the information needed to compare response measures between time periods, detect changes over time, and thereby, provide site-specific information about both the short- and long-term consequences of cetacean tourism.

Moreover, I suggest that management of the cetacean tourism industry rely heavily on findings and recommendations from the best-studied populations where long-term information is available. Studies from those sites can also be used to guide the formulation of the long range strategic monitoring plans and aid in the design of focused impact assessments. A strategic mixture of short, well-focused studies, in combination with some long-term studies at the best-supported sites, seems a prudent way forward in monitoring and managing the cetacean tourism industry.

A cautious approach is particularly important in managing endangered species targeted by cetacean watching operations, e.g., northern right whale (Eubalaena glacialis) and the vaquita (Phocoena sinus). Based on the short- and long-term effects reported here, a precautionary

approach based on extrapolations from this study naturally leads to the question posed by Corkeron (2004:849): "Maybe it is time ... to the question of where whale [and dolphin] watching should not occur".

The difficulty in detecting the population-level effects of human activity on cetaceans has led to a re-evaluation of research focus. Specifically, a recent consensus among scientists resulted in the following recommendation to the Scientific Committee of the International Whaling Commission: "[p]reventing disruption of critical life-history processes at the level of the individual is one way to prevent population-level impacts of whale-watching on cetaceans from ... occurring", therefore, "managers concerned with impact on the level of the populations should be encouraged to minimize impact on individual cetaceans" (IWC 2004:1). A study by Samuels and Bejder (1998, 2004) exemplified how a focus on individuals can enhance rapid detection of detrimental effects of human interaction on local dolphins, thereby facilitating the formulation of timely and relevant recommendations to managers. The value of identifying and monitoring individuals through time was also instrumental to the success of this study, and hence a focus at the level of the individual is conducive to both short- and long term impact assessments.

In summary, in light of the urgent need for sound scientific bases to minimize potential impacts of the ever-growing cetacean tourism industry, a precautionary, adaptive management approach would be prudent. Adaptive management eschews the one-final-solution strategy, and instead, enables managers to move forward in the face of uncertainty, multiple variables, and/or incomplete information about cause-and-effect relationships (e.g., Holling 1978; Walters 1986). Thus, given the continued growth of cetacean watch tourism industry worldwide and the overall scarcity of long-term or population-level perspectives, I urge managers to 1) err on the side of caution when managing a local cetacean watch industry; 2) extrapolate wisely from findings of the few studies in which short-term responses can be translated into biologically-significant processes; 3) design long range strategic monitoring plans that feature repeated, short-term assessments over time; 4) value and support continuous long-term monitoring where it is ongoing, and encourage and support the initiation of strategically-selected long-term monitoring programs elsewhere; 5) encourage and support impact assessment studies that the focus at level of individual; and 6) implement long-term adaptive management monitoring schemes, where results of repeated impact assessments be used to continuously inform and fine-tune management of the industry.

CHAPTER THREE

CUMULATIVE EFFECTS OF LONG-TERM EXPOSURE TO VESSEL ACTIVITY ON BOTTLENOSE

DOLPHIN HABITAT USE AND FEMALE REPRODUCTIVE SUCCESS

INTRODUCTION

The ultimate goal of scientific inquiry into effects of anthropogenic activity on wildlife is to provide mitigation from any negative impacts. In this regard, investigators endeavour to measure wildlife response and reveal those activities that are detrimental to wildlife so to provide practical information that will inform the development of management guidelines specific to the circumstances. However, while the need for regulations that prohibit or mitigate animal injury or death is obvious, a complex and unresolved problem in wildlife management is detecting whether non-lethal, apparently benign human activities, *e.g.*, urban development, recreation (*e.g.*, camping, snowmobiling, hiking, diving) and nature-based tourism activities that specifically targeted wildlife to bring humans into close contact with wild animals, have cumulative effects that are harmful to wildlife populations.

In addition to numerous methodological obstacles to identifying impacts of human activity on wildlife (for review see Bejder and Samuels 2003; Chapter 1), impact assessments are often constrained temporally, financially and logistically. Therefore, they typically focus on short-term behavioural responses that are more readily obtainable than long-term impact measures. However, attempts to regulate human activities based on disruption of wildlife behaviour face difficulties in defining the threshold of harm, *i.e.*, little is known about whether and when short-term responses translate into long-term biologically significant impacts on, for example, reproduction, physical condition, distribution and/or habitat use.

Furthermore, the interpretation of traditional behavioural indices as indicators of disturbance has recently come under fire (e.g., Nisbet 2000; Gill et al. 2001; Beale and Monaghan 2004a,b). For example, animals that remove themselves from disturbance are not necessarily the ones that have been most affected by disturbance, e.g., the animals that leave in the face of disturbance may be those that have sufficient body condition to expend additional energy (e.g., Stillman and Goss-Custard 2002; Beale and Monaghan 2004a); or in another scenario, when disturbance is concentrated in critical habitat, animals may have no other option but to stay (e.g., Creel et al. 2002; Dyck and Baydack 2004).

Fortunately, impact assessment studies have recently begun to incorporate a theoretical framework for predicting and understanding behavioural outcomes of human disturbance (e.g., Gill et al. 1996, 2001; Gill and Sutherland 2000; Frid and Dill 2002; Stillman and Goss-Custard 2002; Beale and Monaghan 2004b). The framework is based on evolutionary theory pertaining to

decision-making under the risk of predation, and is applied to make predictions regarding responses of wildlife to non-lethal forms of human disturbance. By placing wildlife disturbance research within this theoretical context, interpretation of the responses of wildlife to human disturbance is more likely to be based on biologically significant evidence, thereby serving as the basis for better-informed management policies. A further promising development in disturbance research are studies that aim to quantify the energetic costs incurred through short-term behavioural responses and/or use behavioural information to model the long-term effects thereof (e.g., Regel and Putz 1997; Bradshaw et al. 1998; White et al. 1999; West et al. 2002; Lusseau 2004a,b; Bain et al., in review).

While recent developments within the disturbance literature are showing promising venues for interpretation of short-term responses, ultimately, however, these frameworks and models rely heavily on assumptions and simplifications, and in the end, only provide *predictions* of outcomes of anthropogenic disturbances on important measures of population health, *e.g.*, reproduction, survival and habitat use.

Better yet would be to have direct, long-term information on the very measures that models try to predict and to be able to compare these measures to varying levels of disturbance across control and impact sites and to before and after the onset of disturbance.

With this in mind, the Indo-pacific bottlenose dolphin (*Tursiops sp.*) population in Shark Bay, Australia, was identified as a system where possible cumulative, long-term effects of an apparent benign human activity (vessel activity) could be tested on two fundamental measures of dolphin population health. Specifically, due to the long-term nature of the Shark Bay dolphin research project (>20 years) individually specific demographic, reproductive and habitat use information were available for dolphins from a time period before the onset and during the development of vessel-based dolphin-watching tourism in the bay. Using long-term records for individual bottlenose dolphins, I evaluated habitat use and female reproductive success in relation to an increase in the activity of vessels targeting dolphins over a 14-year period. The results presented here have implications in fields as diverse as population biology, wildlife management, education, research ethics and the ecological effects of human activities on wildlife.

METHODS

Overall study design

To evaluate potential long-term effects of research- and tour vessel activity on dolphins, two fundamental measures of population status (habitat use and female reproductive success) were examined in relation to individual dolphins' exposure to vessel activity.

Long-term habitat use by individual dolphins relative to the degree of vessel activity was investigated through a treatment/control experimental-design approach. This entailed defining control and impact (*i.e.*, treatment) sites within a larger study area, and comparing habitat use during three periods of varying tourism intensity (zero vs. one vs. two vessel-based dolphin-watch operators). Potential effects of vessel exposure on female reproductive success were investigated by a correlation-type approach, in which the reproductive success of females was correlated with their cumulative exposure to research and tour vessels, respectively. Thus, different measures of vessel exposure were used to investigate possible effects of vessel activity on dolphin habitat use and female reproductive success.

Field methods

Field site: female reproductive success

Shark Bay is on the west coast of Australia (~ 25°45'S, 113°44'E; Figure 3.1) and is inhabited by a population of approx. 2700 resident Indo-Pacific bottlenose dolphins (*Tursiops* sp.) (Preen *et al.* 1997). The marine habitat consists of shallow sea-grass beds (<4 m depth) that are surrounded by embayment plains (5-13 m depth) and deeper channels (<14m depth). The bay is bisected by Peron Peninsula, dividing it into an Eastern and Western gulf. Since 1984, on-going long-term dolphin behavioural research has been conducted by a number of research teams throughout the Eastern gulf, encompassing an area of 300km² off Monkey Mia Resort (Figure 3.1a). Females residing in these waters were used in the investigation of potential effects of cumulative vessel exposure on female reproductive success.

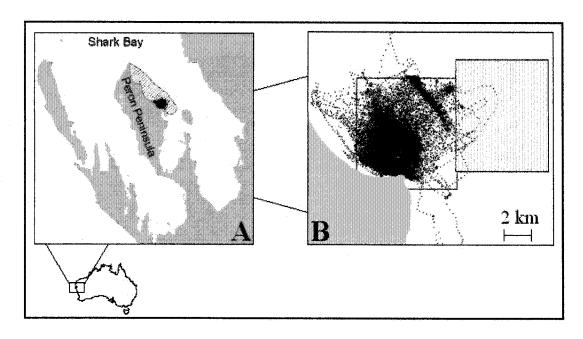


Figure 3.1. Study site. A: Shark Bay and Peron Peninsula. Encircled area depicts the ~300km2 site of long-term dolphin research. Dolphin sightings within this larger area were used in the analysis of female reproductive success in relation to cumulative vessel exposure. B: 36km^2 impact site as defined by automatic GPS downloads during 372 tour vessel trips (black dots). Grey square: an adjacent control site of equal size. These two 36km^2 sites were used in the comparison of dolphin habitat use between time periods T0, T1 and T2.

Field site: defining 'control' and 'impact' sites for habitat use analysis

Comparisons of habitat use across three successive ~4.5-year time periods of varying intensities of vessel activity were made within two sub-sections ('control'- and 'impact' site) of the 300km² long-term study area described above. Two commercial dolphin-watch tour vessels (17 and 19m sailing catamarans equipped with twin turbo140hp engines and twin 50hp engines, respectively; herein referred to as 'tour vessels') have been in operation in the waters immediately off Monkey Mia since May 1993 and August 1998, respectively. The waters in which tour vessels operated defined the 36km² impact site, as measured by automatic Global Positioning System (GPS) downloading of tracks from tour vessel trips (Figure 3.1a,b). Specifically, positions of the two tour vessels were recorded at 75-sec intervals via automatic GPS downloading during a combined total of 372 trips in 2000, 2002 and 2003 (n=188, 84, 100, respectively; 177 and 195 trips per vessel). A control site of equal size adjacent to the impact site containing a substantial number of dolphin sighting records from research vessel surveys was selected to allow for a comparison of dolphin habitat use within an area of similar biological and physical characteristics but low vessel traffic (Figure 3.1b).

Study population and long-term dolphin research

Long-term dolphin behavioural research has identified approximately 800 individual dolphins in the Eastern Gulf through photo-identification and vessel-based focal follow techniques (e.g., Connor and Smolker 1985; Smolker et al. 1992; Connor et al. 1992; Connor and Smolker 1995; Connor et al. 1999; Mann et al. 2000; Figure 3.1a). Based on the long-term database, individually specific demographic (age and sex: e.g., Mann et al. 2000; Krützen et al. 2003, 2004a,b) and habitat use information were available for the dolphins from the time period before and after the onset of vessel-based dolphin-watching tourism in the bay. Furthermore, the long-term database of sighting records provided information on the reproductive success of individual female dolphins since the onset of the dolphin research program in Shark Bay in 1984.

Sighting records:

The data used to analyze individual dolphin habitat use and female reproductive success were based on dolphin group composition data collected from sighting surveys as a part of the longitudinal field study. Since 1988, all dolphin research teams, irrespective of their research goal, have collected information on dolphin group encounters following a standardized sighting survey protocol. Primary goals of the sighting surveys have been to individually identify all animals in encountered groups and document their locations.

Surveys have been conducted from small (4–6 m) outboard-powered boats (6-50 hp). During each survey, standard photo-identification techniques (Würsig and Jefferson 1990) were used to determine group composition. Photograph records were taken of every unknown individual and were compared to an existing catalogue, which now contains over 800 known animals. Animals that were still unidentified after several attempts at identification from the catalogue were labeled as 'unknown'.

A group sighting survey was conducted each time dolphins were sighted and was initiated when the research vessel was close enough to the animals that recognition or photographic-identification was possible. An individual was considered part of a group using a 10-meter 'chain rule' as in Smolker *et al.* (1992): a) if it was within 10m of any other member within the first five minutes of the survey and b) if individual A was within 10m of individual B and B was within 10m of C, then A and C were considered to belong to the same group regardless of the distance between A and C. Sighting survey durations varied from a minimum of five minutes up to over an hour.

Determining sighting location from bearings to known landmarks:

In Shark Bay, dolphin researchers started using GPS in June 1994. When groups of dolphins had been encountered prior to the implementation of the GPS, compass bearings from the group location towards prominent landmarks were obtained. The latitude and longitude of the landmarks were later determined using GPS. It was then possible to convert the location of group encounters containing three or more compass bearings to known land features to latitude and longitude positions using 'Locate II' software [http://www.nsac.ns.ca/envsci/staff/vnams/Locate.htm].

An independent error assessment using 32 positions for which both GPS and compass bearings were taken simultaneously was carried out to calculate the mean difference in distance between the two locations obtained via the two different methods. This analysis showed a discrepancy of, on average, 260m (s.d. = 239m) between the locations documented via the two methods. The GPS locations of dolphin groups were recorded using the WGS84 datum and had a random error of up to 200 m due to selective availability purposely applied by the U.S. government through May 2000. Thus, the precision of the conversions from bearings to latitude and longitude were accurate enough to incorporate the group sighting records obtained prior to the implementation of GPS into analyses.

History of vessel-based tourism

Since the 1960's, several dolphins have frequented the shallow waters off the fishing camp of Monkey Mia to receive fish handouts from humans in knee-deep water (Connor and Smolker 1985). Today, this phenomenon remains the area's main tourist draw card attracting over 100,000 visitors annually, of which 69% come primarily to see dolphins (Reark Research 1995). Currently, four adult females are provisioned on a daily basis under strict ranger supervision. In response to growing demands to experience wild-feeding dolphins away from the provisioning area, one commercial dolphin-watch tour vessel has been in operation since May 1993, and in August 1998, the Western Australian Department of Conservation and Land Management made a second license available (Table 3.1). Since the arrival of the second operator, a combined total of eight trips have been offered almost every day of the year, with each operator running two tours in the morning and two in the afternoon. All tours are 2.5 hours duration with the exception of the first morning tour, which lasts for one hour. In addition to targeting dolphins, the first afternoon tour also targets dugongs.

Methods of analyses

Habitat use

Experimental design:

The temporal pattern in which commercial dolphin-watch licenses were issued guided the design of the investigation of dolphin habitat use within and between control and impact sites. Specifically, this allowed for comparison of individual dolphin habitat use within and between sites during three consecutive ~4.5 year periods in which dolphins were followed by research vessels and no dolphin-watch tour vessels (T0), one tour vessel (T1), and two tour vessels (T2), respectively (Table 3.1). By choosing adjacent impact and control sites, it is unlikely that differences in changes in dolphin habitat use between sites and time periods are attributable to environmental factors (e.g., changes in prey or predator abundances) since the effects of such would probably influence both adjacent sites similarly.

