CETACEAN STUDIES USING PLATFORMS OF OPPORTUNITY
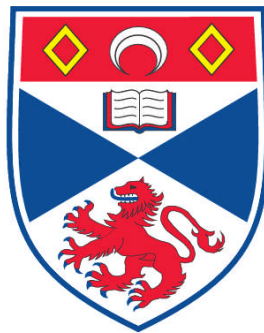
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Chapters 1-5 of this thesis have been updated and subsequently published in multi-authored articles in peer-reviewed journals. If required, citations should be made to these updated articles.

Cetacean studies using platforms of opportunity

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For a project on how to study whales on the cheap, this degree sure was expensive. The three-year cost of foreign-student tuition fees at the University of St Andrews (forget living and travel expenses) exceeded that of oceanfront property near my home in British Columbia, Canada. And it was worth every penny. Several people were instrumental in reducing my costs to study with my mentors at SMRU and CREEM, including: Ted Chamberlin and Carol Finlay (McLean Foundation); Miss Gillam (Newby Trust); Sarah Haney (Canadian Whale Institute – in landlocked Bolton, Ontario); Nancy Mackay (The Russell Family Foundation); Tom and Bonnie Murphy (and their anonymous friend at the Jane Marcher Foundation, with logistical support

ABSTRACT

As human impact on marine ecosystems continues to grow, so too does the need for sound conservation and management strategies that are informed by science. Cetaceans, the whales, dolphins and porpoises, epitomise this challenge, because they are hard to study, they have been heavily exploited in the past, and because some of their habitats, behaviours and life-history strategies make them acutely vulnerable to human activities. Unfortunately, research on free-ranging cetaceans in remote areas is costly, and financial resources are limited.

The approach used in this thesis to acquire inexpensive quantitative information on cetacean populations and behaviour was to seek out platforms of opportunity. Tourism and environmental education projects provided access to remote areas of importance to cetaceans. The topic was explored in two main areas. First, studies were conducted to investigate the use of ships of opportunity in estimating distribution and abundance, namely of Antarctic baleen whales. The second area of interest was the effect of boats on killer whales in the northeast Pacific.

Platforms of opportunity proved valuable for collecting data to model the role of measurement error on abundance estimation. Measurement error was found to be a potential source of bias in four distance estimation experiments. Platforms of opportunity could be used to train observers on protocols, and to learn to use range-finding photogrammetric equipment well before conducting dedicated surveys, which would eliminate this source of bias, as well as estimating abundance in some cases.

Abundance and distribution of three whale species were modelled using data collected aboard Antarctic tourist ships. Spatial modelling techniques were used to model distribution of minke, fin and humpback whales using line-transect data collected from a survey that could not be randomised. Strong gradients in animal density were predicted, which could be used to inform future surveys. In the meantime, rough estimates of abundance were obtained, and this approach shows promise for other areas where lack of resources makes systematic surveys prohibitively expensive.

A government-funded environmental education project provided logistical support for two studies that dealt with effects of boats on killer whale behaviour. One quantified the extent to which a particular style of whalewatching was disruptive to whale behaviour, and commercial whalewatchers agreed to halt this activity. The other found that a protected area conferred benefit to killer whales, even though it protects only a fraction of the whales' habitat for a fraction of the year.

The thesis contains four case studies that illustrate how inexpensive methods may be used to obtain practical quantitative information to aid decision-making about conservation and management of wild cetaceans that interact with (*i.e.*, whalewatching), compete with (*i.e.*, fishing) or are exploited by (*i.e.*, whaling) humans.

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Cetacean studies using platforms of opportunity

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Introduction

"More than any other form of life, whales have come to epitomize the problems of managing our living resources. For the 113 nations assembled in Stockholm in 1972, at the United Nations Conference on the Human Environment, whales became the symbol of our environmental problems as a whole. Whale conservation is a problem of endangered species, but it is far more. The situation of the whales emphasizes the problems of management of living resources in general." (Talbot, 1974)

1.1 Background

In terrestrial ecosystems, humans are an undeniable keystone species (Paine, 1969) – we influence the land around us in glaring disproportion to our biomass. But for centuries, it was held that oceans were too vast and productive for humans ever to leave a mark upon them. That view has been abandoned (Carlton, 1998). Of the 31 species of vertebrates extirpated from the southeastern North Sea during the last two millennia, more than half of the cases were attributable to overexploitation by humans (Wolff, 2000). Bottom trawling in commercial fisheries was estimated to disturb as much as half of the world's continental shelf annually – an analogous situation to clearcut logging of forests, but one that covered 150 times the terrestrial area clearcut each year (Watling and Norse, 1998). Commercial fishing reduced global stocks of predatory fish to 10% of their initial biomass (Myers and Worm, 2003). Our response, to maintain catches by targeting fish at sequentially lower trophic levels, hinders recovery of predatory fish communities in turn (Pauly *et al.*, 1998a).

How did we reach such a state of affairs? An outdated sense of the inexhaustibility of the world ocean certainly played a role. So did, in the case of bottom trawling, an

inability to see the damage caused in the marine environment by a growing human population with increasingly sophisticated technology. Mostly though, each generation viewed the state of the environment it inherited as the norm, which created what Pauly (1995) termed 'shifting baseline syndrome.' Our lack of historical perspective hindered our ability to detect change until perhaps, it became too obvious to ignore.

Our subjective perception of the environment in which we were raised is an untrustworthy tool to enable us to detect subtle, long-term changes. Yet, the need for conservation and sound management has never been stronger. If we want to manage resources sustainably, to meet the needs of a growing human population, or to protect them (conserving either for future use or because ecosystem preservation is deemed morally correct in its own right), then our efforts need to be based on good science. Objective population monitoring (Thompson *et al.*, 1998) and information on survivorship, fecundity and other demographic parameters can help inform conservation and management. By assigning magnitude and direction to population trends, we develop a reliable cure for shifting baseline syndrome.

1.2 The need for conservation and management of marine mammals

Good decisions about wildlife conservation and natural resource management are facilitated by good information about the biological systems they influence. Often, the questions that wildlife biologists pose are simple ones: How many animals? Where are they? Are we disturbing them? What resources do they need? Answering these and related questions, however, can be difficult.

These logistical problems associated with marine conservation and management may be coupled with political concerns. The wide-ranging and migratory habits of marine species (Gell and Roberts, 2003) often make them inhabitants of the territorial waters of more than one nation, or in the case of pelagic species, international waters (United Nations, 1983). The need for treaties (IWC, 1950; CCAMLR, 1980; United Nations, 1983; Kimball, 1999) to manage marine resources in international waters is illustrated by the global decimation of whale stocks through whaling (Laws, 1977; Price, 1985; Gambell, 1999; Whitehead, 2002; Best, 2003), which will be discussed in Section 1.7.

Quantitative research on marine species is important for numerous, and often conflicting, reasons. Marine mammals are of management and conservation concern because they overlap spatially and ecologically with what humans want from the oceans (*inter alia* fish, petroleum, transportation and a carbon sink). Pinnipeds (the seals, sea lions and walruses) are notorious for their interactions with commercial fisheries (Olesiuk, 1993; Fraker and Mate, 1999, Northridge and Hofman, 1999) and salmonid enhancement such as fish hatchery escapement (Yurk and Trites, 2000). Analysis of the scale of commercial fishing in the Pacific Ocean suggested that marine mammals and humans were in competition not only for prey, but also for the primary production required to sustain marine mammals and fisheries (Trites *et al.*, 1995).