Table 3.1. Time periods as dictated by the number of operating commercial dolphin-watch tour vessels.

	Tourism intensity level				
	TO	T1	T2		
	March 1988-	May 1993-	August 1998-		
Time period	April 1993	July 1998	January 2003		
Number of commercial tour operators	0	1	2		
Number of commercial tours offered/day	0	4	8		
Research vessel activity	Yes	Yes	Yes		

Exposure to all vessel types may influence dolphin habitat use, hence both tour- and research vessel activity in the two sites were quantified (total time spent within 50m of dolphins) and summarized according to sites and the three periods (T0, T1, and T2), and subsequently used as a proxy to evaluate their relative contribution to habitat use.

For research vessels, the amount of time spent with dolphins in the two sites in each time period (T0, T1, T2) was directly calculated from the sighting survey records, together with information on the location and duration of focal follows conducted by each research team throughout the long-term research program.

The amount of time tour vessels spent with dolphins in the two sites in each time period was estimated based on extrapolations made from observations obtained in 2000 during the 188 monitored tour vessel trips. During these trips, information on the number, duration and location of dolphin group encounters, *i.e.*, time spent with dolphins, were recorded.

An 'encounter' was defined as when a tour-vessel approached within 50m of the closest dolphin in a group for more than one minute and ended when the vessel moved beyond 50m of the nearest dolphin within the focal group. Situations in which a vessel by-passed a dolphin group without stopping were not considered to be encounters. When more than one group was within 50m of a vessel and the groups were more than 10m apart, one encounter was recorded. The 50m criterion was chosen to define an encounter based on specifications described in the commercial operators' license conditions. Specifically, tour operators are restricted to a 15min limit to be 'in contact with' (*i.e.*, within 50m of) a given dolphin group (Western Australian Wildlife Conservation Notice 1998 (Close Season for Marine Mammals); Western Australian Wildlife Conservation Regulations 1970, Regulation 15 Marine Mammal Interaction License).

Analysis

For the purpose of this analysis, each of the impact and control sites was sub-divided into 36 1km x 1km grid squares. The total number of sighting records and the total number of individually identified dolphins observed in each grid square was calculated for each time period. Therefore, 'habitat use' by an individual dolphin was based upon whether the animal had been observed within a given 1km² grid square in a given time period (T0, T1, and T2).

This analysis explored dolphin habitat use within the impact and control sites between the three times periods (T0 vs. T1 vs. T2), using all group sightings that were recorded within these two sites between March 1988 and January 2003 (n=6008).

A nonlinear logistic model (Eq. 1 and 2) that related the total number of identified individuals within each of the grid squares in each time period to the number of surveys conducted in the square in that time period was fitted to the data. This model included a term for changes in abundance (p) per grid square between time periods. The model was fitted using least squares estimates and parameter estimate confidence intervals were estimated by bootstrapping on grid squares (1000 times).

$$y(j,1) = s(j) * q * x(j,1) / (1+q * x(j,1))$$
 (Eq. 1 and 2)
$$y(j,2) = s(j) * q * x(j,2) * (1+p) / (1+q * x(j,2))$$

where the dependent variable y(j,t) = number of dolphins observed using square j in period t; x(j,t) = number of surveys in square j during time period t.

The model estimated the following parameters:s(j) = number of dolphins using square j in the first period;

p = proportional change in number of dolphins using each square between 1st and 2nd time period (assumed the same for all squares within either the control or impact sites); and

q = a parameter indicating the rate of increase of number of dolphins detected in a square with the number of surveys (assumed the same for all squares and both time periods);

s(i), q and p were estimated by least squares and maximum likelihood.

Female reproductive success:

Potential effects of exposure to vessel activity on female reproductive success were evaluated based on the long-term sighting records of individually identified, sexually mature, adult female dolphins and the extent of their exposure to vessel activity. The analysis that explored the correlation between cumulative vessel exposure and female reproductive success investigated whether there was a relationship between a females' reproductive success and the extent of her exposure to vessels since the onset of tourism, *i.e.*, whether the more vessel-exposed females are more or less successful at reproducing than the less vessel-exposed females.

From the onset of tourism (May 1993) through June 2004, 84 sexually mature adult females residing within the 300km^2 study area (Figure 3.1a) were identified for whom calf survival was known and ≥ 4 years of reproductive data were available. I excluded the food-provisioned females that fulfilled these criteria from further analyses because of the pervasive effects that provisioning has on behaviour and offspring survival (e.g., Mann et al. 2000; Samuels and Bejder 2004). Female reproductive success (as defined below) was calculated from information extracted from >11,000 dolphin group sighting records collected from May 1993 through June 2004, i.e., the last year of this study.

Defining reproductive success:

Female reproductive success was defined as a rate, *i.e.*, the number of offspring surviving to age 3 years divided by the number of years of reproductive data available for that female. The definition of 'successful reproduction' was based on information from the long-term research in Shark Bay. Specifically, of 210 births documented in the study area from 1982-2000 for which survival and weaning status is known, no calves still nursing beyond age three years died while still dependent or nursing. Before age three, 44% died pre-weaning (Mann *et al.* 2000). Only years for which offspring survival status was known were included (including years in which the female had no dependent offspring, but was over 12 years of age).

If a female was of known age, her 'reproductive years' started when she turned 12 years (earliest age of first reproduction documented in Shark Bay (Mann *et al.* 2000)). Otherwise, it started at the time of her first known birth. Year of calf birth was used, not the pregnancy year, as the starting point for those cases for which reproductive years started during or after May 1993 (*i.e.*, onset of T1). If the female still had a calf under age 2 years in June 2004, then her reproductive years stopped in the year that calf was born because it was unknown whether the calf made it to year 3. If a female still had a dependent calf in May 1993 (onset of T1), then her reproductive years began to count in the year the calf was weaned. For example, if a female gave birth to a calf in 1990, but the calf was not weaned until 1994, the female's reproductive years started in 1994 and ended in 2004.

Analysis:

This analysis investigated the correlation between cumulative research vessel exposure and cumulative tour vessel exposure since the onset of tourism and individual female reproductive success. The analysis did not compare the reproductive success of females residing purely in the defined impact site to those residing purely in the defined control site (female home ranges exceed the boundaries of these sites), nor did it compare reproductive success between the three periods defined in the habitat use analysis (T0, T1 and T2). Rather, this analysis investigated the correlation between cumulative research vessel exposure and cumulative tour vessel exposure since the onset of tourism and individual female reproductive success.

Cumulative exposure index (CEI)

To evaluate possible long-term impacts of vessel exposure on individual female reproductive success, a 'cumulative exposure index' was calculated for tour vessels (CEI_{TV}) and research vessels (CEI_{RV}) for each female. These indices are measures of the proportion of time a given female was sighted in a given 1km² square throughout the entire 300km² study area in relation to the proportion of time tour-and research vessels, respectively, spent in that same 1km².

Specifically, a CEI_{RV} was calculated for each female as the proportion of records in which the female was sighted in a given 1km^2 square multiplied by the proportion of all research sighting surveys carried out since the onset of vessel-based tourism (May 1993) within that square, summed over all squares.

A CEI_{TV} was calculated for each female as the proportion of sighting records of the female in which she was sighted in a given 1km² square multiplied by the proportion of GPS positions of tour vessels within that square, summed over all squares. For this analysis, it was assumed that the movements of the two tour vessels, as recorded by automatic GPS downloading during 372 trips in 2000, 2002-03 (also used to define impact site), were representative of tour vessel movements since the advent of vessel-based tourism since May 1993. The movement tracks obtained in 2000, 2002 and 2003 confirmed that the area of tour vessel activity did not change over this period. Furthermore, tour operators confirmed that their area of use had not changed through time.

Hence, for each female, measures of her reproductive success and cumulative exposure to tourand research vessels were available. Correlation analyses were carried out between each female's reproductive success and her CEI_{TV} and CEI_{RV} , respectively. Square-root transformations were used to normalize both CEI_{TV} and CEI_{RV} . Note: the two measures of cumulative exposure to tourand research vessels (CEI_{TV} and CEI_{RV}) are not directly comparable as they were based on different units (GPS positions of tour vessels recorded at 75-sec intervals and dolphin sighting surveys, respectively).

RESULTS

Sample sizes for analyses

Dolphin group composition was obtained from all 6008 sighting records collected during the three time periods in the two sites (control site: n=978; impact site: n=5030). In total, 21240 individual

dolphin identities (including recounts) were documented in the two sites combined. The proportion of dolphins sighted that were identified ranged from 90.4%-94.6% and 71.4%-76.3% in the impact and control sites, respectively (Table 3.2). There was no statistical difference in dolphin identification rates within sites between time periods (Chi-square p = 0.14 for control site and p = 0.11 for impact site). Similar identification rates within sites suggest that potential differences in the number of dolphins between time periods within sites are not artifacts of changes in identification rates.

Table 3.2. Research effort number of dolphins encountered and identification rates.

Time period	Tourism	Research coverage	Number of dolphins (incl. recounts)		Identification	
	Intensity	(% of months			rate	
		with research effort)			(%)	
			Impact	Control	Impact	Control
March 1988 - April 1993	Т0	76	2714	42	90.4	71.4
May 1993 - July 1998	T1	62	6261	1548	90.7	73.2
August 1998 – January 2003	T2	70	8863	1812	94.6	76.3

Throughout the 300km² study area, 84 females fulfilled the criteria for inclusion in the study of reproductive success in relation to cumulative vessel exposure.

Changes in habitat use

Comparing periods of no-tourism (T0) and one-operator (T1) within the impact site, there was no statistically significant difference in numbers of individual dolphins per square kilometer, although the power to detect change was low. As the number of tour operators increased to two (T2) and research vessel activity increased, there was a significant average decline of 14.9% (95% CI = -20.8 to -8.23) in the number of dolphins using any 1km^2 . This equates to displacement of approximately one in every seven individuals from the impact site. Concurrently, there was a non-significant average increase of 8.5% (95% CI = -4.0 to +16.7) in the number of dolphins using any 1km^2 within the adjacent control site (Figure 3.2).

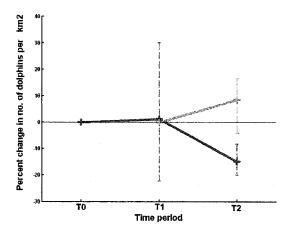


Figure 3.2. Average percent change in number of individual dolphins using each 1km² within impact (red line) and control (green line) sites between time periods. Vertical lines depict 95% confidence intervals.

Impacts on female reproductive success

For this analysis, reproductive rate was used as a measure of reproductive success (expressed as the number of offspring surviving to age three years a given female had divided by the number of reproductive years for that female). Female reproductive rate ranged from 0 to 0.333 surviving calves/year (mean = 0.137; s.d. = 0.098) (Figure 3.3).

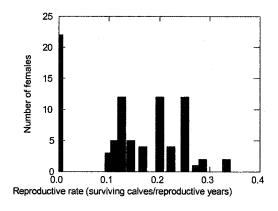


Figure 3.3. Frequency distribution depicting the reproductive rate of the 84 females that satisfied the criteria of this analysis.

Female reproductive rate was significantly negatively correlated with both CEI_{TV} and CEI_{RV} (r = -0.277; P = 0.01 and r = -0.253; P = 0.02, respectively) (Figures 3.4ab). Furthermore, the average reproductive rate of the 42 females with greater than median tour- and research vessel CEIs were 26.1% and 29.2% lower, respectively, than that of females with lower than median tourism- and research vessel CEIs (0.116 vs. 0.157 surviving calves/year and 0.114 vs. 0.161 surviving calves/year, respectively). Of the 22 females that had a zero reproductive rate (Figure 3.3), 17 and 16 had higher than median CEI_{TV} and CEI_{RV} , respectively.

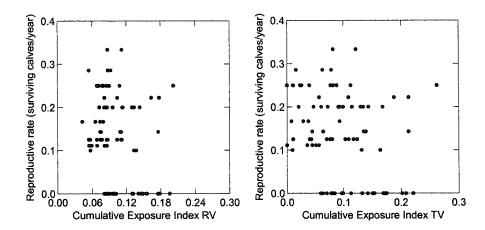


Figure 3.4. Plots depicting the correlation between each of the 84 females' reproductive rate and her cumulative exposure to tour- and research vessels (expressed as CEI). The two figures are not directly comparable as CEIs for the two vessel types had different units. Note: methodologically, it was not possible for a given female to have a value of $CEI_{RV} = 0$ because known individuals are first identified by research vessels. Note: two females had $CEI_{TV} = 0$, which means that they were never seen in the waters in which tours vessels operate between May 1993 – June 2004.

The CEIs for tour- and research vessels were highly correlated (r = 0.95; P<0.0005; Figure 3.5), and hence, the females that had greatest cumulative exposure to tour vessels also had the greatest cumulative exposure to research vessels (and the same applies for the females with low cumulative exposure).

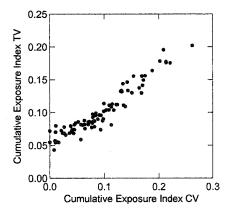


Figure 3.5. Plot of the correlation between each female's tour- and research vessel CEIs.

Inspection of Figure 3.4 suggests that there was no relationship between the reproductive success of the females that reproduced successfully and their cumulative vessel exposure, *i.e.*, if a female reproduced successfully, her reproductive rate was not affected by vessel exposure. In fact, when the females with zero reproductive rates were excluded from correlation analyses, there was no correlation between reproductive rate and CEIs (r = 0.036; P = 1.00 and r = 0.092; P = 1.00, for r = 0.092; P =

CEI_{TV} and CEI_{RV} respectively). Thus, the significant negative correlation between cumulative vessel exposure and female reproductive rate was attributable to the individuals that have a non-zero reproductive rate (Figures 3.4ab). To highlight this effect, the 84 females included in the analysis were ranked based on their cumulative exposure indices and were subsequently categorized into CEI quartiles, *i.e.*, four groups of 21 individuals – with Quartile 1 consisting of the 21 females with lowest cumulative exposure indices and Quartile 4 consisting of those with the highest cumulative exposure indices. The proportion of individuals that reproduced successfully, *i.e.*, those with a non-zero reproductive rate, was calculated for each quartile (Figure 3.6). One hundred percent (n=21) of the females in the first quartile (least cumulative vessel exposure) reproduced successfully, while only 47.6% (10 of 21) of the females in the fourth quartile (highest cumulative vessel exposure) reproduced successfully. Ten of the eleven females (90.9%) in Quartile 4 that did not reproduce successfully did give birth to calves, however, none of them survived to year 3. On average, these ten females gave birth to 1.6 calves (SD = 0.84) during the time period of investigation.

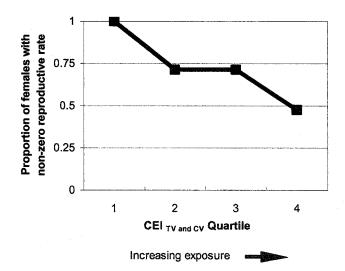


Figure 3.6. Proportion of females in CEI Quartiles that had non-zero reproductive rates (n=21 females per quartile). Quartile 1 consists of the 21 females with lowest cumulative exposure indices while Quartile 4 consists of those with the highest cumulative exposure indices. The composition of the quartiles, whether they were based on CEI_{TV} or CEI_{RV} rankings, was the same because the females that had greatest cumulative exposure to tour vessels also had the greatest cumulative exposure to research vessels.