Marine mammals themselves form a natural resource. Canada's harp seal hunt is the largest existing hunt for marine mammals, and its sustainability is in question (Johnston *et al.*, 2000). Cetaceans are a natural resource to the fishermen who use Ganges River dolphin (*Platanista gangetica*) as an attractant in more lucrative

fisheries (Sinha, 2002), to aboriginal subsistence whalers (Price, 1985) and to commercial whalewatchers (Hoyt, 1997).

Public support for granting special protection to marine mammals has grown tremendously in recent decades (Nielsen, 1986). Large animals are popular (Ward *et al.*, 1998). However, there are also sound ecological reasons for monitoring marine mammal populations. Marine mammals can serve as totem or umbrella species, so that by protecting their habitat, we also protect habitat for less charismatic marine taxa (Zacharias and Roff, 2001), to protect fisheries resources (McClanahan *et al.*, 1999), and to protect marine wilderness for the sake of conserving marine biodiversity (Brailovskaya, 1998).

From the herbivorous sirenians to the seal-eating polar bear (*Ursus maritimus*), marine mammals can illustrate how complex marine ecosystems (Mangel and Hofman, 1999) function across a wide range of trophic levels (Pauly *et al.*, 1998b). Like humans, marine mammals are thought to exert stronger influence on marine communities than their numbers would appear to warrant (Bowen, 1997).

The opposite effect is also evident: changes in the marine ecosystem can bring about changes in marine mammal populations and vital rates, so studying one can inform decision-making about the other. As consumers of high trophic level prey, marine mammals are subject to accumulation of fat-soluble contaminants (Ross *et al.*, 2000). These contaminants have been linked to immune system compromise in harbour seals

(*Phoca vitulina*, Ross *et al*., 1996). Response of marine mammals and their populations to these contaminants can be used to signal expected results, and to pre-empt them, in human populations, in a way that is far more convincing than laboratory studies (Ross, 2000).

Status of an Antarctic fur seal (*Arctocephalus gazella*) population mirrored variability in the waters around South Georgia (Boyd and Murray, 2001). Fur seals and other predators that breed on South Georgia could be studied more easily and more reliably than the fluctuating krill (*Euphausia superba*) to which the vertebrate populations were responding (Boyd, 2002), thereby acting as a proxy for ecosystem functioning as a whole. Similar efforts are ongoing to model how the decline of Steller sea lion (*Eumetopias jubatus*) may be used to make inferences about changes in the marine ecosystems on which they rely (NAS, 2002; Springer *et al*., 2003). Incorporating information about marine predators will become increasingly part of a wildlife biologist's job as managers shift toward ecosystem approaches to managing marine resources, and as biologists struggle with what is meant by the term (Larkin, 1996).

In addition to their role in marine resource management, marine mammals present a strong case for conservation in their own right. Ehrenfeld (1970) outlined life-history traits of animals that lend themselves inherently vulnerable to extinction: *inter alia* large body size; long gestation period; small litter size or maternal care; formation of large breeding aggregations; high commercial value for body parts and (or) an unregulated hunt; highly restricted distribution or distribution in international waters; and trans-boundary migration. This description, in whole or in part, describes most

endangered marine mammal populations (*e.g.*, vaquita, *Phocoena sinus*, Vidal, 1995; Hawaiian monk seal, *Monachus schauinslandi*, Ragen and Lavigne, 1999; northern right whale, *Eubalaena glacialis*, Clapham *et al*., 1999; southern resident killer whale, *Orcinus orca*, Baird, 2001; Steller sea lion, NAS, 2002). The vaquita has the smallest range of any marine dolphin or porpoise (Vidal, 1995) and the distribution of Hawaiian monk seal haulouts is restricted to a few square kilometers in the Northwestern Hawaiian Islands (Ragen and Lavigne, 1999). The live-capture industry for killer whales in the northeast Pacific was very lucrative (Bigg and Wolman, 1975).

1.3 The difficulty of studying cetaceans

Cetaceans, the whales, dolphins and porpoises, represent a particular challenge for population monitoring (Talbot, 1974; Donovan, 1986; Bowen, 1997; Berggren *et al*., 2002a). Their ranges are vast. Their habitat is daunting to human observers. The animals spend small fractions of their time at the surface, and even then, only small fractions of the animals' bodies are visible. Cougar (*Felis concolor*) are similarly cryptic, but they leave tracks that can be used to model population trends (Smallwood and Fitzhugh, 1995). Cetaceans do not. Unlike pinnipeds, of which some fraction of the population can be counted annually when the animals haul out to breed and moult, cetaceans spend their entire lives at sea. Despite these obstacles, and perhaps in part because of them, they are of great interest to people. While it is neither more nor less important to monitor cetacean populations than pinnipeds, monitoring cetacean populations presents a unique task for wildlife biologists.

Arboreal marsupials are difficult to study (Lindenmayer *et al*., 2003), but one can walk in their habitat. Studying pelagic cetaceans requires a ship. So cetaceans are not only difficult to study, but also they are costly to study (Burns and Wandesford-Smith, 2002; Hammond *et al*., 2002). Ideally, information necessary for cetacean conservation and management would be acquired from well-designed, well-executed and well-analysed studies. Biologists, though, are asked to provide increasingly sophisticated information (*e.g.*, predictive models and strategies that incorporate uncertainty in risk-averse plans) on tighter and tighter budgets. Canada's new Species at Risk Act, for example, aims to protect species at risk of extinction, but legislates no funding for surveys to identify which species are at risk (Smallwood, 2003).

These issues, the complexity of monitoring free-ranging cetaceans and the problem of limited resources, are exemplified best by the case of freshwater cetaceans. River dolphins are among the world's most endangered cetaceans (Perrin, 1999). The developing countries in which river dolphin habitat is often found are unlikely to have the resources needed for river-basin-wide surveys. Even if resources were available, the best survey methodology to use on these cryptic animals in muddy rivers is still in the developing stages (Vidal *et al*., 1997). At its 2000 meeting in Adelaide, Australia, the International Whaling Commission's (IWC) Sub-Committee on Small Cetaceans urged quantitative scientists to visit a range of field sites to develop appropriate methods to generate rigorous abundance estimates for these species (IWC, 2001).

Unfortunately, at a time when creative solutions to human impacts are needed most, it seems prohibitively expensive to obtain them. In the United States, it cost an

estimated \$32-42 million (1997 United States Dollars) annually to protect the habitat of known endangered species against exotic species invasion and disruption of natural fire regimes (Wilcove and Chen, 1998). In other words, after paying to identify species at risk and to protect their habitat, steep expenses remain simply to prevent those gains from disappearing over time, even in the absence of continued anthropogenic threats. Identifying and protecting endangered species cannot be allowed to be beyond the reach of developing countries. How, in the face of escalating human pressure on species around the world, can scientists' limited resources and time be used to provide the data needed to make the best possible decisions?

1.4 Platforms of opportunity

One response to the problem of limited resources is the use of platforms of opportunity. Traditionally, the term 'platforms of opportunity' has been used to describe opportunistic sightings, rather than platforms. Opportunistic sightings can be used simply to confirm presence of cetacean species in a given area, as killer whale sightings were used from the United States' Platforms of Opportunity Program (Braham and Dahlheim, 1982).