To investigate possible sampling biases, a further analysis (Figure 3.7) was carried out to try to identify the mechanism causing the documented negative correlation between female reproductive success and cumulative vessel exposure. Specifically, no change in the proportion of a females' sighting records within the impact site between the two time periods would suggest that the

amount of time she spent in this area did not change between T1 and T2. Therefore, the proportion of an individual females' sightings that were recorded within the impact site in T1 was plotted against that in T2 for 67 of the 84 females (who were sighted five or more times during each of T1 and T2).

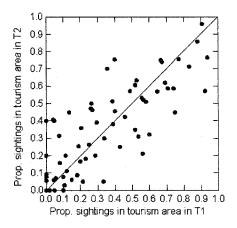


Figure 3.7. The correlation between the proportion of all sighting records of each female (n=67) that was recorded within the impact site between T1 and T2. The diagonal represents the 1:1 ratio line on which points would be expected to fall if females spent an equivalent amount of time within 36km² impact site between T1 and T2.

There was a highly significant correlation between the proportions of each females' sightings recorded within the impact site between the two time periods (r = 0.803; P < 0.0000). This indicates that the observed negative correlations between individual female reproductive rate and cumulative vessel exposure were not due to a segregation of better fit- or more experienced females away from the impact site, *i.e.*, a sampling bias. Rather, this suggests that the negative correlation is caused by a reduced ability of the females with greater cumulative exposure to successfully produce or raise offspring compared to the females with lower cumulative vessel exposure. Furthermore, this result suggests that the displacement of individuals from the impact site between T1 and T2 were not adult females.

Time spent with dolphins by tour- and research vessels

A total of 349 encounters between tour vessels and dolphin groups were observed during the 188 trips in which information on encounter duration and location were recorded. The average number of encounters per trip was 1.86 (s.d. = 1.07) dolphin groups with an average duration of 10 min 38 sec (s.d.= 7 min 20 sec). On average, 2.5 (of 4 possible) and 5.5 (of 8 possible) trips were carried out daily during T1 and T2, respectively (D. Charles, Acting Parks and Visitor Services coordinator, pers. comm.).

Based on these numbers, the daily and total amount of time tour vessels spent with dolphins (<50m) in the impact site was extrapolated based on the assumption that dolphin encounter rates and durations were constant through periods T1 and T2 (one and two tour operators, respectively). Specifically, tour vessels spent 0, 1558 and 2937 hours or 0, 0.82 and 1.81 hours/day with dolphins during T0, T1 and T2, respectively (Figure 3.8). Research vessels spent 1018, 792 and 1255 hours or 0.54, 0.41 and 0.77 hours/day with dolphins during T0, T1 and T2, respectively (Figure 3.8).

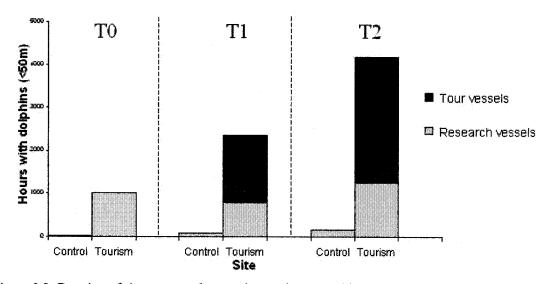


Figure 3.8. Duration of time tour- and research vessels spent within <50m of dolphins in the impact and control sites in T0, T1 and T2. Tour vessel values are based on extrapolations; research vessel values are based on direct measures.

At the control site, tour vessels were not observed within 50m of dolphins during the three time periods. In comparison, research vessels spent 11, 75 and 161 hours with dolphins during T0, T1 and T2, respectively (Figure 3.8).

As researchers spend little time in the impact site when not observing dolphins (pers. obs.), these measures are good approximations of the total time they spent within this site irrespective of whether they are within 50m of dolphins. In comparison, tour vessels spent 4.4 and 9.6 hrs/day during T1 and T2, respectively, in the impact site (estimates based on average trip duration and average number of trips per day), *i.e.*, an order of magnitude more than that of research vessels.

The total amount of time research vessels spent with dolphins in the impact site decreased by 22% between T0 and T1, and increased 1.58 fold between T1 and T2. In comparison, tour vessels spent 1.89 times more time with dolphins between T1 and T2 in the impact site. And overall, in the impact site from T1 and T2, there was a 1.78 fold increase in time spent with dolphins, of which 74.9% could be attributed to tour vessels (Figure 3.8).

DISCUSSION

Effects of vessel activity on long-term habitat use – should I stay or should I go?

There were ~15% fewer individual dolphins per square kilometer in the impact site after the number of tour vessels increased from one to two and as research vessel activity increased. This is equivalent to a decline of approximately one out of every seven individuals. There was a concomitant average increase of 8% more individual dolphins per square kilometer in the adjacent control site. Though this was not statistically significant, it does suggest a permanent shift in dolphin habitat use from areas of high to low vessel traffic. It is unlikely that the documented decline is attributable to environmental factors or an overall population decline, since the effects of such would probably influence both adjacent sites similarly.

Avoidance occurs on a continuum of temporal and spatial scales. For example, both immediate, short-term horizontal (Bejder et al. 1999, Chapter 2; Nowacek et al. 2001a, 2004; Williams et al. 2002a,b; Lusseau 2003a) and vertical (Nowacek 2001a; Lusseau 2003a; Janik and Thompson 1996; Williams et al. 2002a,b) avoidance responses have been documented for delphinids exposed to vessel activity. In these cases, animals typically remain in the area of disturbance, while allocating time and energy avoiding physical and/or acoustic disturbance factors. Spatial displacement and area avoidance has also been documented where marine mammals avoid areas in times of heavy vessel traffic (e.g., Trites et al. 1995; Allen and Read 2000; Lusseau 2003b, 2004a), animals typically re-inhabiting these areas during periods of less vessel traffic. Lastly, long-term displacement and site abandonment has also been documented for which all/or a subset of animals permanently avoided once-preferred areas where disturbance is on-going (e.g., Gerrodette and Gilmartin 1990).

When disturbed, individuals must evaluate the costs and benefits of relocating to a less disturbed location – a decision influenced by the quality of the area currently being occupied, distance, quality and availability of alternative sites, relative predation risk, nutritional condition, and density of competitors and mates (Frid and Dill 2002; Gill *et al.* 2001; Beale and Monaghan

2004a,b). This is analogous to decision making under the risk of predation, *i.e.*, an animal's decision of whether to relocate in response to predation risk is influenced by the availability, distance and quality of suitable habitat elsewhere (Lima and Dill 1990; Frid and Dill 2002; Beale and Monaghan 2004b). In situations in which animals switch from short-term behavioural avoidance tactics to long-term area avoidance in response to increasing disturbance, the cost of remaining and tolerating disturbances has likely exceeded the benefits of remaining in the previously preferred habitat. These results suggest that some individuals' tolerance levels were exceeded with the introduction of the second tour vessel resulting in permanent displacement of 15% of individuals away from the impact site.

Irrespective of the explanatory mechanism behind the decreased usage of the impact site by individual dolphins in response to increasing vessel activity, it raises concerns for the long-term sustainability of the dolphin-watching industry at this site.

Displacement and sociality

The consequence of displacement on energy budgets, survival and reproductive success is currently unknown. Nevertheless, it is likely that permanent habitat shifts in response to disturbance will have significant consequences, especially for social animals. Disruption of social bonds through displacement of individuals based on a continuum of levels of tolerance may have far-reaching repercussions for socially complex species like bottlenose dolphins that exhibit longterm, individually-specific bonds (e.g., Smolker et al. 1992; Connor et al. 1992, 1999; Owen et al. 2002). For example, Lusseau and Newman (2004) showed the vulnerability of a population of bottlenose dolphins in Doubtful Sound, New Zealand, to removal of key individuals. Specifically, two dolphin sub-communities (20 and 42 individuals, respectively) affiliated by a few common individuals, fissioned as a result of the disappearance of a key member. Her reappearance 13 months later (Lusseau et al., pers. comm.), seemingly was related to the two communities once again spending more time with one another. Furthermore, Silk et al., (2003) recently showed that the quality of social bonds between wild female baboons (Papio cynocephalus) is positively associated with offspring survival. Unintentional changes to social bonds brought about by a segregation of individuals due to vessel disturbance may diminish the ability of individuals to rely upon long-term social networks with unknown long-term repercussions.

Effects of cumulative vessel exposure on female reproductive success

Female bottlenose dolphin reproductive success was significantly negatively correlated with cumulative exposure to both tour- and research vessels. This study represents the first documented evidence of negative effects of long-term disturbance on cetacean reproductive success.

Many factors, such as age (e.g., Stalmaster and Newman 1978; Constantine 2001; Müllner et al. 2004), sex (e.g., Williams et al. 2002a; Lusseau 2003a), reproductive condition (e.g., Culik and Wilson 1995; Nellemann et al. 2000; Parent and Weatherhead 2000) and prior experience (e.g., Burger and Gochfeld 1999), may influence either singly or in combination, how individual animals respond to anthropogenic activity. Therefore, possible explanatory mechanisms behind the observed effect of cumulative vessel exposure on reproductive success could include segregation between females based on fitness, experience and/ or differing tolerance levels. That is, the animals displaced from the impact site between periods T1 and T2 (one and two tour operators, respectively) could have been the more fit females who had sufficient body condition, greater tolerance and/or experience to distinguish habitat conditions. In turn, this would cause a segregation of more fit females leaving the less fit females behind and thereby causing the latter to acquire disproportionately higher cumulative vessel exposures. However, analyses suggest that the documented detrimental impact of cumulative vessel exposure was not because of a segregation of better fit- or more experienced females away from the impact site.

A more likely explanation for the documented effect of cumulative vessel exposure on female reproductive success is the reduced ability of females to successfully produce or raise offspring when exposed to disturbance over the long-term. Reproductive success of the females of greater exposure could have been reduced by a variety of mechanisms, either singly or in combination, e.g., lower conception rate, inability to complete pregnancy, decreased calf survival via malnutrition or increased disease susceptibility, or decreased calf survival via increased predation. The females with highest cumulative vessel exposures are giving birth to calves, but the majority of these calves are not surviving to weaning. This suggests that the explanatory mechanism behind the negative correlation between vessel exposure and reproductive success is decreased calf survival via malnutrition, increased disease susceptibility or increased predation.

In the impact site, dolphin groups had heightened rates of fission and fusion in response to experimental vessel approaches (Chapter 2). This automatically entails the segregation of dolphin groups into smaller sub-groups with a concomitant increase in predation risk. For some terrestrial

and avian species, human disturbance has resulted in separation of mothers from their young and increased predation on unprotected offspring (e.g., Dall sheep, *Ovis dalli dalli*: Nette et al. 1984; Eider ducks, *Somateria millissima*: Keller 1991; mountain goats: Côté and Beaudoin 1997; numerous species of water birds: Carney and Syderman 1999).

The risk of predation to bottlenose dolphins in Shark Bay is evident from body scars caused by sharks (Heithaus 2001). In fact, the frequency of scars is higher in this population than reported in any other dolphin population. Here, 74.2% of non-calf dolphins bear evidence of mainly tiger shark predation attempts and the estimated unsuccessful attack rate is at least 11-13% of dolphins in the study area attacked per year (Heithaus 2001). Thus, for Shark Bay dolphins whose risk of predation by sharks is exceptionally high, frequent and forced separation of calves from their mothers in response to vessel disturbance, may cause increased predation rates, with a concomitant decrease in female reproductive success.

The explanatory mechanism behind the significant negative correlation between cumulative vessel exposure and female reproductive success is unknown, but similarly to decreased use of the impact site by individual dolphins in response to increasing vessel activity, it raises concerns for the long-term sustainability of the dolphin-watching industry at this site.

Relative contribution of tour- and research vessels

In addition to focusing attention on the potential effects of tourist vessels on targeted cetaceans, this study draws attention to another dilemma, *i.e.*, the research that documented detrimental effects necessarily increased the animals' exposure to vessels. There are several reasons to justify intervention with wildlife for proper management and conservation of study subjects, but this study highlights the need to carefully weigh the relative contributions of research activity on documented detrimental effects on individual cetaceans.

Besides the physical presence of vessels, it is also important to consider the potential effects of acoustic stimuli produced by vessels on dolphins given that cetaceans rely so heavily on acoustic vocalisations for communication and orientation, and for detecting conspecifics, predators and prey (e.g., Richardson et al. 1995; Tyack 1998). Engine noise from vessels can overlap with frequencies used by cetaceans, and lead to masking of their vocalisations or a modification of vocal behaviour (e.g., Myberg 1990; van Parijs and Corkeron 2001, Erbe 2002; Buckstaff 2004;

Foote et al. 2004). Therefore, acoustic disturbance is likely to be a significant contributor towards the documented decline in habitat use in the impact area during T2.

Acoustically, research vessels are less intrusive than tour vessels because of their smaller and quieter engines (6-50hp, 4-stroke engines) compared to that of tour vessels (twin turbo 140hp and twin 50hp engines, respectively). Although the two tour vessels are sailing catamarans, they change motor activity (in and out of gear), on average, every 21sec when within 50m of dolphins (Bejder 2000) – an activity that produces excess noise. This is despite the fact that tour operators in Shark Bay work under permit regulations that state the 'licensee shall approach a dolphin by manoeuvring their vessel so as to be able to drift downwind from a distance of 100 meters, and their vessel's engines are not placed into drive or engaged until 100 meters beyond the closest dolphin'.

The decline in habitat use in the impact site occurred as exposure to both tour- and research vessels increased. However, as tour vessels spent an order of magnitude more time in the impact site and 2.4-fold more time within 50m of dolphins (1.81 vs. 0.77 hrs/day) within this site during the time of habitat use decline, than did research vessels, coupled with their larger physical size (17 and 19m compared to 4-5m, respectively) and louder engines, it is reasonable to assume that tour vessel impact is substantially more significant.

The relative contribution from cumulative tour- and research vessel exposure towards decreased female reproductive success could not statistically be teased apart, because tour- and research cumulative exposure indices were highly correlated. The reason for this is that both vessel types depart and arrive from the same location. This, coupled with small home-range sizes of adult females in Shark Bay (Watson-Capps *et al.*, in prep) causes both vessel types to encounter the females residing in the waters close to the launch site disproportionately more often then females animals residing further afield.

However, because female reproductive success was significantly negatively correlated with cumulative vessel exposure coupled with the fact that the females that tour vessels spent most time with were also the females that research vessels spent most time, means that the females with lowest reproductive success were the ones residing predominately in the impact site. Thus, because tour vessels are physically and acoustically more intrusive and spend substantially more

time in the impact site, tour vessel impact is likely to be more significant towards documented detrimental effects on female reproductive success.

Management implications

A devil's advocate might argue an often-used phrase: 'correlation does not prove causation', and maintain that this study does not prove a cause-and-effect relationship. While it is correct that statistical correlation does not definitively prove causation, this study does provide strong evidence that both dolphin habitat use and female reproductive success are significantly negatively influenced by vessel exposure, and that commercial dolphin watch vessels are likely the biggest contributors towards this effect in Shark Bay. Considering the conservational, ethical and economical stakes involved, preventive measures to mitigate detrimental effects are essential based on the present findings.

Local implications

The Department of Conservation and Land Management (CALM) is entrusted to manage lands and waters in Western Australia. The Shark Bay Marine Reserves Management Plan 1996-2006 (CALM 1996), developed by CALM and approved by the Australian Ministers of the Environment, Fisheries and Mines, states that the principal goals for CALM in the management of Shark Bay Marine Park include to: a) conserve ecological values; b) facilitate recreation and tourism in a manner compatible with conservation and other goals; c) ensure that commercial uses are managed in a manner that minimizes impacts on its values; and d). seek and provide an up-to-date and sound scientific basis for the Department's conservation and management activities.

Of particular interest in regards to the present study are the strategies outlined to meet the management objectives specifically in regards to wildlife interaction, bottlenose dolphins, tourism and recreation (CALM 1996). The strategies include: to license commercial operations where they are compatible with the management plans; to license acceptable commercial operations involved with wildlife interaction and determine appropriate conditions; to monitor visitor numbers and control, if necessary, to preserve the quality of the interaction experience and to protect the dolphins; and to monitor pubic visitation and impacts on wildlife events and take action where adverse impacts are occurring.

Low-impact of dolphin watch operations in Shark Bay on target animals is vital, not only from dolphin welfare-, conservation- and management perspectives, but also given the importance of dolphin-tourism towards the regional economy of Shark Bay (CALM 1993). Although declines within the impact site may not end in jeopardizing the large, genetically-diverse Shark Bay dolphin population (Krützen *et al.* 2004b), current trends are likely unsustainable for the long-term continuation of the local dolphin-watch industry, and are clearly not compatible with local management objectives. Given the documented effects, coupled with the conservation and management objectives of the local wildlife governing body, immediate management intervention is well-justified.

Given the apparent small contribution of research vessel activity towards documented effects, coupled the inevitability of research vessel exposure to study animals to identify potential problems regarding dolphin welfare, which is turn, allows for management that is informed by sound scientific evidence, there is no evident need to decrease the exposure of dolphins to research vessel activity. However, it is recommended that research activity should be monitored and controlled if it increases substantially (e.g., see Clutton-Brock 2003).

Given the likely significant contribution of tour vessel activity towards documented effects and considering management strategies outlined by CALM to meet their conservation objectives, the results of this research support the option of decreasing the exposure of dolphins to tour vessels. A range of management options are available to reduce the current level of exposure of individual dolphins to tour vessels. These include: to reduce the number of licensed operators or to maintain the current number of licensed operators but reduce the time they spend with dolphins within the impact site. In theory, the latter can be accomplished by creating zones of exclusion, reducing the daily number of allowable trips and/or reducing the allowable time with dolphins per encounter. A feasibility analysis will be needed to examine whether or not these options are viable both financially and practically.

Global implications:

If the findings at this site of low-level tourism be extrapolated to the many high-level tourism sites around the world (e.g., killer whales in British Columbia, Canada: Williams et al. 2002a; Foote et al. 2004; bottlenose dolphins in Bay of Islands and Fjordland, New Zealand: Constantine et al. 2004, Lusseau 2004a; bottlenose dolphins in Port Stephens, Australia: Allen 2001; spinner dolphins in Hawaii, USA: Forest 2001) one is forced to conclude that cetacean watch tourism may

not be as low-impact as previously presumed. And given the scale of the cetacean-focused tourism industry and its continued proliferation worldwide (Hoyt 2001), coupled with the dearth of available long-term studies evaluating impacts of cetacean tourism, it is imperative that in management considerations strong inference be drawn from the best-studied populations, such as this one, where long-term information is available (Chapter 2).

CHAPTER FOUR

AN ETHOLOGICAL FRAMEWORK FOR DEFINING HABITUATION, SENSITISATION AND TOLERANCE
TO ANTHROPOGENIC STIMULI

ABSTRACT

An important goal of scientific inquiry into effects of anthropogenic activity on wildlife is to provide a sound foundation for wildlife conservation and management efforts. This objective, however, is often jeopardized by misinterpretation of the very science that professes to safeguard wildlife. In particular, imprecise or lax use of the terms, habituation, sensitisation and tolerance can lead to misinterpretation of research findings with unintended and potentially dire consequences for wildlife communities. The most noticeable example is colloquial use of the term behavioural habituation, to refer to any form of moderation in wildlife response to human disturbance. Because habituation is widely assumed to be a positive outcome for wildlife, such a misclassification can lead to inappropriate management decisions including an easing of conservation efforts. Clear definitions of terms, and rigorous methods for distinguishing among them are provided, thereby demonstrating that most cases of presumed habituation or sensitisation actually represent differences in the tolerance levels of wildlife to anthropogenic activity. This distinction is important because there are various mechanisms by which different tolerance levels can arise and by which habituation- and sensitisation-type responses can be explained. By characterizing explanatory mechanisms as learning, physiology, selection or ecology, it is shown that only one mechanism will result in true behavioural habituation (or sensitisation), while others will have detrimental outcomes for targeted animals. A framework is provided for literal and standardized use of terminology, and an empirical technique for discerning among explanatory mechanisms to detect true habituation and sensitisation responses is offered.

INTRODUCTION: Interpreting wildlife response to human disturbance: the importance of semantics

The ultimate goal of scientific inquiry into effects of anthropogenic activity on wildlife is to provide mitigation from any negative impacts. To this end, investigators endeavour to measure wildlife response and reveal those activities that are threatening to wildlife; to make clear the links between cause and effect and between short-term response and long-term biological significance; and ultimately, to provide practical information that will inform the development of management guidelines specific to the circumstances. But, with regard to wildlife and human activity, the field of impact assessment is a science in the early stages, and accomplishment of these objectives has often been jeopardized by misapplication and misinterpretation of the very science that professes to safeguard wildlife. In reference to wildlife tourism targeting marine mammals, Gales (1999) raised an issue that is pivotal to this problem, stating, "...the demand and growth of this industry has significantly outstripped the ability of scientists to develop and implement sufficiently sensitive tools that might provide some sound basis for management decisions". Here, this sentiment is built upon to point out that, in impact assessment research and wildlife management, not only are refinements in methodology needed (e.g., Bejder and Samuels, 2003; Chapter 1), but an important facet of open channels of communication is careful attention to the translation of research findings into management guidelines. In particular, I caution that imprecise or lax use of terminology can lead to misinterpretation of findings, with unintended and potentially dire consequences for wildlife communities.

These are issues of significant concern for scientists and wildlife managers alike, because the rate at which people and wildlife come into close contact, and the consequent potential for conflict, are on the rise. Spatial overlap between people and wild animals has increased through encroachment of wildlife habitats as a result of urban development and expansion of industry, settlements and infrastructure, as well as direct consumption of natural resources. In addition, human intrusion into wildlife habitat has been promoted by leisure activities, such as camping, snowmobiling, mountain biking, hiking, and diving, that take place in proximity to, but are not focused on, wildlife. Further activities have specifically targeted wildlife to deliberately bring humans into close contact with wild animals. For example, tourism in the form of wildlife viewing and/or wildlife interaction (e.g., feeding, touching), often involves sustained, repeated, close-up encounters with wild animals.

In response to the expansion and intrusion of human activity into natural areas, a number of investigations have been undertaken to try to evaluate what the potential impacts might be. A range of animal attributes has been suggested to influence, either singly or in combination, the responsiveness of animals to human activity. These factors include: species (e.g., Gutzwiller et al., 1998), age (e.g., Stalmaster and Newman 1978; Constantine 2001), sex (Williams et al. 2002a; Lusseau 2003a) reproductive condition (e.g., Culik and Wilson 1995; Nellemann et al. 2000; Parent and Weatherhead 2000), nutritional condition (e.g., Doenier et al. 1997; Beale and Monaghan 2004a) and prior experience (e.g., Burger and Gochfeld 1999) (for an overview see: Samuels et al. 2003). In addition, wildlife response to human activity has been documented to take many forms, expressed via changes in: home range size and habitat use (e.g., Altmann and Muruthi 1988; McLellan and Shackleton 1989; Albert and Bowyer 1991; Chapter 3), foraging behaviour (e.g., Galicia and Baldassarre 1997; Gander and Ingold 1997), reproductive success (e.g., Safina and Burger 1983; Giese 1996; Müllner et al. 2004; Chapter 3), body condition and disease susceptibility (e.g., Altmann et al. 1993; Phillips-Conroy et al. 1993; Nizeyi et al. 1999, Woodford et al. 2002; Müllner et al. 2004), sex ratio (e.g., Clout et al. 2002), daily activity period (e.g., Griffiths and van Schaik 1993), social development (e.g., de la Torre 2000), and mating system and social structure (e.g., Lacy and Martins 2003).

Apparent "habituation" is another often-claimed response of wildlife to human activity – an outcome that is sometimes actively sought by humans (e.g, Nisbet 2000). For example, in field studies of animal behaviour, habituation of wildlife to human presence may be desirable when researchers want to study behaviour that is relatively unaffected by their own presence (e.g., Goodall 1986; Tutin and Fernandez 1991; Johns 1996). A common theme in studies of habituation is a stimulus-specific response that weakens after exposure to repeated stimuli in the study subject (but see later for working definition).

The premise to strive for wildlife habituation is based on the general perception that it indicates that the activities have no or little effect on the animal itself – in contrast to the impacts listed above. However, there is considerable disagreement as to whether or not habituation compromises the well being of wildlife (e.g., McLellan and Shackleton 1989; Spradlin et al. 1998, 2001; Nisbet 2000; Stone and Yoshinaga 2002; Woodford et al. 2002). Here, I make no judgement as to the pros and cons of wildlife habituation, and its counterpart - sensitisation - to human activity, but rather, discuss the unfortunate trend in the mis-identification of wildlife habituation and sensitisation to anthropogenic stimuli in impact studies.

Specifically, in the literature pertaining to effects of anthropogenic activity on wildlife – habituation, sensitisation and tolerance – have come into colloquial use, resulting in applications that are variously loose, inappropriate, and even, interchangeable. This trend is unfortunate because there are management implications of imprecise terminology, in particular, a potential for misinterpretation of the impacts of human activity on wildlife.

Misuse of the term, habituation, is perhaps the most noticeable example because behavioural habituation is widely considered to be a positive outcome for wildlife. Wrongful application of this label with its positive connotations can mislead wildlife managers to conclude that a given human activity had neutral, or even benign, consequences for wildlife, when, in fact, the impacts were negative. With harmful effects going unrecognised, management plans might erroneously call for no corrective action, an easing of conservation efforts, or worse, an increase in human activity. Inappropriate use of the term, habituation, can, therefore, seriously undermine management plans and may even counteract conservation goals.

Thus, the goal of this paper is to highlight the potentially damaging effects of imprecise language to the formulation of wildlife management plans, and to propose a framework for the literal and standardized use of terminology for categories of behavioural response to human disturbance within the fields of wildlife management and conservation.

Categories of behavioural response: defining habituation, sensitisation and tolerance

Habituation, and its counterpart, sensitisation, are adaptive behavioural modifications exhibited by animals in response to exposure to human activity that is repetitious or continuous. As these are processes occurring over time, the terms, habituation and sensitisation, do not refer to specific behavioural responses. Behavioural habituation is "the relative persistent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement" (Thorpe, 1963:61) (Table 4.1). Habituation is, therefore, a process involving a reduction in response over time as individuals learn that there are neither adverse nor beneficial consequences to occurrence of the stimulus. Conversely, sensitisation is "[i]ncreased behavioural responsiveness over time when animals learn that a repeated or ongoing stimulus has significant consequences for the animal" (Richardson *et al.*, 1995:543) (Table 4.1). These processes are based on learning and the cumulative experience of individual animals, which will include the number and outcome of

exposures to anthropogenic stimuli over the course of each animal's lifetime (Knight and Temple, 1995).

Table 4.1. Working definitions for categories of behavioural response and requirements for their demonstration.

Term	Definition	Time course of response	Requisites to demonstrate response
Habituation Sensitisation	"the relative persistent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement" (Thorpe 1963:61) "[i]ncreased behavioural responsiveness over time when animals learn that a repeated or ongoing stimulus has significant consequences for the animal" (Richardson et al. 1995:543)	Longitudinal Process	Sequential measures taken from same individuals over time
Tolerance	"the intensity of disturbance that an individualtolerates without responding in a defined way" (Nisbet 2000:315)	State	Instantaneous measurement

Despite formal definition of habituation and sensitisation as processes, the term, habituation, has come into colloquial use to categorize moderation in wildlife response to human disturbance. In many such cases, however, the moderate responses described were not habituation, but instead, increases in tolerance levels (Nisbet 2000). Tolerance is defined as "the intensity of disturbance that an individual....tolerates without responding in a defined way" (Nisbet 2000:315) (Table 4.1). Tolerance levels can be measured instantaneously and are, therefore, more readily demonstrated than the longer term processes of habituation or sensitisation. In fact, habituation and sensitisation are identified, and distinguished from each other, by the direction of change indicated by repeated measures of tolerance taken over time. For example, over the course of a habituation process, individual tolerance levels will be on the increase, and conversely, as individuals become sensitised to specific stimuli, their tolerance levels will decrease. Thus, demonstrating, at one point in time, that animals in one group or area are more tolerant than others to disturbance provides one piece of evidence in documenting that habituation may have occurred, but does not rule out other plausible explanations. Confirmation that habituation has occurred would necessarily require longitudinal, sequential measurements of responses of individuals to controlled stimuli (Nisbet 2000), a rigorous assessment technique that has rarely been employed (but see, e.g., Tutin and Fernandez1991; Johns 1996).

Impact assessment research typically documents differences in levels of tolerance – not habituation or sensitisation

Due to practical and financial constraints, the vast majority of impact assessment studies are constrained to the evaluation of a limited number of points in time - constraints that necessarily restrict opportunities to document long-term processes such as habituation and sensitisation. As a result of these limitations, assessment of the impacts of human disturbance typically follows one of two study designs: (1) instantaneous comparison at one point in time of responses between communities that have different histories of exposure (e.g., duration, frequency, intensity) (Figure 4.1a); or (2) sequential comparison at two points in time of responses within one community (Figure 4.1b). For example, in Figure 4.1a, the goal would be to evaluate effects of anthropogenic activity on animals that have been exposed to a given stimulus ("impact" group; Figure 4.1a-1), by comparing them with animals having little or no history of exposure ("control" group; Figure 4.1a-2). In Figure 4.1b, members of the same community would be sampled at different exposures to the anthropogenic disturbance. In both designs, documenting differing levels of tolerance within or between communities of animals is readily achieved, but this is not the case with respect to habituation or sensitisation. Proof of behavioural habituation or sensitisation is feasible only by employing the latter design, and then, only when the same individual animals are sampled through time. This second criterion, in particular, is one that is seldom met. Animal identities are rarely taken into account in impact assessment research, and as a result, even when sequential observations are taken within a community, it is not possible to detect behavioural change in individuals. Thus, without longitudinal monitoring, sequential measures of the same individuals, and/or pre-exposure observations, it is difficult to meet the conditions required to detect behavioural habituation or sensitisation.