Commercial whaling statistics can be considered another form of data from a conventional platform of opportunity, although the wealth of life-history data associated with these allows researchers to ask a wider variety of biological questions from the data than from sightings alone. Whaling catch data have been used to describe diet of fin, sei and sperm whales (Flinn *et al.*, 2002). Similar data have been used to model timing of migration and population structure from whales that were once abundant, but now rarely seen, in the coastal waters of British Columbia (BC), Canada (Gregr *et al.*, 2000). Those models were later used to predict critical habitat

for five cetacean species: likely places to look for those whales as populations recover from overexploitation (Gregr and Trites, 2001).

A platform of opportunity study could be defined as one in which the platform is opportunistic, but the research is dedicated. A platform of opportunity can be defined as any resource whose primary objective is not one's own project, but a resource that can carry one's project along with it. Multidisciplinary cruises and synoptic surveys are examples of platforms of opportunity studies (*e.g.*, the IWC-CCAMLR synoptic krill survey provided IWC with an opportune platform, although the collaboration and analyses were planned in advance). Studies conducted from platforms of opportunity should be proactive, where researchers seek out research projects or other programs to share costs or provide logistical support for novel, complementary studies.

Marine mammals themselves can serve as platforms of opportunity to collect interesting oceanographic information, such as salinity, on attached dataloggers, without having to hire a ship to survey an ocean basin (Hooker and Boyd, 2003). More commonly, the platform is a ship, in which case the platform can be referred to as a Ship of Opportunity. A ferry crossing the Strait of Georgia was used to collect effort and sightings data that described seasonal variation in relative abundance of marine mammal species (Keple, 2002). An Antarctic tourist ship was used to provide a researcher with access to killer whales (*Orcinus orca*) for photo-identification and biopsy, which lead to the interesting and important finding that three ecotypes of killer whale inhabit the Southern Ocean (Pitman and Ensor, In press).

1.5 This thesis

This thesis explores these topics in two main areas: estimating cetacean abundance and distribution, mainly of balaenopterid whales in the Antarctic, and measuring the impact of disturbance on killer whales in the northeast Pacific. The following studies were aided logistically by a resource whose primary role was unrelated to the research. The platforms included ships whose main aim was carrying tourists to wild places where whales happened to be, ship time on other research projects, and a government-funded on-the-water environmental education contract to teach boaters about killer whales and whalewatching guidelines. In each of these cases, rigorous study design and data analysis methods were crucial in deriving useful data that addressed the limitations inherent in such platforms. They may be considered, loosely, to pertain in turn to the four questions often asked of wildlife biologists: How many animals? Where are they? Are we disturbing them? What resources do they need?

1.6 Estimating abundance and distribution

Chapters 2 and 3 consider one of the cornerstones of cetacean conservation and management: providing information on abundance, population size and/or trends in abundance. A census is rarely possible for free-ranging cetaceans, so techniques have been developed to sample areas or populations, and to use the sample to make inferences about the area or population from which the sample was drawn.

Two families of sampling methods to estimate cetacean abundance have developed in recent decades (Schwarz and Seber, 1999; Seber, 2002). The first is an individual-based approach. Mark-recapture statistics can be applied to biopsy samples of genetic material, or more commonly, to photo-identification data from individually recognisable animals (Hammond *et al.*, 1990). In fact, even the complete enumeration

of a population through identification catalogues can be considered a special case of mark-recapture studies, where researchers ensure that capture probability for all individuals was certain (Bigg *et al*., 1990).

The second approach, the family of distance-sampling methods (Buckland *et al*., 2001), measures animal density in terms of number of animals (or schools of animals) per unit area in a number of random samples, and uses these data to infer population size. Terrestrial surveys often use circular plots, but the most commonly used distance-sampling method to estimate cetacean abundance is a line-transect survey (*e.g*., Buckland, 1985; Buckland and Turnock, 1992; Vidal *et al*., 1997; Branch and Butterworth, 2001a,b; Hammond *et al*., 2002; Matsuoka et al., 2003a,b). A general approach to systematic shipboard line-transect surveying is to define a study area, and to place tracklines in such a way that the sampled area provides representative coverage of that area (Strindberg, 2001). The ship's route follows transects placed randomly (or systematically with a random start point), and a team of observers record effort and sightings along the way. The goal is to estimate whale density, $\hat{D}$, in each transect. Conceptually, the approach is simple: animal density is the number of animals per unit area [Equation 1.1],

$$\hat{D} = \frac{n \cdot \hat{f}(0) \cdot \hat{E}(s)}{2L} \qquad \text{[Equation 1.1]}$$

where:
    n is the number of schools observed within truncation distance, w, of the trackline;
    $\hat{f}(0)$ is the estimated probability density function of perpendicular distances, evaluated at zero distance (and is the reciprocal of the effective strip half-width);
    $\hat{E}(s)$ is the estimated mean school size; and
    L is the total length of trackline.

The area searched in the survey is estimated at the analysis stage. The length searched is the total trackline length, which can be calculated from nautical charts, or recorded using GPS. The width of the strip effectively searched for cetaceans is estimated by fitting a detection function to histograms of perpendicular distances (Buckland, 1985), because detection probability decreases with increasing distance from the trackline. Perpendicular distance is calculated from the radial distance and angle to each whale spotted. The function is scaled to model detection probability, and the value of this probability density function at zero distance (*i.e.*, $\hat{f}(0)$) is the inverse of the effective strip half-width, the width of the strip that was effectively searched either side of the trackline. The area sampled in a sightings survey, then, is twice the effective strip half-width multiplied by trackline length [Equation 1.1].

A variety of functional forms have been described for perpendicular distance line-transect models (summarised in Buckland *et al.*, 2001). Two commonly used models are the half-normal and hazard-rate models. The half-normal function [Equation 1.2] models the probability of detecting an animal (or school) at perpendicular distance, *x*, as

$$p(x) = \exp\left\{\frac{-x^2}{2\sigma^2}\right\}$$
[Equation 1.2]

where σ^2 is a parameter to be estimated. The hazard rate function [Equation 1.3] models the probability of detecting an animal at perpendicular distance, *x*, as

$$p(x) = 1 - \exp\left\{-\left(\frac{x^2}{\theta_1}\right)^{-\theta_2}\right\}$$
[Equation 1.3]

where θ_1 and θ_2 are parameters to be estimated. Note that in both cases, $p(0)=1$.

Many factors affect the distance at which cetaceans can be seen (Barlow *et al*., 2001). The most obvious example is species: a blue whale is visible at greater distance than a harbour porpoise. Less obvious examples are sea state, precipitation, swell, platform height and observer experience. These can be treated by stratifying (Buckland *et al*., 2001) or introduced as covariates (Marques, 2001). Covariates thought to have minor influence on detection probability may be ignored, since distance sampling methods are, to a great extent, 'pooling robust' (Buckland *et al*., 2001).

The following conditions must be met in order to ensure that the density estimates in the sample are unbiased (Buckland, 1985; Buckland *et al*., 2001):

1. All animals or groups on the transect line are detected. The detection function is referred to as *g(x)*, where *x* is perpendicular distance from the trackline. Hence, this assumption is often referred to as the g(0)=1 assumption. Estimates of abundance are negatively biased in proportion to g(0). For example, if g(0)=0.25, true abundance is 4X the uncorrected abundance estimate.

2. Animals or groups are distributed uniformly throughout the survey region. While this is rarely true of any cetacean population, in practice, violation of this assumption is not problematic, as long as the study is designed to give all areas equal probability of being sampled, and robust variance estimation methods are used.

3. No animal movement occurs prior to detection. Random movement of animals prior to detection causes minimal positive bias when ship speed is fast relative to animal movement (Hiby, 1982). Movement in response to the ship, though, can cause large bias in either direction (*e.g.*, Palka & Hammond, 2001).