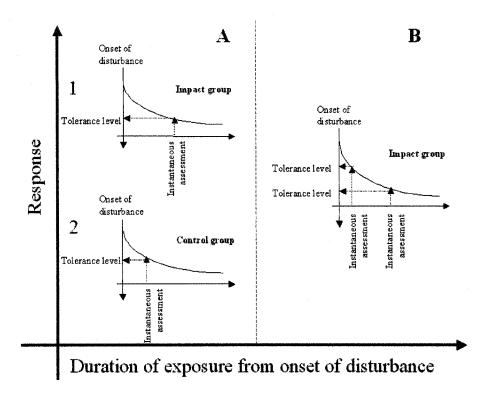


Figure 4.1. Examples depicting two study designs typically used for assessment of anthropogenic impact on wildlife. The origin represents the time of onset of the disturbance factor and, hence, the x-axis denotes duration of exposure to the stimulus, and the y-axis represents corresponding levels of response to the stimulus. Figure 4.1a depicts an instantaneous comparison at one point in time of responses between an "impact" (1a-1) and a "control" (1b-2) group that have different durations of exposure. Figure 1b depicts a sequential comparison at two points in time of responses measured within one community at different exposure levels. Note direction of y-axis in small insert figures: tolerance levels increase as response levels decrease (large y-axis).

If it is levels of tolerance that are typically detected in impact assessment studies, how are these findings to be interpreted? Further inspection of Figure 4.1a, shows that there are several ways in which the differences in observed tolerance levels between impact and control groups can occur. In one scenario, members of the impact group have truly become more tolerant to disturbance through a gradual process of behavioural habituation, *i.e.* learned habituation. In this case, additional, temporally spaced observations are needed to confirm that true waning of responsiveness has occurred. In a second scenario, a segregation of the less tolerant members of the impact group occurred prior to onset of the assessment, resulting in biased sampling of constituents of the impact group. In such a case, an assessment would not reflect the avoidance responses of the less tolerant group members that moved away from the area of disturbance;

instead, only responses of more tolerant individuals remaining in the area would be measured (e.g., Griffiths and van Schaik 1993; Fowler 1999; Chapters 2 and 3). In a third scenario, a response resembling habituation occurred through physiological or ecological means rather than through learning. For example, animals may exhibit reduced responsiveness to a given stimulus because of physiological impairment, e.g., deafening due to repeated or prolonged exposure to loud acoustic stimulus. Or, animals may exhibit reduced responsiveness to an element in their ecosystem other than the given stimulus. For example, the focal species may respond to the habituation of prey species or displacement of predators in response to the human disturbance, rather than to the disturbance directly. And, in a fourth scenario, a habituation-type response was the result of habitat differences between impact and control sites, that is, with no suitable habitat elsewhere to which animals at the impact site could move, they were compelled to remain in proximity to the disturbance (Gill et al. 2001). In this case, criteria for habitat suitability might include abundance of predators, prey or shelter, social factors, etc. In only one of the four scenarios presented above could behavioural habituation be invoked, and in that case, confirmation would require additional sampling. Analogous explanations can give rise to differences in tolerance levels within one population or community measured at two different times (Figure 4.1b).

Thus, interpreting the findings of impact assessment research for management purposes is not entirely straightforward. What is clear, though, is that common presumptions do not hold up. When results indicate that responses of the impact group are more moderate than those of the control group, it is often assumed that behavioural habituation has occurred. When results indicate that the impact group has greater tolerance than the control group, it is often assumed that there are no detrimental impacts on members of the impact group. Are either of these interpretations correct? As the analysis of Figure 4.1a, above, shows, other explanations are equally plausible and more information is needed (see also Chapters 2 and 3).

Discerning between explanatory mechanisms: would the real 'Habituation' please stand up?

In an ideal world, impact assessment research would be initiated prior to the onset of anthropogenic activity, would feature sequential monitoring of responses, and would focus on the same individual animals over time. In this model, a waning or waxing of wildlife response to human activity could be readily identified. Unfortunately, such ideal monitoring conditions rarely exist. Even under the best of circumstances, confirming that the documented response is truly

behavioural habituation or sensitisation is problematic, given the various mechanisms that can explain observed decreases or increases in responsiveness over time.

As an example, consider Figure 4.2a, which depicts a "habituation-type" response. With the introduction of a given stimulus, behaviour, as measured by some response variable, changes (y-axis). With repeated occurrence of the stimulus over time (x-axis), the cumulative exposure grows with a concomitant decline in the response variable, which ultimately approaches the pre-stimulus level. The observed pattern conforms to Thorpe's (1963) ethological definition of habituation: with increased exposure, an animal learns that the stimulus has neither adverse nor beneficial effects, and the animal's responsiveness to that stimulus wanes.

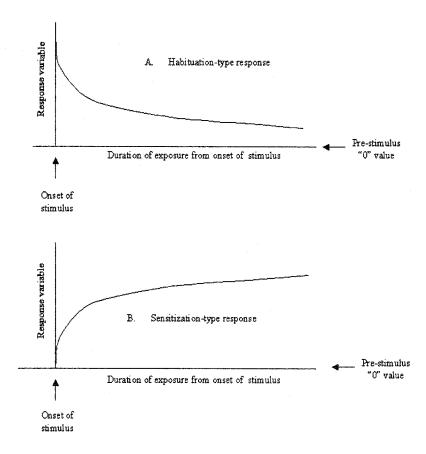


Figure 4.2. Illustration of 'habituation-type' response (A), and 'sensitisation-type' response (B). As in Figure 4.1, the origin represents the time of onset of the stimulus and, hence, the x-axis denotes duration of exposure to the stimulus, and the y-axis represents corresponding levels of response to the stimulus.

Still looking at Figure 4.2a, now consider that, as is common in studies of anthropogenic effects on wildlife, the response variable (y-axis) is actually a measure of the mean population response.

In the ideal monitoring scenario, the behaviour of randomly-chosen members of the population would be measured at intervals following the introduction of the stimulus, and a curve, the same as that shown in Figure 4.2a, would be drawn from the resulting data set. From these two examples, it is clear that a number of different mechanisms can produce the curve shown in Figure 4.2a. Explanatory mechanisms include:

learning: individual animals learn with repeated exposure not to respond to a given stimulus, i.e. true behavioural habituation; physiology: animals exhibit reduced responsiveness to a given stimulus because repeated or prolonged exposure results in physiological impairment, e.g. deafening in the case of a loud acoustic stimulus; selection: animals exhibit individual variation in responsiveness to a given stimulus such that the most responsive individuals are disproportionately vulnerable and are removed from the study population through death, morbidity, spatial displacement, or reduced reproductive success. For example, if the less tolerant individuals move out of a region in response to human activity, a reduction in the average density of animals, and therefore, a more moderate average response among animals within the disturbed area would be observed (Fowler 1999; Chapters 2 and 3). ecology: animals exhibit reduced responsiveness to an element in their ecosystem other than the given stimulus, e.g., habituation of prey species, or displacement of predatory species.

All of these mechanisms can result in the habituation-type curve depicted in Figure 4.2a, but only the one that invokes learning by individual animals – true behavioural habituation – is likely to have no direct detrimental consequences for the long-term fitness of the community and/or population. However, it is important to note that some scientists believe that behavioural habituation can result in harmful outcomes for wildlife, for example, through increased exposure to disease or loss of wariness to vehicular activity (e.g., Spradlin et al. 1998; Stone and Yoshinaga 2000; Woodford et al. 2002).

The three other mechanisms that produce habituation-type curves are unlikely to denote good news for targeted animals. Ecological factors may sometimes have benign or neutral effects, as when target animals respond to the habituation of their prey to a given stimulus, rather than to the stimulus itself. But outcomes of physiological damage and selection are likely negative.

For sensitisation, a parallel but opposite schema can be generated, with a "sensitisation-type" response that increases with cumulative exposure (Figure 4.2b). The same range of mechanisms can be called upon to explain this type of curve:

j	learning: individual animals learn with repeated exposure to respond to a given stimulus,
	i.e., true behavioural sensitisation;
	physiology: animals exhibit increased responsiveness to a given stimulus because
	repeated or prolonged exposure results in physiological sensitisation (e.g. chemical
	sensitisation);
	selection: animals exhibit individual variation in responsiveness to a given stimulus such
	that the least responsive individuals are disproportionately vulnerable to dire
	consequences, e.g., those that take the least evasive action suffer the greatest mortality,
	morbidity, etc;
	ecology: animals exhibit increased responsiveness to an element in their ecosystem other
	than the given stimulus, e.g., an increase in the abundance of predatory species.

Now consider the variety of ways in which the habituation- and sensitisation-type curves depicted in Figure 4.2 could have been produced. Various units of analyses could have been used. These include sequential measures of the same individuals, communities or populations over time; or comparisons at one point in time between individuals, communities or populations with differing cumulative exposure. Depending on the unit of analysis used, and which of the four mechanisms is in operation (learning, physiology, selection, or ecology), the observed response may or may not be depicted as a habituation- (or sensitisation-) type curve. So, assume a habituation-type response (as in Figure 4.2a), and consider different possibilities for the response variable measured on the y-axis and the response curve shown:

- 1. The response curve is the trajectory of the mean response of a population measured over time: This could result from any of the four mechanisms.
- 2. The response curve is the mean trajectory of the responses of known individuals measured over time: This could be caused by learning, physiology, or ecology, but not selection because the trajectory is based on measurements at the level of the individual, not the population.
- 3. The response curve is fitted through points calculated for several different populations with different cumulative exposure: This could result from any of the four mechanisms.

- 4. The response curve is fitted through points calculated for subsets of one population from different areas within its range, each area having differing cumulative exposure, with all measurements made at the nearly the same time. In this scenario, movement of individuals between subpopulations is assumed: This could result from an ecological effect, or possibly a type of selection in which the animals exhibiting the greatest response avoid the areas of greatest impact. This could not result from learning or physiological damage because variation in response by area depends on each area's exposure history rather than the exposure history of the entire population.
- 5. The response curve is fitted by comparing the responses of a set of known individuals in different areas with differing cumulative exposure within their range, with all measurements made at the nearly the same time and with the same instantaneous level of exposure (i.e., same individuals being examined in different areas within their home range the different areas having different levels of exposure): This could only result from an ecological effect because variation in responses of individual animals depends on each area's exposure history, not the exposure history of the individual animals.

Table 4.2. Combinations of units of analysis and explanatory mechanisms that produce habituation- or sensitisation-type response curves, i.e., curves depicting decreasing or increasing response with increased

cumulative exposure.

Timeframe of		Explanatory Mechanism				
Comparison	Unit of analysis	Learning	Physiology	Selection	Ecology	
Over time	1. Population mean	Y	Y	Y	Y	
Overtime	2. Same individual(s)	Y	Y		Y	
	3. Separate populations with differing cumulative impacts	Y	Y	Y	Y	
At one point in time	4. Subsets of same population from areas with differing cumulative impacts			Y?	Y	
	5. Same individual(s) but from areas with differing cumulative impacts				Y	

These scenarios are summarised in Table 4.2. The converses also hold true. For instance, if animals do not change their behaviour as they enter different parts of their range that have different cumulative exposure, then an ecological mechanism can be ruled out as a cause of a habituation-type response of the mean population trajectory over time.

This analysis suggests ways in which the underlying mechanism for a habituation- or sensitisation-type response can be identified. Take, for example, a situation in which the population mean shows a habituation-type response when plotted over time (first scenario, above), but the trajectories of individual animals do not (converse of second scenario, above), then selection becomes the most plausible mechanism.

As another example, consider a case in which individuals exhibit a habituation-type response to a given stimulus over time, ruling out selection as a mechanism (second scenario, above). Additionally, if the response of each individual is similar in different areas that have different levels of cumulative exposure (converse of fifth scenario, above), then an ecological factor can also be ruled out, leaving learning and physiological damage as plausible mechanisms for the habituation-type response.

Using this method of analysis, responses caused by physiology and learning cannot be distinguished by behavioural investigation, as these columns are identical in 4.2. To discriminate between physiology and learning, psychological or physiological investigations would be needed, and/or examination of multiple response variables. For instance, a habituation-type response based on auditory, but not visual, response variables would point to physiological damage (hearing impairment) rather than learning as the causative mechanism. Thus, by focusing on the responses of individual animals, and comparing their behaviour in different areas, it is possible to eliminate confounding selection and ecological explanations, but a multifaceted approach may be needed to distinguish between physiological and learning as explanatory mechanisms.

Proceed with caution: Behavioural habituation can be inferred only for the type of response that has been monitored

Practical and financial constraints not only reduce the number of points typically measured in impact assessment research, but also restrict such monitoring to observable, behavioural responses, rather than, for example, physiological responses that typically have no visible, external sign and are not as readily detectable as behaviour in free-ranging animals. Such an emphasis on one modality of response effectively limits the scope of conclusions that can be drawn from the investigation. Thus, even after other explanatory mechanisms have been ruled out and true behavioural habituation has been confirmed, findings must still be handled with caution because the conclusion is likely to be specific only to the response variable(s) that have been monitored.

Accordingly, the most effective course of action would be to complement behavioural assessment by monitoring an animals' physical condition and such physiological measures as heart rate, body temperature, and/or hormonal levels. The strength of this course of action is affirmed by studies in which both behavioural and physiological responses were monitored simultaneously. These have produced the disconcerting result that, although typically easier to document, behaviour, in and of itself, may not always be a sufficiently sensitive or timely indicator of the effects of disturbance (Beale and Monaghan 2004a,b). For example, several studies have shown that, at the same time that animals exhibited little or no behavioural sign of disturbance, physiological evidence of their distress could be detected (e.g., Moen et al. 1982; Culik et al. 1990; Wilson et al. 1991; Nimon et al. 1995; Regel and Putz 1997; Ratz and Thompson 1999; Müllner et al. 2004). Thus, it is clear that animals can respond in one modality but not another, and therefore, likely that animals may become habituated in one modality but not another.

Research on killer whales and human disturbance further highlights the complexities involved in interpreting wildlife responses and demonstrating behavioural habituation. Williams *et al.* (2001) documented a decline from the 1980s to the 1990s in the overt avoidance of vessels by resident killer whales (*Orcinus orca*). The data, however, were insufficient to discriminate among explanatory mechanisms. Plausible explanations include: the whales became habituated to boat traffic through individual experience (learning), or became less responsive through hearing impairment inflicted by vessel noise (physiology). Additionally, the result may be related to ecological change, such as salmon abundance, that may or may not be related to vessel activity (ecology). Or, the result may be a product of sampling biases, *e.g.*, whales having differing tolerance levels or experiencing vessel operators of differing abilities were sampled in the two time periods. Thus, despite long-term monitoring, the case for behavioural habituation to vessels by killer whales is equivocal.

The situation is further confounded by additional experimental evidence obtained in 1998 showing that killer whales at that time still responded with avoidance to vessels both in compliance or in violation of local whale watch guidelines (Williams *et al.* 2002a,b). One plausible explanation of the apparently contradictory findings is that animals can show signs of habituation to one aspect of human disturbance, while at the same time responding negatively to a different feature of the same activity. The overall waning in avoidance to vessels does not rule out the possibility of detrimental acoustic impacts of the same activity. For example, apparent

behavioural habituation, expressed as a reduction in physical avoidance, would not necessarily mitigate effects of acoustic masking by boat noise on the whales' acoustic sensitivity and/or their detection of prey and conspecifics (e.g., Bain and Dahlheim 1994; Erbe 2002; Foote et al. 2004). Thus, documented behavioural changes in one response variable over time do not, in and of themselves, confirm that other responses (e.g. physiological ones) or impacts (e.g. acoustic masking) are not occurring.