4. Distances and angles are measured accurately. Accurate estimation of $\hat{f}(0)$ is conditional on the model being fitted to accurate perpendicular distance data. The abundance estimate is not robust to systematic bias in estimating distance.

The decision to use line-transect or capture-recapture methods to estimate abundance must be made based on the animal and the system being studied (Thompson *et al*., 1998; Schwarz and Seber, 1999). Line-transect methods were chosen over capture-

recapture methods to estimate abundance of the New Zealand reptile, tuatara (*Sphenodon* spp.), because surveys were less invasive and stressful to animals than the handling that capture-recapture would have demanded for this species (Cassey and Ussher, 1998). Line-transects can provide abundance estimates with one complete survey, whereas capture-recapture studies require at least two. The disadvantage of conventional distance-sampling surveys is that they rarely provide the individual life-history data gained from long-term photo-identification study (Hammond *et al*., 1990).

Two chapters in this thesis address abundance estimation in a line-transect framework. Chapter 2 addresses the fourth assumption, that distances are measured without error. This study represents use of ships of opportunity to gain information on the abundance estimation process, rather than about the animals. This is a good use of a ship of opportunity, because sighting a whale, and measuring range to it, may be unrelated to placement of tracklines. Exploring measurement error from a non-randomised survey can provide information of use to future designed surveys. By addressing a source of error that can bias abundance estimates, studies of how observers err when measuring distance will contribute to more precise and accurate abundance estimates in future.

Chapter 3 addresses the second assumption, that the survey has been designed to take into account the non-uniform distribution of animals in the study area. The high cost of chartering a large research vessel to cover large areas precludes their use for some areas. However, model-based methods to map animal distribution and estimate animal abundance make no assumption about placement of tracklines, except that they provide reasonable coverage. "Reasonable coverage" may be defined as a sampling method in which observations represent well the range of values of the explanatory

variables. Spatial modelling methods provide the ability to acquire information on cetacean distribution from free ship time, by modelling heterogeneity in animal density from data collected in non-randomised surveys.

Conventional distance-sampling methods can provide locations of sightings along the trackline, but how does one interpolate animal density between tracklines? Spatial modelling (Hedley *et al*., 1999; Bravington, 2003) provides an objective analytical method for predicting smooth density surfaces from observed line-transect sightings and effort data. Spatial modelling allows abundance estimation by summing predicted density across the study area.

In addition to knowing how many animals are found in an area, it is important to know how animals are distributed within that area. Data on distribution are valuable from a research perspective. Areas of high density can be targeted to make biopsy, photo-id or line-transect surveys more cost-effective or precise. Data on distribution are valuable also from a conservation and management perspective. Areas of high density can be closed to commercial fishing, if by-catch is a problem, or set aside as a protected area in the case of a food-limited population.

1.7 Antarctic balaenopterids
The subject of Chapter 3 is the information that spatial modelling methods can provide on distribution and abundance of Antarctic baleen whales (Order Cetacea, Sub-order Mysticeti) using data collected from tourist ships in the Scotia Sea. Balaenopterids (Rice, 1998) in the Southern Ocean include five species: blue (*Balaenoptera musculus*), fin (*B. physalus*), sei (*B. borealis*), Antarctic minke (*B. bonaerensis*), humpback (*Megaptera novaeangliae*) whales.

Marine mammals play an important role in the ecosystems in which they have been studied (Bowen, 1997). Baleen whales are no exception. As fish and krill eaters, they occupy a relatively high trophic level in the marine ecosystem (Pauly *et al*., 1998b). The typical baleen whale life-history strategy is to winter on low-latitude mating and calving grounds, and to summer on high-latitude feeding grounds. The Southern Ocean provides rich summer feeding grounds for Antarctic balaenids and balaenopterids (Laws, 1977). In particular, the waters off the western Antarctic Peninsula shelf have interesting physical properties (Smith and Klinck, 2002) that lead to seasonal blooms in productivity (Bathmann *et al*., 1997). The result is a summer peak in krill (primarily *Euphausia superba*) abundance that enables baleen whales to increase their mass by 50% by the end of the feeding season (Lockyer, 1972).

The lipid stored in the blubber serves as a reserve on which the whales subsist during migration to winter mating and calving grounds. It has been suggested that this annual migration is linked to reducing predation risk from killer whales (Corkeron and Connor, 1999). However, attacks of killer whales on large whales are rarely observed (Jefferson *et al*., 1991). Photo-identification studies suggest that killer whale predation on baleen whales occurs mostly in their first migration, prior to arrival on the high-latitude feeding grounds (Clapham, 2001).

Humans, on the other hand, were important predators of Antarctic baleen whales (Laws, 1977; Mizroch, 1984; Gambell, 1999; Burns and Wandesford-Smith, 2002; Best, 2003). Approximately two million whales were removed from the Southern Ocean in the previous century (Baker and Clapham, 2002) until a moratorium on

commercial whaling took effect in 1985-6 (Gambell, 1999). The history of exploitation of baleen whales in the Southern Ocean is discussed in more detail in Chapter 3. However, the importance of monitoring recovery of Antarctic baleen whales (Best, 2003; Branch and Williams, 2003) relates to the ecosystem consequences of such a large perturbation as widespread commercial whaling (Laws, 1977; Branch and Williams, 2003; Springer *et al.*, 2003). After all, monitoring the outcome of management actions, even unintended ones, is a crucial part of marine resource management (Butterworth and Punt, 1999).

Chapter 3 also represents an opportunity to try out new spatial modelling techniques on data collected from an inexpensive platform. The results are of biological interest, because the platform covers an important area for balaenopterid whale populations that are still recovering from overexploitation. The methods are of general interest, because the analytical techniques require good but not randomised coverage, and the models can be applied to changing geographic areas to suit changing management needs. The framework allows survey data to serve multiple sub-areas as stock boundaries are redefined (*e.g.*, as genetic info becomes available, as photo-identification studies find more matches, and as animals change historic distribution and range patterns). It also allows assessment of multiple surveys to compare abundance estimates or to detect trends in abundance over time, when the survey areas overlap, but are not identical.

1.8 Killer whales and whalewatching in the northeast Pacific

Chapters 4 and 5 address issues relating to killer whales in the northeast Pacific. Killer whales represent an ideal case study with which to explore conservation and

management of marine mammals. In recent decades, a dramatic shift has occurred in the way that people relate to these animals. Plans to 'cull' killer whale populations on the British Columbia (BC) coast were considered as recently as 1960 (Ford *et al.*, 1994). Today, such plans would be unthinkable. Indeed, many people are concerned that the killer whale is now too popular, and may be suffering from too much attention from people in boats (JSKWC, 1991; Kruse, 1991; Baird, 1999, 2001; Williams *et al.*, 2002, Meinhold, 2003).

What changed? People's attitudes certainly changed in response to live-capture of killer whales for display (Newman and McGeer, 1966; Bigg and Wolman, 1975). Undoubtedly, concern over the number of killer whales being captured between 1962-1973 prompted a killer whale photo-identification study to estimate abundance. The study found quickly that the number of killer whales in BC waters was far smaller than expected, and in the process, discovered that three sympatric ecotypes inhabit the region (Bigg et al., 1990; Ford, 1989; Ford *et al.*, 1994, 1998, 2000). The live-capture fishery was quickly regulated (Bigg and Wolman, 1975).

At the species level, killer whales are high trophic level feeders (Pauly *et al.*, 1998b; Springer *et al.*, 2003). On the level of the population, killer whales in the northeast Pacific show strong dietary preference (Ford *et al.*, 1998). Mammal-hunting transients were cited as the cause of the decline of sea otters (*Enhydra lutris*) in the northeast Pacific (Estes *et al.*, 1998). Recent modelling efforts indicated that if a fraction of killer whales switched from preying on large whales (which were decimated by commercial whaling in the Pacific) to smaller marine mammals, killer whales could

account for large, chronological population declines in northern fur seals (*Callorhinus ursinus*), harbour seals, Steller sea lions and sea otters (Springer *et al.*, 2003).

On the one hand, it is important to monitor killer whales because they may exert tremendous influence over their marine ecosystem. On the other, killer whales themselves represent a species of special conservation concern. For the fish-eating resident whales (Ford *et al.*, 1998), their preferred salmon (*Oncorhynchus* spp.) prey is in limited supply (Allendorf *et al.*, 1997). Extremely high levels of anthropogenic contaminants in lipids of mammal-hunting transients, and residents to a lesser extent (Ross *et al.*, 2000), could be contributing to population decline (Baird, 2001). Nonetheless, people continue to go out in noisy boats to watch killer whales, which may affect killer whales' ability to echolocate prey (Bain and Dahlheim, 1994).

Chapters 4 and 5 address effects of vessel activity on whales. Whalewatching is a vital component of the economies of small coastal communities (Duffus and Dearden, 1993; Hoyt, 1997). At the same time, concern is mounting that the industry may benefit at the expense of 'disturbance' to whales (as a proxy for fitness) and whale populations. Iterative management of whalewatching may compromise, by identifying whalewatching practices that minimise disturbance to whales and promoting these practices in the form of guidelines or regulations. Identifying appropriate sites and setting up field camps, though, can be time-consuming and expensive.

Chapter 4 describes an attempt to cut the cost of experimental research on the effects of one type of human activity on the behaviour of northern resident killer whales (Ford *et al.*, 2000), by combining the research with an environmental education contract

designed to mitigate negative effects of boat traffic on whales. Government commitment to the education contract provided boats and a field camp, and legislated access to a restricted vantage site. Chapter 4 illustrates a cost-effective way of getting information needed for management, while minimising the costs of logistical support.

Chapter 5 expands the discussion of human disturbance, but considers the value of excluding all human activity from a protected area of importance to the whales. Note that this chapter does not address whalewatching *per se*, but presence of any form of vessel traffic, including commercial fishing boats. A key question regarding human disturbance to whales is whether short-term avoidance behaviour carries an energetic cost. Whalewatching guidelines were designed to mitigate disturbance as evidenced by short-term behavioural reactions to boats, but it is unknown whether disturbance carries energetic cost to whales or disruptions to daily activity budgets. Chapter 5 presents a case study where it was possible to estimate roughly the energetic demand of killer whales in the presence and absence of boats, at a minimal cost.

The study took place near Robson Bight – Michael Bigg Ecological Reserve in Johnstone Strait, British Columbia, Canada, which was established as a killer whale sanctuary in 1982. The Reserve reflects the view that while guidelines are an integral component to managing whalewatching, no guidelines are as effective as a no-boat zone. A study of the effectiveness of the Reserve's no-entry policy showed near-perfect boundary compliance among commercial whalewatchers and near-perfect indifference among commercial fishermen (Wong and Williams, 1998).

Twenty-one years after its creation, the Reserve's benefit to whales remains largely unexplored. This chapter assesses whether one benefit might be the conservation of rare behaviour. Similarly, is there an energetic benefit to whales of a temporary refuge from whalewatch boats? Can one measure such a benefit without tagging animals? Would benefits increase if fishing boats and other non-whale-oriented traffic avoided the Reserve as well? Managers want answers to those questions, but fieldwork is costly. Chapter 5 represents attempts to answer these questions by piggybacking dedicated research on an environmental education project. The study represents a model that other researchers could use to look for overlap between whales and fishing, or to assess the utility of a marine protected area that is respected by a fraction of boaters and used by a fraction of the whale population for a fraction of the year.

1.9 Synopsis

This thesis describes four attempts to use inexpensive ways to obtain useful quantitative information to inform conservation and management for cetacean populations that have been, or still are, subject to anthropogenic impact of some kind. Managers and conservationists alike need information on cetacean abundance, distribution, human disturbance and energetic needs. Multipurpose studies are an attractive means of acquiring some of the information that is most expensive to obtain. The limited resources allocated to conservation work create an obligation to do the best we can with the means at our disposal.

Conducting research from a platform whose role, by definition, takes precedence over one's research is not without its difficulties. In the following chapters, four cases are presented that share a common theme of rigorous honing of study design,

methodology, analysis when using limited financial and human resources. In each of the four cases, flexible study design and data analysis methods were crucial in deriving useful data from these platforms, mostly because sampling effort was restricted by the platform.

Common aspects of the four studies will be presented, in an effort to answer questions affecting species where they meet humans as their competitors, predators and sometimes-intrusive followers. The goal of the thesis was to explore how inexpensive methods may be used to obtain useful quantitative information to aid decision-making about conservation and management of wild cetaceans that interact with (*i.e.*, whalewatching), compete with (*i.e.*, fishing) and are exploited by (*i.e.*, whaling) humans.

Chapter 2

Measurement error in cetacean sightings surveys

ABSTRACT

Line-transect estimates of abundance assume that distances and angles to animals are measured without error. Biased distance measurements will lead to corresponding bias in abundance estimates. Efforts to address this have been made, but measuring distance to cetaceans at sea remains problematic. Four distance estimation experiments were conducted from ships of opportunity to explore relationships between estimated and measured distance. Heteroscedasticity was found in all four cases. Preliminary evidence suggested that one observer differed in the ability to judge distance to fixed, continuously visible cues and ephemeral, cetacean cues. Two studies found visual estimates to be positively biased, and two studies found reticule measurements to be negatively biased. The data indicated that correction factors varied widely by observer, and were sometimes non-linear. Errors in three studies showed positive skew, suggesting that ranges were overestimated to a larger degree than they were underestimated. If reticule and photogrammetric measurements yield log-normally distributed (or positively skewed) errors generally, then a least-squares regression will always overestimate the correction factor, underestimate range, and overestimate abundance. Photogrammetric methods to measure range to cetaceans performed well, and their use is encouraged. When measurements cannot be made to all sightings, however, it is recommended that ample ship time be committed to distance estimation experiments that generate sufficient sample size (of the target species and conditions typically encountered in the survey) to assess error distributions, examine evidence for non-linearity, and consider inter-observer differences. Ships of opportunity may be used as cost-effective platforms for fine-tuning survey protocols, and for training observers to measure distance accurately.

2.1 INTRODUCTION

2.1.1 Estimating animal abundance

Information on animal abundance and trends in abundance plays a key role in any wildlife conservation or resource management strategy (Thompson *et al*., 1998). Although the information is crucial, acquiring it is often difficult. This holds especially true for cetaceans, the whales, dolphins and porpoises, which occupy a challenging marine habitat and display diving behaviour that makes abundance estimation particularly problematic. Complete censuses have been conducted for some killer whale populations (Bigg *et al*., 1990; Ford *et al*., 2000), however in most cases,

complete enumeration is not possible. The alternative is to design a survey to sample animals or their habitat, and to use the survey results to make inferences about the population from which the samples were drawn.