Clearly, if research findings are to be effective in forming management plans for killer whales, it is important to discriminate among competing mechanisms in order to explain the observed effect. Without rigorous analysis, an apparent waning in response would likely be interpreted to show that habituation had occurred, and the subsequent management plan might specify that no whalewatch guidelines or protected areas were needed (a conclusion that might also have been drawn from this study without access to the long-term datasets – Chapters 2 and 3). Instead, a more informed synthesis of several studies, looking at a number of response variables, indicated that guidelines and boat exclusion zones can, and should, play a beneficial role in recovery plans for threatened killer whale populations (Baird 2001). In the killer whale example, changes in whale behaviour were noted on a scale of tens of years, but longitudinal replication of studies on known individuals would be required to determine the root cause of the behavioural change.

CONCLUSION

In the realm of scientific inquiry into effects of human activity on wildlife, managers and scientists alike tend to operate under the assumptions that: (1) it is relatively easy to demonstrate behavioural habituation of wildlife to anthropogenic stimuli, and (2) habituation-type responses imply that there is an absence of detrimental consequences for targeted animals. This chapter endeavours to show that neither assumption is entirely correct, and that the misinterpretation of scientific findings resulting from reliance on these false premises can have detrimental consequences for wildlife. Thus, to classify wildlife response as habituation should not be done without considerable scrutiny, as this classification is likely to have serious management ramifications, even an easing or cessation of conservation efforts. Therefore, I urge conservation biologists, ethologists and wildlife managers to use care in assigning the label, habituation, without fulfilling the stringent requirements of carrying out sequential monitoring over time of the responses of individuals to a given stimulus. I further caution against extrapolating from habituation demonstrated for specific response variable(s) to variables or modalities that have not been assessed.

Instead, in many instances, a designation of varying levels of tolerance, which carries no a priori stigma, is more appropriate and correct than using the labels, habituation or sensitisation. I have shown that demonstrating, at one point in time, that animals in one group or area are more or less tolerant than others to anthropogenic stimuli provides one piece of evidence to suggest that behavioural habituation or sensitisation has occurred, but does not rule out other plausible explanations. Similar habituation- and sensitisation-type response curves can occur through other mechanisms, such as physiology, selection and ecology, none of which are likely to signify positive outcomes for targeted animals.

In the present paper, a methodological framework for distinguishing among explanatory mechanisms for given habituation- or sensitisation-type responses is provided. This method will help to clarify appropriate designation of behavioural habituation and sensitisation, and conversely, to prevent inappropriate designation thereof. This empirical technique is offered in the hope that it will enhance conservation attempts by promoting sound scientific evidence as the basis for informed management policies.

CHAPTER FIVE

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Regional economic significance of cetacean-watch activities

In Australia, tourism is the largest single earner of foreign exchange (Hoyt 2001). Wildlife tourist activities, such as cetacean-watching, are at the top of the visitor attraction list. In 1998, 46 communities, involving 223 commercial operators, offered cetacean-watching tours (Hoyt 2001). More than 730,000 tourists engaged in cetacean-watching producing a total revenue of \$56 million USD (Hoyt 2001). In Western Australia, in 1998, there were 87 commercially licensed cetacean-watching operators and two 'swim-with-dolphin' operators in 13 communities with an additional 23 operators offering dolphin-watching as part of other activities, *e.g.* fishing and sightseeing (Hoyt 2001), producing a total revenue of \$13.7 million USD (Hoyt 2001).

Since the 1960's, several dolphins have frequented the shallow waters off the fishing camp of Monkey Mia, Shark Bay to receive fish handouts from humans in knee-deep water. Today, this phenomenon remains the area's main tourist draw card attracting over 100,000 visitors annually (Figure 5.1). One commercial dolphin-watch company offering to experience non-provisioned, wild-feeding dolphins away from the provisioning area has been in operation sine May 1993. In August 1998, the Western Australian Department of Conservation and Land Management (CALM), the governing body responsible for management of cetacean-watch tourism within Western Australia, made a subsequent license available for a second operator.

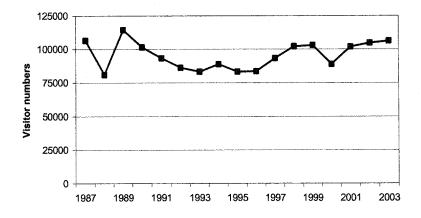


Figure 5.1. Visitor numbers to Monkey Mia, Shark Bay. Source: Department of Conservation and Land Management.

Sixty nine percent of visitors come to Shark Bay specifically to see dolphins and 98% of all visitors to Shark Bay go to Monkey Mia (Reark Research 1995). Hence, these animals are of extreme economic significance to the local community. As stated in the Monkey Mia Reserve Draft Management Plan (CALM 1993), "... because of its popularity and importance, Monkey

Mia's long-term protection and the protection of the values it support is essential to maintaining a healthy tourism industry and strong regional economy in Shark Bay".

The need for impact assessment

Given the character of the cetacean-watch industry such that specific communities of animals are repeatedly sought out for prolonged, close-up encounters, there is a potential for detrimental consequences for targeted animals, in particular, for resident animals with small home ranges.

Despite the scale of the cetacean tourism industry and its world-wide exponential growth, our current understanding of impacts on targeted animals and current methods of evaluating impacts are in their infancy. With respect to impact assessment, Gales (1999) noted that "management... has proceeded without clear scientific guidance. As is the case with most marine mammal/human interactions the demand and growth of this industry has significantly outstripped the ability of scientists to develop and implement sufficiently sensitive tools that might provide some sound basis for management decisions."

The present study was conducted in collaboration with the Western Australian Department of Conservation and Land Management to provide a scientific basis for informed management of vessel-based dolphin tourism in Shark Bay, with a goal of identifying potential impacts on targeted dolphins. By developing scientifically-based plans for minimising detrimental impacts of vessel activity, CALM will be better equipped to ensure the welfare of targeted dolphins and the sustainability of the local tourism industry.

In the following, I briefly outline the conservation objectives of CALM and the results of this research. Subsequently, based on the results and the conservation objectives of the managing body, I provide several options for management.

Management framework in Shark Bay Marine Park relating to Conservation, Tourism and Recreation

CALM is entrusted to manage lands and waters in Western Australia. CALM operates under two principal Acts: the CALM 1984 Act and the Wildlife Conservation Act. With regards to marine

reserves, the Wildlife Conservation Act provides for the protection of flora and fauna, while the CALM 1984 Act provides the legislative basis for regulating activities of recreation and tourism.

The Shark Bay Marine Reserves Management Plan (1996-2006), developed by CALM and approved by the Ministers of the Environment, Fisheries and Mines, states that the principal goals for CALM in the management of the Shark Bay Marine Park include to:

- 1. Conserve ecological, cultural and scenic values;
- 2. Facilitate recreation and tourism in a manner compatible with conservation and other goals;
- 3. Ensure that commercial uses are managed in a manner that minimizes impacts on the reserves' values;
- 4. Seek and provide an up-to-date and sound scientific and information basis for the Department's conservation and land management activities.

Of particular interest in regards to the present study are the strategies outlined to meet the management objectives in regards to:

Tourism and recreation:

- 1. Ensure that recreation developments and activities do not detract from or adversely impact on conservation values of the reserve;
- 2. License commercial operations where they are compatible with the management plan.

Wildlife Interaction:

- License acceptable commercial operations involved with wildlife interaction and determine appropriate conditions;
- 2. Monitor pubic visitation and impacts on wildlife events and take action where adverse impacts are occurring.

Bottlenose Dolphins:

- 1. Monitor visitor numbers and control if necessary to preserve the quality of the interaction experience and to protect the dolphins;
- 2. Regularly review interaction procedures and the feeding strategy for the dolphins and recommend changes to Monkey Mia Management Committee as required.

While the latter point refers specifically to the dolphin-provisioning program at Monkey Mia, it may equally apply to interactions between dolphins and tour vessels in the waters off Money Mia. In fact, the overall management goals within the Monkey Mia Reserve, as outlined by the CALM and the Shire of Shark Bay include to: "protect the Monkey Mia dolphin population and habitat from adverse impacts" (Monkey Mia Reserve - Draft Management Plan (CALM 1993)).

Study design and summary of results pertaining to exposure of dolphins to vessels

The main goals of the study were to:

- identify potential effects of vessel activity on dolphins in the waters immediately off Monkey Mia in Shark Bay;
- develop recommendations, pertaining to vessel activity, to minimise impacts on targeted animals that, in turn, will help ensure the sustainability of the industry.

Study design

In a review of the literature pertaining to the evaluation of impacts of nature-based tourism on cetaceans, I identified factors that, to date, have limited the utility of this research and pinpointed factors that allow for effective impact assessment.

With this in mind, I designed a multi-faceted study that evaluated short-term responses and long-term effects of vessel activity on bottlenose dolphins off Monkey Mia, Shark Bay. Specifically, I incorporated the following key research attributes into the impact assessment: 1) use of multiple types of research platforms, 2) applied appropriate behavioural sampling techniques, 3) monitored multiple response measures simultaneously, 4) supplemented opportunistic observations with controlled experiments, and 5) took advantage of historical data.

Experimental vessel approaches to groups of dolphins were carried out in two adjacent study sites (control and impact sites) where dolphins have had different histories of exposure to vessel activity. Multiple behavioural response measures were monitored from land-based observation platforms before, during and after each experimental approach. Individual dolphins involved in experiments were photographically identified and information about their age and sex was obtained from long-term records (>20 years) of the Shark Bay dolphin research project.

These short-term responses to vessel activity were interpreted within the longitudinal perspective provided by long-term research on Shark Bay dolphins. Specifically, due to the long-term nature of the Shark Bay dolphin research project where individually specific demographic, reproductive and habitat use information were available for dolphins from a time period before the onset and during the development of vessel-based dolphin-watching tourism in the bay. Using long-term records for individual bottlenose dolphins, I evaluated habitat use and female reproductive success in relation to an increase in the activity of vessels targeting dolphins over a 14-year period.

Strictly speaking, this study evaluated the additional effects of tour vessel activity to dolphins already exposed to research vessel activities. In this study, we recognize that the cumulative exposure to all vessels that repeatedly target prolonged interactions with dolphins (tour- and research vessels) and other anthropogenic activities may be a contributing factor to the observed detrimental impacts.

Summary of results

Experimental vessel approaches elicited significant short-term changes in patterns of sociality and movement of targeted dolphins at both control and impact sites. Responses at the control site were stronger, more prevalent, and longer lasting than those at the impact site.

Subsequent analyses showed that the moderation in the short-term responses at the impact site was likely not the result of habituation to vessel activity, but could be better explained by a displacement of sensitive individuals during the development of the tourism operations. Specifically, there was a statistically significant average decline of 14.9% in numbers of individual dolphins per square kilometer within the area of tourism, when comparing two four-and-a-half year periods in which the number of tour vessels increased from one to two (1993-1998, 1998-2003). This is equivalent to a decline of approximately one out of every seven individuals within the impact site.

During this period, there was a 1.84-fold increase in the time tour- and research vessels spent with dolphins (<50m) in the impact site, of which 76% could be attributed to tour vessels. In other words, from 1998-03, in the impact site, tour vessels spent an order of magnitude more time

within this area and 2.4-fold more time with dolphins (<50m) within this area than did research vessels. At the same time, there was an average increase of 8% in the numbers of individual dolphins within an adjacent control site rarely used by tour vessels. Although the latter trend was not statistically significant, it does corroborate the finding that there has been a long-term shift in dolphin habitat use away from the impact site, a region of high vessel activity, to a site of lower vessel traffic.

Female bottlenose dolphin reproductive success was significantly negatively correlated with cumulative exposure to both tour- and research vessels. This negative correlation was likely caused by a reduction in the ability of highly exposed females to successfully produce or raise offspring rather than a segregation of better fit- or more experienced females away from the impact site.

Because tour- and research vessel exposure rates were highly correlated, the effect of each contributing factor could statistically not be teased apart. These measures were highly correlated because of the coupled effect of both vessel types departing and arriving from the same location, and small home-range sizes of adult females causing both vessel types to encounter the females residing in the waters close to the launch site disproportionately more often then females animals residing further afield.

Because female reproductive success was significantly negatively correlated with cumulative vessel exposure coupled with the fact that the females that tour vessels spent most time with were also the females that research vessels spent most time with, meant that the females with lowest reproductive success were the ones residing predominately in the impact site.

Although the explanatory mechanisms are not yet definitively confirmed, the findings are clear. There has been a significant decline in use of the impact site by individual dolphins during a period of increasing vessel activity, and the reproductive success of females with greater exposure to vessels is lower than that of less-exposed females.

The declines in habitat use and decreased reproductive success within the impact site may not end in jeopardizing the large, genetically-diverse Shark Bay dolphin population, but current trends are likely unsustainable for the long-term continuation of the local dolphin-watch industry. Given the conservation and management objectives of the local wildlife governing body, coupled with the ethical and economical stakes involved, immediate management intervention is well-justified.

Relative contributions from research- and tour vessels toward documented impacts

In the evaluation of the contributions of research- and tour vessels towards documented detrimental effects on dolphin habitat use and reproductive success, all of the following points need be taken into consideration:

- 1. Tour vessels spent an order of magnitude more time in the impact site than did research vessels during the period of decreased habitat use (Chapter 2).
- 2. Tour vessels spent 2.4-fold more time with dolphins in the impact site than did research vessels during the period of decreased habitat use (Chapter 2).
- 3. Acoustically, research vessels are less intrusive because of their smaller and quieter engines (6-40hp, 4-stroke engines) compared to that of tour vessels (twin turbo 140hp and twin 50hp engines, respectively).
- 4. Tour operators change motor activity (e.g., in and out of gear), on average, every 21sec when within 50m of dolphins an activity that produces excess noise (Bejder 2000).
- 5. Physically, research vessels are less intrusive because of their smaller size (4-5m dinghies) compared to tour vessels (17 and 19m, respectively).
- 6. Research vessels typically operate seasonally while tour vessels operate year-round.
- 7. Researchers are likely to detect signs of behavioural disturbance more quickly than other vessel operators because their attention is dedicated to observing dolphin behaviour.
- 8. Research vessels typically spend anywhere from 5min to 3hrs with the same individuals, whereas tour vessels are restricted to 15min encounters per dolphin group.

Conclusion regarding relative contributions from research- and tour vessels toward documented impacts

The decline in habitat use in the impact site occurred as exposure to both tour- and research vessels increased. However, as tour vessels spent an order of magnitude more time in the impact

site and spent more that twice as much time within 50m of dolphins within this site during the time of habitat use decline, than did research vessels, coupled with their larger physical size and louder engines, it is reasonable to assume that tour vessel impact is substantially more significant.

Because female reproductive success was significantly negatively correlated with cumulative vessel exposure coupled with the fact that the females that tour vessels spent most time with were also the females that research vessels spent most time, means that the females with lowest reproductive success were the ones residing predominately in the impact site. Thus, because tour vessels are physically and acoustically more intrusive and spend substantially more time in the impact site, tour vessel impact is likely to be more significant towards documented detrimental effects on female reproductive success.