2.1.2 Assumptions of design-based surveys based on perpendicular distance-sampling methods

The simplest distance-sampling methods to estimate cetacean abundance (which multiply estimated mean animal density by the total study area) assume that the sample is representative of the area from which it was drawn, and that animal density was measured accurately. The former assumption is satisfied at the survey design stage (Buckland *et al*., 2001) of a design-based survey. The latter assumption is addressed, among other ways, by ensuring that distances and angles are measured accurately in the field (Buckland *et al*., 2001, Chapter 1). Accurate estimation of $\hat{f}(0)$ is conditional on the model being fitted to accurate perpendicular distance data. The abundance estimate is not robust to systematic bias in estimating distance.

Thus, a fundamental assumption underlying distance-sampling techniques is that radial distances and angles to animals are measured without error (Chen, 1998; Barlow *et al*., 2001; Buckland *et al*., 2001; Palka and Hammond, 2001). Analysis of measurement error in a wooden stake dataset in which true and estimated distances were known revealed that systematic bias in underestimating distance caused much greater bias in abundance estimates than the random error associated with rounding (Alpízar-Jara *et al*., 2001). In general, line-transect methods are thought to be robust to small random errors in distance estimates, as long as no systematic bias is present (Chen, 1998; Chen and Cowling, 2001). More recent work, however, challenged this relaxed assumption. Marques (2003) found that even random error in perpendicular distance measurements

caused overestimation of density in both simulated and real datasets. It is this error in radial distance estimation that is the focus of this study.

The importance of addressing measurement error in sightings surveys becomes clearer when realising that people generally are unable to judge distance accurately at sea (Schweder, 1996, 1997; Baird and Burkhart, 2000). While trackline length, L, is measurable directly, $\hat{f}(0)$ must be estimated from the sightings data. Bias in perpendicular distance data, x, leads to proportional bias in the resulting estimate of effective strip half-width. For radial distance methods, bias in the abundance estimates is proportional to the square of the bias in distance. Abundance estimates from cue counts of North Atlantic minke whales were positively biased by 25% when measurement error exceeding a CV of 10% was ignored (Borchers, 2002).

A distinction must be drawn between surveys designed to estimate absolute abundance, and those surveys from which relative abundance estimates will be used to detect population trends over time. If the latter is the case, then measurement error can be ignored if it remains constant over time (*e.g.*, if the same observers are employed on each survey, and if their ability to judge distance does not change with age and experience). Relative abundance estimates were used to identify that Greenland beluga (*Delphinapterus leucas*) populations were declining (Heide-Jørgensen and Reeves, 1996). However, ignoring measurement error for this reason may be counter-productive. Unmodelled measurement error in this scenario will remain a source of variance that will confound analysis of trends over time, especially if observers vary in their ability to judge distance (Baird and Burkhart, 2000). If an absolute abundance estimate is required, to calculate harvest levels (Johnston *et al*., 2000) or to assess

whether by-catch exceeds some threshold (Wade, 1998; Berggren *et al.*, 2002b; Hammond *et al.*, 2002), then measurement error becomes more problematic.

In summary, measurement error has the potential to introduce large bias in abundance estimates from line-transect sightings surveys. Considering its relative importance, it has received surprisingly little treatment from an analytical point of view. Perhaps this reflects conventional wisdom that it is better to collect accurate distance data in the field than to develop analytical methods for coping with biased data. However, measurement error has also received infrequent attention in terms of developing new field methods.

2.1.3 Field methods to collect unbiased distance measurements

It is difficult to measure distance to free-ranging animals from a moving platform (Quang and Becker, 1996; Schweder, 1997; Alpízar-Jara *et al.*, 2001; Branch and Butterworth, 2001a,b; NAMMCO, 2001; Bravington, 2002; Hammond *et al.*, 2002; Thiele *et al.*, 2002; Marques, 2003; Matsuoka *et al.*, 2003a,b). Methods for measuring distance require typically a stationary platform (*e.g.,* for theodolites) or a stationary target (*e.g.,* for laser rangefinders). In shipboard sightings surveys, the platform pitches and rolls, and the animals provide a challenging, ephemeral target.

Although considerable efforts have been made in some studies to ensure that unbiased distance measurements are collected in the field (*e.g.*, Thompson and Hiby, 1985; Lerczak and Hobbs, 1998; Leaper and Gordon, 2001; Hammond *et al.*, 2002), measuring distance to cetaceans on shipboard surveys remains problematic. Sightings surveys that rely on visual estimates of range tend to devote substantial time to

training observers (Hammond *et al*., 2002), however observer training is limited by the expense of ship time.

Many cetacean sightings surveys use binoculars marked with reticules to measure distance. Trained observers can collect unbiased distance estimates to buoys using reticule binoculars under good conditions (Lerczak and Hobbs, 1998). Without adequate training, however, these measurements can introduce a systematic bias that may vary among observers (Thompson and Hiby, 1985).

One recent technological advancement that addresses errors in distance estimation is the development of photogrammetric methods for measuring range (Leaper and Gordon, 2001). This technique involves mounting a video camera to binoculars, and allows unbiased distance measurement to free-moving cetaceans. Video-tracking techniques also allow observers to make extensive voice notes and to archive sightings for subsequent re-analysis as new questions arise. This technique offers promise for widespread future use on sightings surveys.

2.1.4 Distance estimation experiments
If the distance to sightings can only be estimated by eye, some fraction of the survey can be used to conduct experiments that compare estimated and measured distance to the same target. Distance estimation experiments can also allow reticule measurements of distance to be compared with 'truth,' as measured by radar. Experiments can also play a valuable role in training observers.

The role of the distance estimation experiments in this study was to allow simple measurements (such as visual estimates) to be related to better (but perhaps costlier in

terms of time or money) measurements, and to use that relationship to develop an appropriate correction factor to remove bias from the remaining estimates. Indeed, estimated distance and angle experiments have become part of the International Whaling Commission's (IWC's) standard methods for cetacean sightings surveys (IWC, 1994b; Burt and Stahl, 2000).

In a typical distance estimation experiment, a number of reflective marker buoys are launched through which the ship travels at the same speed as under typical searching conditions. Observers record distance to these objects using the methods used to measure range to cetaceans under normal survey conditions. At the same time, a measurement to the object is made using radar, and observers are not provided with feedback on the true distance. Subsequently, the relationship between observers' estimates and radar measurement is used to develop observer-specific correction factors. Although these radial distances are often measured using reticule binoculars, on some surveys, observers are trained also to estimate distance with naked eye (Hammond *et al.*, 2002; Schweder, 1996).

2.1.5 Potential problems with distance estimation experiments

Cetacean sightings surveys may differ in several respects from the conditions under which experimental data typically are collected. There may be qualitative differences in the way that the human eye perceives distance to fixed, continuously visible targets such as floats, and transient cues such as a whale's blow or body. Similarly, observers using reticule binoculars may have more time to measure range to fixed targets than to cetaceans, thereby improving apparent performance. Environmental conditions such as sea state may remain constant while distance experiments are conducted, but vary throughout the survey. Simple linear correction factors may be overly simplistic if

underlying relationships are non-linear. Mean-variance relationships may violate the assumptions of a least-squares regression. Errors may be related to unmeasured covariates, such as sea state, target size, aspect or bearing. Addressing these problems will require a large number of observations to choose the best correction factor. However, the expense of ship time on systematic surveys may make it difficult to collect sufficient sample size to investigate any deviation from assumptions of linearity and normal error distributions, or to model covariates that may affect error.

2.1.6 This study

The primary goal of the work presented in this Chapter was to use photogrammetric methods to develop a suitable correction factor for an observer's radial distance estimates to free-moving cetaceans on a sightings survey in the Southern Ocean (Chapter 3). The secondary goal was to explore other concerns inherent in using fixed-target experiments to correct radial distance estimates – namely inter-observer and methodological differences; non-linear relationships between estimated and measured range; and mean-variance relationships that violate the assumptions of a least-squares regression – using data from sightings surveys on a wide range of targets under a wide range of conditions. This chapter presents four case studies where radial distances to the same objects have been made using two methods simultaneously. It makes use of data collected from four Platforms of Opportunity. A brief synopsis of each study is given below.

2.1.6.1 Study 1

The study aimed to collect sufficient sample size to look for a relationship between estimated and measured range that was best described by models other than least-squared regression techniques, as evidenced by non-linear relationships or non-

normality of errors. The primary goals of the distance estimation component of Study 1 were to:

1. assess the relationship for one observer between estimated distance (using naked eye) and measured distance (using photogrammetric methods) to free-ranging animals at sea,

2. test whether the relationships between measured and estimated differences were similar for fixed and transient cues,

3. assess whether performance was affected by sea state,

4. correct radial distance estimates to on-effort sightings, and

5. assess the effect of correcting radial distance estimates on estimates of effective strip width for two target species; minke and humpback whales.

2.1.6.2 Study 2
The primary goals of the distance estimation component of Study 2 were to:

1. assess the relationship between estimated (using naked eye) and measured (using laser rangefinders) distance to fixed objects (namely floating vegetation and life preservers), and

2. test for inter-observer variation in relationships between estimated and measured distance to fixed objects for six observers.

2.1.6.3 Studies 3 and 4
The primary goal of the distance estimation component of Studies 3 and 4 was to assess the relationship for one observer between distances measured to free-moving animals at sea using reticule binoculars and photogrammetric methods.

A summary is shown in Table 2.1. In all four cases, the data came from distance estimation experiments, rather than distance training exercises. Therefore, observers were given no feedback on their performance during the trials. This Chapter presents results from four sets of experiments (Table 2.1) designed to assess how observers measured range to a variety of targets, using visual, reticule, laser range-finding and photogrammetric methods.

Study	Cue type	Measurement process	Observers
1	Fixed and transient	Naked-eye vs. photogrammetric measurement	1
2	Fixed	Naked-eye vs. laser rangefinder measurement	6
3	Transient	Reticule vs. photogrammetric measurement	1
4	Transient	Reticule vs. photogrammetric measurement	1

Table 2.1. Summary of four distance-estimation experiments conducted during this study.

2.2 METHODS

2.2.1 Study 1
2.2.1.1 Data collection

The first distance estimation experiment was conducted from a Ship of Opportunity in the Scotia Sea. Study 1 was a small component of a larger opportunistic sightings survey being conducted aboard m/v *Explorer* during the austral summer of 2001-2002 (Chapter 3). *Explorer* is an ice-strengthened ship that takes up to 99 passengers from Ushuaia, Argentina or Port Stanley, Falkland Islands [Islas Malvinas] on expedition-style cruises to the Antarctic Peninsula and nearby sub-Antarctic islands.

The calibration experiment was conducted between 5 December 2001 and 12 February 2002. The range-finding apparatus was a Canon Elura 2 (NTSC) mini-digital-video (DV) camcorder mounted to Tasco 7X50 binoculars and stabilised with a monopod. Camera height was 13.8m above sea level. Measurements were made from the primary platform to two points on the ship's bow (Figure 2.1), and these points were

used to calibrate across the range of magnifications used in the study (Leaper and Gordon, 2001). One observer (Rob Williams) was used in the experiment.
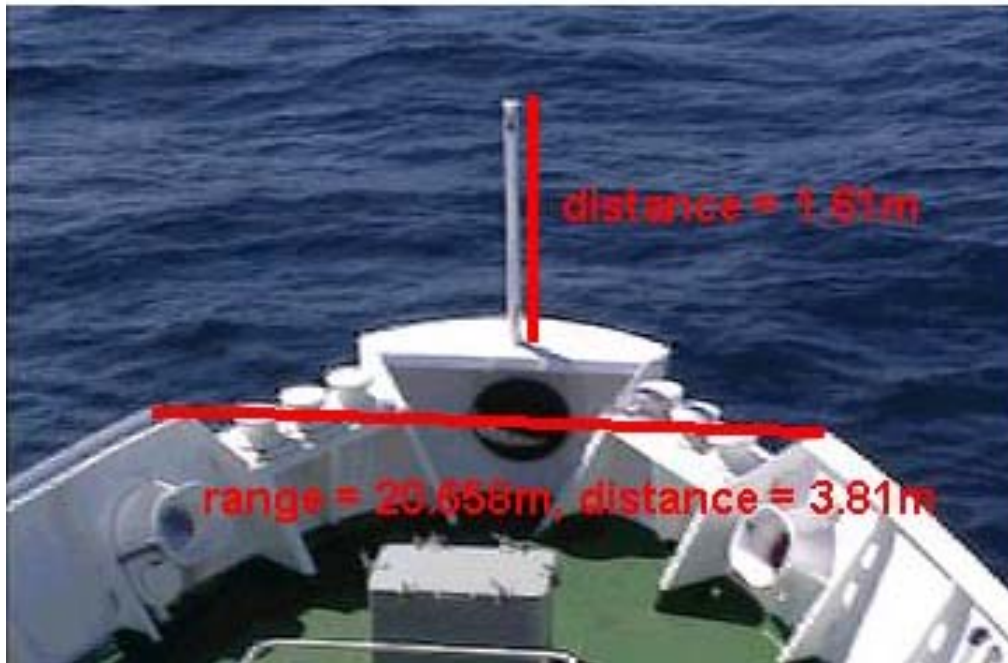
Figure 2.1. Two calibration points on the bow of m/v *Explorer*. This still was captured from the primary searching platform at a camera height of 13.79m. A similar calibration shot was made after each sighting at each level of magnification used in the experiment.

The distance estimation experiment was conducted when the ship was engaged in activities that were unsuitable for the primary sightings survey, and are subsequently referred to as 'off-effort' conditions. Typically, the ship was deemed to be 'off-effort' when it deviated from a trackline to engage in whalewatching activity, or when it was following a very short (*i.e.* less than 30 minutes) or convoluted trackline between anchorage sites, where passengers were sent ashore in Zodiacs (inflatable boats) for land-based wildlife viewing activities.

While the ship was moving at cruising speed, the observer scanned from the primary platform with naked eye. When an object was detected, the observer began recording

on the camcorder and making simultaneous voice notes on the same DV cassette using an external microphone. The observer decided whether the object in question formed a fixed cue (*i.e.* it remained visible at the surface for the entire time it took to find it, judge distance, and record the object and the distance estimate voice note on the video cassette). Cues were deemed to be transient cues if the object submerged at least once during this procedure. Transient cues targeted for this exercise included cetaceans, pinnipeds and penguins. Fixed cues included fur seals and penguins resting on the surface, Zodiacs and chunks of ice that were approximately whale-sized or smaller.

When a fixed target presented itself, or when an animal surfaced presenting a transient cue, the observer made a voice note of the estimated range in metres. Immediately following each video sequence of a surfacing, the observer captured a digital still image of one of the two calibration points on the ship's bow at the same level of magnification. Whenever the level of magnification allowed it, the horizontal line in Figure 2.1 was used. Whenever a sighting required a degree of magnification such that the default calibration points could no longer fit in the field of view, the vertical line in Figure 2.1 was used for calibration.