Management and Recommendations

The following recommendations to mitigate detrimental effects of vessel exposure are based purely from a biological and conservation perspective, with CALM's *conservation* objectives in mind. However, it is recognised that factors other than dolphin conservation need be taken into consideration (e.g., local economy) when implementing management in regards to mitigating detrimental effects to dolphin habitat use and reproductive success. Furthermore, it is important to note that management options and recommendations presented here are based purely on number of vessels and/or the duration of exposure to vessels. Vessel disturbance in the form of vessel behaviour (manoeuvring) in vicinity of animals, e.g., speed and heading, proximity and acoustic impacts were not evaluated in this study.

There are three overall management options available in response to the results of this study: increase, maintain or decrease the current level of exposure of dolphins to vessels that target repeated, prolonged interactions in the waters off Monkey Mia.

Increase the level of exposure:

Considering management strategies outlined by CALM to meet their conservation objectives, the results of this research *do not support*, from a purely biological perspective, the option of increasing the exposure of dolphins off Monkey Mia to any vessel activities.

Maintain the current level of exposure:

Considering management strategies outlined by CALM to meet their conservation objectives, the results of this research *do not support*, from a purely biological perspective, the option of maintaining the current level of exposure of dolphins off Monkey Mia to vessel activities.

Decrease the level of exposure:

Considering management strategies outlined by CALM to meet their conservation objectives, the results of this research *support*, from a purely biological perspective, the option of decreasing the current level exposure of dolphins off Monkey Mia to vessel activities.

Recommendations to mitigate dolphin exposure to vessel activity

Decreasing the level of exposure to vessels that specifically target prolonged and repeated interactions with dolphins in the waters immediately of Monkey Mia could be achieved either by decreasing the time research- and/or tour vessels spend with dolphins in these waters.

Research vessel activity:

While acknowledging that research vessels likely contribute to the documented detrimental effects, their relative contribution is likely less significant than that of tour vessels.

Considering management strategies outlined by CALM to meet their conservation objectives, e.g., "seek and provide an up-to-date and sound scientific and information basis for the Department's conservation and land management activities", coupled with the inevitability of research vessel exposure to study animals to identify potential problems regarding dolphin welfare, coupled with the apparent small contribution of research vessel activity towards documented effects, there is no evident need to decrease the exposure of dolphins off Monkey Mia to research vessel activity.

However, it is recommended that the exposure of dolphins to research vessels is not further increased, and that research vessel activity be monitored (see below for recommendations for further research).

Tour vessel activity:

Given the likely significant contribution of tour vessel activity towards documented effects coupled with the management strategies outlined by CALM to meet their conservation objectives, the results of this research *support*, from a purely biological perspective, the option to decrease the exposure of dolphins to tour vessel activity off Monkey Mia.

Options for reducing exposure to tour vessels:

In theory, a range of management options is available to reduce the current level of exposure of individual dolphins to tour vessels. However, a feasibility analysis will be needed in order to evaluate which of these options are most viable ethically, practically and financially.

Options include to:

- 1. maintain the number of licensed tour operators and the number of trips offered per day per operator, but restrict the number of trips that can occur within the tourism area;
- 2. maintain the number of licensed tour operators and the number of trips offered per day per operator, but restrict the allowable time with animals within the tourism area;
- 3. maintain the number of licensed tour operators, but decrease the number of trips allowable per operator per day;
- 4. reduce the number of licensed tour operators;
- 5. eliminate all tour vessel activity.

Recommendations for further research:

In order to ensure the sustainability of the vessel-based dolphin watch industry in Shark Bay, by minimising impacts on targeted animals, it is recommended that the monitoring of potential effects of vessel activity on dolphins off Monkey Mia be continued, and that a long-term adaptive management monitoring scheme be implemented. An adaptive management approach should rely on further impact studies in which the results of such be used to continuously inform and fine-tune management of the industry.

Specifically, it is recommended that further research:

1. re-evaluate individual dolphin habitat use within and between control and impact sites (as defined in Chapter 3) after another 4.5-year period, *i.e.*, August 2007.

- 2. investigate explanatory mechanisms behind the negative correlation between cumulative exposure to vessels and female reproductive success (testable hypotheses are outlined in Chapter 3).
- 3. investigate acoustic impacts of vessel activity on dolphins off Monkey Mia, Shark Bay.
- 4. investigate how vessel disturbance in the form of vessel behaviour (maneuvering) during interactions, e.g., speed, heading and proximity, affect dolphins.
- 5. investigate effects of prolonged research vessel interactions with dolphins especially with adult females.
- 6. monitor outcomes of management actions taken in response to this and future impact assessments.

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APPENDIX ONE

Research Abstracts (see Chapter 1)

Allen, M.C. and Read, A.J. (2000). Habitat selection of foraging bottlenose dolphins in relation to boat density near Clearwater, Florida. *Marine Mammal Science* 16, 815-824.

Allen and Read (2000) conducted opportunistic observations of bottlenose dolphins (Tursiops truncatus near Clearwater, Florida, USA, to assess potential effects of vessel traffic on foraging behaviour and habitat selection. Although this study does not specifically evaluate effects of cetacean-based tourism, it illustrates a good design for comparing disturbance situations. Focalanimal sampling of identified individual dolphins from an independent research vessel was used to compare dolphin behaviour between two sites that varied in degree of human use and vessel density, and between two time periods (weekdays, weekends) that varied in vessel density. Within follows, instantaneous sampling was used to quantify dolphin behaviour (foraging vs. not foraging), dolphin location, and number of vessels underway within 800m. Collection of finescale data on both spatial and temporal scales enabled researchers to quantify short-term responses of dolphins to changes in vessel traffic. Research findings included: (1) dolphin foraging frequencies did not differ between the two time periods despite greater vessel activity on weekends; and (2) habitat selection by foraging dolphins differed between the two time periods, e.g., at one site, foraging dolphins showed significant preferences for certain habitats during low vessel activity but habitat preferences were not apparent during periods of high vessel activity. Results suggest that dolphins may shift habitat use either to directly avoid areas of high vessel traffic or in response to vessel traffic.

Barr, K. and Slooten, E. (1998). Effects of tourism on dusky dolphins at Kaikoura. International Whaling Commission Scientific Committee, SC/50/WW10, pp. 30.

Barr and Slooten (1998) conducted opportunistic observations of groups of dusky dolphins (Lagenorhynchus obscurus) at Kaikoura, NZ, to quantify exposure and responses to commercial and private dolphin watch vessels. From a clifftop vantage point, the following information was recorded for dolphin groups: movement patterns and group dispersion were recorded via theodolite; surface behaviour, swimmer activity, and vessel activity were recorded via scan sampling. Although the goal was to record these data in the presence and absence of vessels, dolphins were seldom without boats nearby: i.e., dolphins were accompanied by vessels during 72% of observations. Other findings included: (1) nearly 10% of vessel approaches to dolphins violated national Marine Mammal Protection Regulations; (2) numbers of leaps and directional changes were significantly higher when a mix of vessels types was present; and (3) substantial changes in dolphin behaviour occurred when vessels were present during the afternoon. These findings led to conclusions that (1) despite long term exposure to vessels, dolphins still reacted to boat activity; (2) it would be difficult to determine whether boats and swimmers affect dolphin behaviour when periods without boats and swimmers were so few; and (3) dolphins may be more sensitive to disturbance in the afternoons, which is their normal resting period.

Bejder, L., Dawson, S.M., and Harraway, J.A. (1999). Responses by Hector's dolphins to boats and swimmers in Porpoise Bay, New Zealand. *Marine Mammal Science* 15, 738-750.

Bejder et al. (1999) conducted opportunistic observations of Hector's dolphins (Cephalorhynchus hectori) in Porpoise Bay, NZ, to quantify responses to casual swimmers and to a commercial dolphin watch operation. The location, orientation and spread of a focal group of dolphins relative to swimmers or vessels were tracked by theodolite from a clifftop vantage point. Findings included: (1) swimmers and the dolphin watch vessel were present during 11% and 12% of observations, respectively; (2) 43% of in-water encounters were at least "potentially disturbing", i.e., dolphins moved >200m away within 5 min of an approach by swimmer(s); (3) dolphins were more tightly bunched when the dolphin watch vessel was in the bay; and (4) dolphins appeared to be initially attracted to the dolphin watch boat but tended to orient away from the vessel if the encounter lasted >70 min. Given the importance of this bay to the small, resident dolphin population (Bejder 1997, Bejder et al. 2001), Bejder et al. (1999) suggested that some individual dolphins may be disproportionately affected by cetacean-focused tourism, and the potential for increased disturbance through an increase in tourism to the area may be cause for concern.

Constantine, R. and Baker, C.S. (1997). Monitoring the commercial swim-with-dolphin operations in the Bay of Islands, New Zealand. Department of Conservation, Wellington, New Zealand. pp. 59.

Constantine and Baker (1997) used commercial tour vessels as the research platform to monitor responses of groups of common and bottlenose dolphins (*Delphinus delphis and Tursiops truncatus*) to swim-with-dolphin operations in the Bay of Islands, NZ. They recorded predominate group activity upon the first sighting of a group (around 400m), and this was subsequently reassessed when the tour vessel was within 100m. Their findings included species-specific differences in response to vessel approaches, *e.g.*, 32% of vessel approaches to bottlenose dolphins resulted in changes in group activity with feeding being the activity least likely to be disrupted and socialising most likely; whereas, 52% of approaches to common dolphins resulted in behavioural change with resting least likely and socialising most likely to change. They also evaluated responses of dolphin groups to specific swimmer placement methods, finding that the "line abreast" strategy resulted in lowest rates of avoidance but also low rates of swim success; in contrast, "in path" resulted in highest rates of avoidance.

Constantine, R. (2001). Increased avoidance of swimmers by wild bottlenose dolphins (*Tursiops truncatus*) due to long-term exposure to swim-with-dolphin tourism. *Marine Mammal Science* 17, 689-702.

Constantine (2001) conducted opportunistic observations to document behavioural responses of groups of bottlenose dolphins in Bay of Islands, NZ, to swim attempts by commercial swim-with-dolphin tour operators during 1997-98. To obtain a longitudinal perspective, these data were compared with findings from an earlier study conducted in 1994-95 in the same location using the same methods (see: Constantine and Baker 1997). Photo-identification and survey techniques were used to estimate the exposure of individual dolphins to swim-with activities in this region. Behavioural response measures included "interaction", "neutral", and "avoidance", recorded during swim attempts using systematic scan sampling of dolphin groups from a vantage aboard commercial tour vessels. Dolphin response was also evaluated with respect to method of swimmer placement in the water, e.g., "line abreast", "in path", or "around boat". Research findings included (1) tour operators' success with swim attempts decreased from 48% to 31% between study periods; (2) avoidance by dolphins to swim attempts increased from 22% to 31% between study periods; (3) dolphin response varied according to swimmer placement; (4) during successful

swim attempts, juveniles were significantly more likely to interact with swimmers than adult dolphins; and (5) the "average" dolphin in this region was estimated to be exposed to 31 swim attempts per year, a level of exposure which suggests that dolphins have become sensitised to swim attempts.

Culik, B.M., Koschinski, S., Tregenza, N., and Ellis, G.M. (2001): Reactions of harbor porpoises *Phocoena phocoena* and herring *Clupea harengus* to acoustic alarms. *Marine Ecology Progress Series* 211, 255-260.

Culik *et al.* (2001) conducted experiments to study responses of small groups of harbour porpoises to gillnets with and without acoustic alarm devices (pingers) in Clayoquot Sound near Vancouver Island, Canada. Although this study does not specifically evaluate effects of cetacean-based tourism, it illustrates a good design for experimentally determining effects of an acoustic (or disturbance) stimulus on cetacean behaviour. Porpoise behaviour was recorded during three controlled conditions in a before/during/after design: (1) an artificial non-lethal gillnet with no acoustic pinger (5 days), (2) the same net with a continuously operating pinger (5 days), and (3) the same net after removal of the pinger (2 days). Assessment of responses to the acoustic stimulus was based on tracking movement patterns of small groups of porpoises via theodolite from land. Findings included that porpoises did not appear to react to presence of an experimental net, but pinger operation resulted in an exclusion zone around the net. Avoidance distance during pinger operation (median = 530m) was estimated to correspond to the audible range of the acoustic alarm.

Goodson, D.A. and Mayo, R.H. (1995). Interactions between free-ranging dolphins (*Tursiops truncatus*) and passive acoustic gill-net deterrent devices. In 'Sensory Systems of Aquatic Mammals'. (Eds. R.A. Kastelein, J.A. Thomas, and P.E. Nachtigall) pp. 365-379. (De Spil Publishers, Woerden: The Netherlands).

Goodson and Mayo (1995) observed bottlenose dolphins under controlled conditions in the Moray Firth, Scotland, to test the potential effectiveness of passive acoustic reflectors in preventing gillnet entanglement. Although this study does not specifically evaluate effects of cetacean-based tourism, it illustrates a good design for controlled experiments that mimic an impact situation. One or more simulated gillnets with acoustic reflectors attached was tethered at a near-shore location frequented by dolphins on a daily basis. To record dolphin responses to the experimental

"net", the movements of one or more dolphins were tracked by theodolite from land, and vocal behaviour was monitored using moored sonobuoys and a seabed hydrophone array cabled to shore. These observations were used to establish ranges at which dolphins could detect acoustic reflectors via sonar, to test responses of dolphins to acoustic reflectors, and to relate echolocation behaviour to avoidance responses. Findings included: (1) all echolocating dolphins appeared to detect the barriers at ranges of >50m and modified their travel paths to avoid collisions; (2) detection echolocation behaviour was evidenced by a sudden increase in sonar activity and subsequent "locked-to-target" patterns; and (3) non-echolocating dolphins travelling in association with others appeared to follow the course of the group and thereby avoid collision; however, a small percentage of solitary non-echolocating animals remained at risk of collision despite acoustic reflectors.

Janik, V.M. and Thompson, P.M. (1996). Changes in surfacing patterns of bottlenose dolphins in response to boat traffic. *Marine Mammal Science* 12, 597-602.

Janik and Thompson (1996) conducted opportunistic observations of the surfacing patterns of groups of bottlenose dolphins (Tursiops truncatus) to assess responses to boat traffic in the Moray Firth, Scotland. A narrow channel frequented by dolphins and vessels provided an opportunity to conduct video surveillance from shore, thereby recording all occurrences of a specified behavioural event, "surfacing" within a circumscribed area. Surfacings could be counted readily from the video record and total numbers compared before and after (± 1 min) vessel approaches. As a control, surfacing numbers were also calculated for random 1-min periods when no boats were present. Findings included: (1) the dolphin watch vessel was responsible for the majority of boat-dolphin encounters and differed from other vessels in its movements around dolphins; and (2) the total number of dolphin surfacings decreased significantly after the dolphin watch vessel approached; however, no such pattern was apparent in encounters with other vessels or in the control data. Although the behaviour of individual animals was not recorded in this study, the decrease in the number of surfacings can clearly be interpreted to indicate that at least some of the dolphins were diving for longer periods and/or moving away from the dolphin watch vessel. Janik and Thompson (1996) speculated that this result may be due to differences in the behaviour of the dolphin watch vessel, e.g., this vessel typically remained in the channel for longer periods and attempted to stay close to dolphins.

Laist, D.W., Knowlton, A.R., Mead, J.G., Collett, A.S., and Podesta, M. (2001). Collisions between ships and whales. *Marine Mammal Science* 17, 35-75.

Laist *et al.* (2001) analysed historical records to quantify the frequency of ship strikes on large whales and investigate contributing factors. Historical records of collisions for the early 1600s into the 20th century were gleaned from newspaper reports, scientific publications, and early stranding records. More recent accounts were obtained from computerised stranding databases, scientific publications, a survey conducted in the 1970s, and a recent request for information on "Marmam". Specific details were recorded for each collision report. Historical information on the speed and number of vessels was obtained from Lloyds Register of Shipping. Findings included: (1) 11 species of great whales (*i.e.*, baleen and sperm whales) are known to be hit by ships, with fin whales being struck most often; (2) fatal ship strikes first occurred in the late 1800s when ships attained speeds of 13-15kn, and increased during the 1950-70s as vessel numbers and speed increased; and (4) factors contributing to ship strikes include length and speed of vessel, with most injurious collisions involving vessels that are ≥80m in length and/or travelling at speeds of >14kn.

Lesage, V., Barrette, C., Kingsley, M.C.S., and Sjare, B. (1999). The effect of vessel noise on the vocal behaviour of belugas in the St. Lawrence River Estuary, Canada. *Marine Mammal Science* 15, 65-84.

Lesage et al. (1999) conducted controlled experiments to study effects of vessel noise on the vocal behaviour of beluga whales (Delphinapterus leucas) in the St. Lawrence River Estuary, Canada, a location where whales are chronically exposed to vessel traffic. Although this study does not specifically evaluate effects of cetacean-based tourism, it illustrates a good design for controlled experiments and careful handling of acoustic data. Vocal and surface behaviour of beluga groups were simultaneously recorded during preexposure, exposure and postexposure conditions. The exposure condition consisted of controlled approaches by two familiar but different potential sources of acoustic disturbance: an outboard motorboat moving rapidly and erratically, and a ferry moving slowly and on a predictable path. Acoustic recordings were made from a hydrophone installed at 3-6m on the sea bottom. Vocalisations were classified using a scheme developed for arctic belugas (Sjare and Smith 1986), and exceptional care was taken to include only those samples in which all calls could be counted. Thus out of 77 experiments, only six satisfied the criteria for acoustic analysis. Despite a small sample of experiments with suitable recording quality, results showed that both vessels induced changes in calling rates, increased call

durations, an upward shift in the frequency range, and a tendency to emit calls repetitively, an increase in call duration, with responses to the larger ferry being more persistent.

Mann, J. and Smuts, B. (1999). Behavioural development in wild bottlenose dolphin newborns *Tursiops* sp. *Behaviour* 136, 529-566.

Mann and Smuts (1999) conducted opportunistic behavioural observations of bottlenose dolphins in Shark Bay, Western Australia, to the evaluate effects of food provisioning on maternal and calf behaviour during the first 10 weeks of the calves' lives. Focal sub-group sampling (mom and calf) was carried out in which the behaviour of provisioned dolphins within a human-interaction area on shore was compared with the behaviour of the same dolphins as well as wild-feeding dolphins away from the human-interaction area. Because of the unusual circumstances in which specific dolphins visit a resort beach on a near-daily basis to be food provisioned by humans, Mann and Smuts (1999) were able to obtain detailed behavioural records for individual dolphins from shore. Focal follows of individually-identified mothers and calves away from the human-interaction area were conducted using an independent vessel as research platform. The time calves spend in echelon swim with the mother was used as a behavioural measure of maternal care, as the calf may derive energetic benefits from swimming in contact with, or in the slipstream of, the mother. Mann and Smuts (1999) found that, although echelon swimming with the mother was common away from the human-interaction area both for provisioned and wild-feeding dolphins, the proportion of time calves spent in echelon swim position was significantly lower when provisioned dolphins were in the human-interaction area. Furthermore, away from shore, mothers foraged and socialized more often than mothers did while in the human-interaction area.

Miksis, J.L., Connor, R.C., Grund, M.D., Nowacek, D.P., Solow, A.R. and Tyack, P.L. (2001). Cardiac responses to acoustic playback experiments in the captive bottlenose dolphin (*Tursiops truncatus*). *Journal of Comparative Psychology* 115, 227-232.

Miksis et al. (2001) conducted controlled experiments to assess the cardiac responses of two captive bottlenose dolphins to acoustic playback stimuli at the Mystic Aquarium, Connecticut, USA. Although this study does not specifically evaluate effects of cetacean-based tourism, it illustrates the potential use of physiological measures to evaluate cetacean responses to anthropogenic stimuli. Three categories of playback stimuli were used: (1) pool noise; (2) signature whistles from familiar poolmates; and (3) agonistic jaw claps from familiar poolmates.

Heart rate responses were measured acoustically using a suction-cup hydrophone that each animal was trained to wear while remaining at station. This set-up allowed for continuous acoustic monitoring of cardiac activity before, during and after playback trials. By comparing the spacing and duration of the 10 heart beats preceding each acoustic stimuli with those of the 20 heart beats following playback stimuli, researchers found: (1) during the first set of 10 heart beats following the playback, all three acoustic stimuli elicited accelerated heart rates, with a significant increase in heart rate in response to jaw claps; and (2) during the subsequent 10 heart beats following the playback, pool noise responses returned to baseline whereas responses to conspecific vocalisations continued to accelerate. Results indicated "patterns of defense and startle response consistent with those observed in humans and nonhuman primates".

Miller, P.J.O., Biassoni, N., Samuels, A., and Tyack, P. (2000). Whale songs lengthen in response to sonar. *Nature* 405, 903.

Miller et al. (2000) conducted controlled experiments to assess effects of man-made underwater sound (specifically, low-frequency active (LFA) sonar) on the vocal sexual displays (song) of male humpback whales (Megaptera novaeangliae) near the Big Island, Hawaii, USA. Although this study does not specifically evaluate effects of cetacean-based tourism, it illustrates a good design for conducting controlled experiments at sea. A small, independent observation vessel was used to conduct focal-animal follows of individual whales before, during and after sound playbacks; strictly speaking, the study evaluates effects of LFA sonar on a whale already being followed by a research vessel. Non-vocal behaviour of the focal whale was recorded using systematic behavioural sampling, techniques while the vocal behaviour of the focal was recorded using a towed, calibrated hydrophone array. Each focal whale was typically followed for the duration of two or more songs before and after the sound playback; a playback typically consisted of ten 42-s LFA signals, broadcast at less than full strength at 6-min intervals, transmitted from a separate vessel. A variety of responses were identified, including: (1) in nine of 18 playback experiments, the focal singer stopped singing; in at least five of these, cessation of song appeared to be a response to the sound playback; and (2) songs of whales who sang continuously throughout experiments were 29% longer during LFA playbacks, suggesting that whales sang longer songs to compensate for acoustic interference. Additional details about methods are provided in Biassoni et al. (2000).

Nowacek, S.M., Wells, R.S., and Solow, A.R. (2001a). Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science* 17, 673-688.

Nowacek et al. (2001a) studied behavioural responses of individual bottlenose dolphins to controlled experimental vessel approaches and opportunistic approaches by passing vessels. The study population is resident to Sarasota Bay, Florida, USA, where dolphins are regularly exposed to high levels of vessel traffic: on average each dolphin is approached by vessels to within 100m once per six minutes during daylight hours. Assessment of dolphin responses was based upon focal-animal follows of 33 individually-identified dolphins of known age and sex from an independent research vessel; systematic behavioural sampling techniques were used to quantify dolphin behaviour in the presence and absence of vessel approaches. Opportunistic observations provided information about dolphin behaviour observable at the water's surface (inter-breath intervals, IBI). Controlled experiments made it possible for researchers to use a tethered blimp mounted with an overhead video system (Nowacek et al. 2001b) in order to assess sub-surface measures of behavioural response (inter-animal distance, heading and speed via fluke stroke counts). Observations of individually identified dolphins whose histories were well-known (Wells et al. 1987) made it possible for researchers to compare responses of different classes of dolphins. Findings included: (1) dolphins had longer IBI during vessel approaches compared to control periods; (2) during vessel approaches, IBI length was inversely correlated with distance to nearest boat; (3) dolphins decreased inter-animal distance, changed heading, and increased swimming speed more often during vessel approaches than during control periods; and (4) females without calves and inexperienced mothers had significantly different IBI from experienced mothers, with experienced mothers having the longest IBI of any class of dolphin during vessel approaches.

Richter, C.F., Dawson, S.M. and Slooten, E. (2001). Sperm whale watching off Kaikoura, New Zealand: Effects of current activities on surfacing and vocalisation patterns. Final Report for Research Investigation No. 2370.

Richter et al. (2001) conducted opportunistic observations of individual sperm whales (*Physeter macrocephalus*) near Kaikoura, NZ, to assess effects of whale-watch vessels on vocal and non-vocal behaviour. Whale movement patterns were recorded via theodolite from land; at other times, visual and acoustic behaviour was recorded from an independent research vessel (strictly speaking, boat-based observations considered the additional impact of whale-watch vessels on whales already being followed by a research vessel). In boat-based follows, individual whales

were tracked acoustically underwater using directional hydrophones. During each surfacing, the following information was recorded for the focal whale: initial and final position, timing of surfacing/dive, blow intervals, initial and final heading, all occurrences of specified aerial behaviours, presence/absence of whale-watch vessels and aircraft, and identification via fluke photos. Following each dive, the time elapsed from fluke-out to first click was also recorded. In the presence of whale-watch vessels (1) whales significantly increased time spent at the surface and frequency of heading change; (2) whales decreased frequency of aerial behaviours; (3) transient whales significantly increased the time to first click, whereas resident whales did not. The findings of Richter *et al.* (2001) highlight individual variation in behaviour of sperm whales and they suggest that resident whales are more tolerant of vessels than transient whales.

Samuels, A. and Bejder, L. (1998). Habitual interaction between humans and wild bottlenose dolphins (*Tursiops truncatus*) near Panama City Beach, Florida. Marine Mammal Commission, Silver Spring, Maryland, pp. 13.

Samuels, A. and Bejder, L. (2004). Chronic interactions between humans and free-ranging bottlenose dolphins (*Tursiops truncatus*) near Panama City Beach, Florida, USA. *Journal of Cetacean Research and Management*. 6(1): 69-77

Samuels and Bejder (1998, 2004) conducted opportunistic observations of bottlenose dolphins near a state recreation area in Panama City Beach, Florida, USA, where dolphins have regular inwater encounters with members of the public and commercial tour operators. Photo-identification combined with behavioural assessment of all dolphins encountered were used to estimate what proportion of the local dolphin community was involved in interactions with humans. In addition, focal-animal follows of individual dolphins and small groups of dolphins from an independent research vessel were used to compare the behaviour of members of the same dolphin community that did and did not have interactions with humans. During follows, systematic behavioural techniques were used to quantify dolphin behaviour and proximity to human activity. Findings included: (1) 7 of 89 dolphins encountered had habitual interactions with humans and were classified as "habituated"; (2) habituated dolphins engaged in interactions with humans during 77% of observation time; whereas, unhabituated dolphins never exhibited any human-dolphin interaction behaviours; (3) habituated dolphins remained in a small area where tourists congregate, whereas unhabituated dolphins travelled distances of several nautical miles during follows; (4) a high rate of food provisioning by humans indicated that human-dolphin encounters

at this location were likely to be sustained by feeding; and (5) a focus on one juvenile dolphin revealed that this immature dolphin was at risk of injury or death once per 12 min as a result of proximity to humans, and was fed by humans once per 39-59 min.

Waples, K.A. and Gales, N.J. (2002). Evaluating and minimizing social stress in the care of captive bottlenose dolphins (*Tursiops aduncus*). Zoo Biology 21, 5-26.

Waples and Gales (2002) monitored the behaviour and physical health of individual captive bottlenose dolphins held at Atlantis Marine Park, Western Australia, during the months leading up to one case of illness and two cases of mortality within the group. Although this study does not specifically evaluate stress and distress as a consequence of cetacean-based tourism in the wild, it illustrates the potential for correlating behavioural and physiological measures to evaluate stress. Specifically, a detailed study of the behaviour of individual animals was complemented by periodic blood samples from the same individuals as well as their health records. The behavioural data documented changes in social dynamics and association patterns within the group (measured by close proximity, physical contact, and synchronous movements between individuals); these behavioural measures were correlated with physiological measures of stress and health. Waples and Gales (2002) suggested that stress resulting from social instability, either from the perceived threat from group members or from changes within dominance hierarchy, contributed to documented mortalities and illnesses.

Watkins, W.A. (1986). Whale reactions to human activities in Cape Cod waters. *Marine Mammal Science* 2, 251-262.

Watkins (1986) reviewed historical, anecdotal records to assess changes in whale responses to vessels near Cape Cod, Massachusetts, USA, from 1957 to 1982. *Ad libitum* descriptions of whale behaviour were based on opportunistic observations of scientists on research cruises in the region. By comparing data collected before (17 years) and after (8 years) the advent of commercial whale-watch activities, Watkins (1986) was able to look at long-term trends and show gradual changes in whale behaviour in relation to vessels. Watkins (1986: 252) noted that although "the records are largely anecdotal and not readily quantifiable... they are representative and fairly depict the observable whale reactions." Findings included: (1) whales apparently reacted to three kinds of stimuli produced by human activities: underwater sound, light reflectivity, and tactile sensation; (2) whale reactions were related to their perception of stimuli as interesting or

disturbing, expected or unexpected, and as moving towards or away; and (3) exposure to presence of human activities resulted in some species-specific behavioural changes, *i.e.*, avoidance responses by humpback whales (*Megaptera novaeangliae*) prior to whale watch activities have largely been replaced with "positive" curious responses; whereas, initially positive responses by minke whales (*Balaenoptera acutorostrata*) have changed to avoidance with exposure to whale watch activities.

Williams, R.M., Trites, A.W., and Bain, D.E. (2002a). Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: Opportunistic observations and experimental approaches. *Journal of Zoology (London)* 256, 255-270.

Williams et al. (2002a) studied responses of killer whales to whale-watch vessels in Johnstone Strait, British Columbia, Canada. Specifically, they tested the relevance of the 100m minimum approach distance specified in a voluntary code of conduct. Twenty-five individually-identified whales of known age and sex were tracked one at a time by theodolite during near-shore foraging (when animals are spread out searching for food); at the same time, observers recorded all occurrences of specified "surface-active" behaviours by the focal whale. Observations were conducted from an elevated clifftop from which whales could be observed both within a reserve where there was relatively little boat traffic and within adjacent waters where whale-watch vessels congregated. These methods provided information about dive times, swim speed, "directness" of travel, and frequency of specified behaviours for individual whales under several conditions: (1) no vessels within 3 km, (2) experimental vessel approaches, and (3) opportunistic approaches of vessels. Experimental approaches followed a "before/during" design in which 20 min of no-boat observations were followed by a controlled approach in which the experimental vessel mimicked vessel behaviour specified in local whale-watching guidelines. Findings included: (1) male whales swam significantly faster than females, indicating the potential for sex-specific responses to vessel traffic; (2) whales responded to experimental approaches by swimming in a less direct path; and (3) females responded by swimming faster and increasing the angle of successive dives.

APPENDIX TWO

Publication

Chapter 1 draws on material that also appears in:

Bejder, L. and Samuels, A. (2003). Evaluating impacts of nature-based tourism on cetaceans. *In* Marine Mammals: Fisheries, Tourism and Management Issues (eds N. Gales, M. Hindell and R. Kirkwood), pp. 229-256. CSIRO Publishing, Collingwood.