At the end of the experiment, the videotape was reviewed by linking the camcorder to a PC equipped with InterVideo WinCoder software. When the voice note indicated a surfacing where a simultaneous naked-eye estimate was made, a digital still image was captured and stored as a bitmap file (Figure 2). Program LENRAN was used to convert these bitmaps, given the camera height and magnification calibration, into range estimates (Leaper and Gordon, 2001).

Figure 2.2. Digital still from a video sequence of a fin whale surfacing during the distance estimation experiment. LENRAN requires input regarding two points (1,2) on the horizon, one at the object of interest (3), plus camera height and magnification. Range to the whale is calculated from the trigonometric relationships described by Leaper and Gordon (2001).

2.2.1.2 Data analysis

A dataset was compiled from all paired observations (those estimated by eye versus those calculated using photogrammetric methods) of both fixed and transient cues. These data were analysed in program R using a variety of linear- and non-linear modelling techniques (Krzanowski, 1998) to regress estimated range on measured range. The decision to include cue type (fixed versus transient) as a covariate was driven by a variation on Akaike's Information Criterion (AIC; Akaike, 1973), in which models carry a penalty for additional parameters. The variant used in this study adjusted the penalty to account for small sample size (AIC_c; Burnham and Anderson, 2003).

Model selection was guided by the desire for an explanatory model that best fitted the data, rather than a mechanistic model to explain plausibly how the errors were generated. Recall that the requirement for distance sampling is a model that produces corrected radial distance estimates that are unbiased on average (Chen and Cowling, 2001). Model selection was aided by visual methods that assessed which model fit the data best across the entire range of observations (*i.e.*, models were favoured when diagnostic plots of their residuals showed uniform spread across the x- and y-axes).

A three-stage model selection protocol was used. First, a least-squares regression was made of estimated range on measured range. If residuals indicated a relationship between range and variance, then the data were log-transformed and the model refitted. If residuals of the second model showed evidence of non-linearity, then a generalised additive model (GAM) was fitted using package mgcv for R (Wood, 2001), with variance proportional to range. GAM-fitting in mgcv uses cross-validation to select automatically the optimum degree of smoothing, with penalties for unwarranted smoothing. If the estimated degrees of freedom (e.d.f.) optimised by the smoothing process in mgcv for the measured range term was greater than one, then the model was selected. If the e.d.f. was near 1, then the log-transformed linear regression was selected. More details of mgcv are given in Chapter 3.

The selected model was used to transform estimated radial distances from a survey (Chapter 3). These and measured angles were used to calculate perpendicular distances, which were modelled in DISTANCE 4.0 Release 2 (Thomas *et al.*, 2001). A half-normal model (Equation 1.2) was fitted to both sets of perpendicular distances (*i.e.*, uncorrected and corrected) to explore how the probability of sighting an animal

decreased with increasing perpendicular distance from the trackline. This estimated the extent to which correcting an observer's ability to judge radial distance altered the estimates of strip half-widths effectively searched for whales.

2.2.2 Study 2
2.2.2.1 Data collection
Study 2 was conducted from a small (c. 15m length, 5m eye height) boat during off-effort legs of a survey for boto (*Inia geoffrensis*) and tucuxi (*Sotalia fluviatilis*) in the Amazon River (S. Hedley, F. Trujillo and R. Williams, unpublished data). Six forward-facing observers conducted the experiment from the main sightings platform on 1 April 2002. A data recorder chose fixed targets only to which observers judged range, because dolphins proved to be inadequate targets for rangefinders. Each observer wrote down the trial number (22 trials), target position (*i.e.*, ahead, port, starboard, abeam), and estimated distance, in order to retain observer independence. The data recorder measured true distance using Bushnell rangefinders. Sea state was not recorded, because the river remained calm throughout the experiment.

2.2.2.2 Data analysis
A dataset was compiled from paired observations (visual estimates versus rangefinder measurement) for each observer. These data were analysed in program R using the three-stage model specification protocol described for Study 1. The decision to include the observer as a covariate was aided by AIC_c.

2.2.3 Study 3
2.2.3.1 Data collection
Study 3 was conducted from a small ship at the discretion of the cruise leader during off-effort legs of a dedicated sightings survey for killer whales (*Orcinus orca*) and balaenopterid whales in the Gulf of Alaska (Zerbini et al., 2003). One observer (Alex

Zerbini) was used in the study, and the experiment was conducted from a small cargo ship named *Coastal Pilot* (length 53m and camera height 9.18m). The observer scanned using 7X50 binoculars to which a digital camcorder was mounted. At first sight of a cetacean school, a voice note was made onto the videotape to record species and reticule reading. Next, a calibration shot of the ship's bow was taken. Reticule readings were converted to range using the trigonometric relationships described in Lerczak and Hobbs (1998). A digital still image was taken from the video at the time of the surfacing to which the reticule reading applied, and converted to range using program LENRAN using the methods described for Study 1.

2.2.3.2 Data analysis
A dataset was compiled from all paired observations (those measured using the reticule binoculars versus photogrammetric methods) to transient cues for each of three cetacean species. These data were analysed in R using the three-stage model specification protocol described for Study 1, where photogrammetric measurements were treated as the independent variable. Species was introduced as a candidate covariate, and the decision to include the term in the model was driven by AIC_c.

2.2.4 Study 4
2.2.4.1 Data collection
The last distance estimation experiment was conducted during off-effort segments of a sightings survey on *James Clark Ross* between 5 January and 10 February 2003. One observer (Russell Leaper) collected the data. Reticule and photogrammetric measurements were made to cetaceans using methods described for Studies 1 and 3, except that species identification was not available to be used in this analysis. Reticule distances were corrected for refraction (Leaper and Gordon, 2001).

2.2.4.2 Data analysis

A dataset was compiled from all paired observations (those measured using the reticule binoculars versus those measured by photogrammetric methods) to transient (*i.e.*, cetacean) cues. These data were analysed in program R using the three-stage model specification protocol described for Study 1, where photogrammetric measurements were treated as the independent variable.

2.3 RESULTS

2.3.1 Study 1

A total of 222 paired comparisons were made between naked-eye distance estimates and photogrammetric measurements to transient cues across a range of animal sizes. Of these, the majority (188) were observations of the target species of the primary sightings surveys (minke, humpback and fin whales). The remaining observations included small cetaceans (16), penguins (12) and fur seals (6). The experiment was conducted across a similarly wide range of sea states: Beaufort 1 (1 observation), 2 (43 observations), 3 (139 observations), 4 (22 observations) and 5 (17 observations). An additional 59 paired comparisons were made between naked-eye range estimates and photogrammetric measurements to fixed cues, of which most (38 observations) were zodiacs or chunks of ice and the remainder (21 observations) were animals (fur seals or birds) that were continuously visible while resting at the surface of the water.

A scatterplot of measured against estimated distance showed a roughly linear relationship (Figure 2.3; upper left) where estimated distances were overestimated by approximately 25% (estimated=1.25*measured; model fit was improved by dropping the intercept term). The variance of estimated distance increased with true range (Figure 2.3, upper right). This relationship is termed heteroscedastic (Zar, 1996). The

observed heteroscedasticity indicated that least-squares regression, which assumes constant variance, would be an inappropriate model. Generalised linear models that have other mean-variance relationships (McCullagh and Nelder, 1989) could be explored, however a simpler approach is to transform the variables (Zar, 1996).
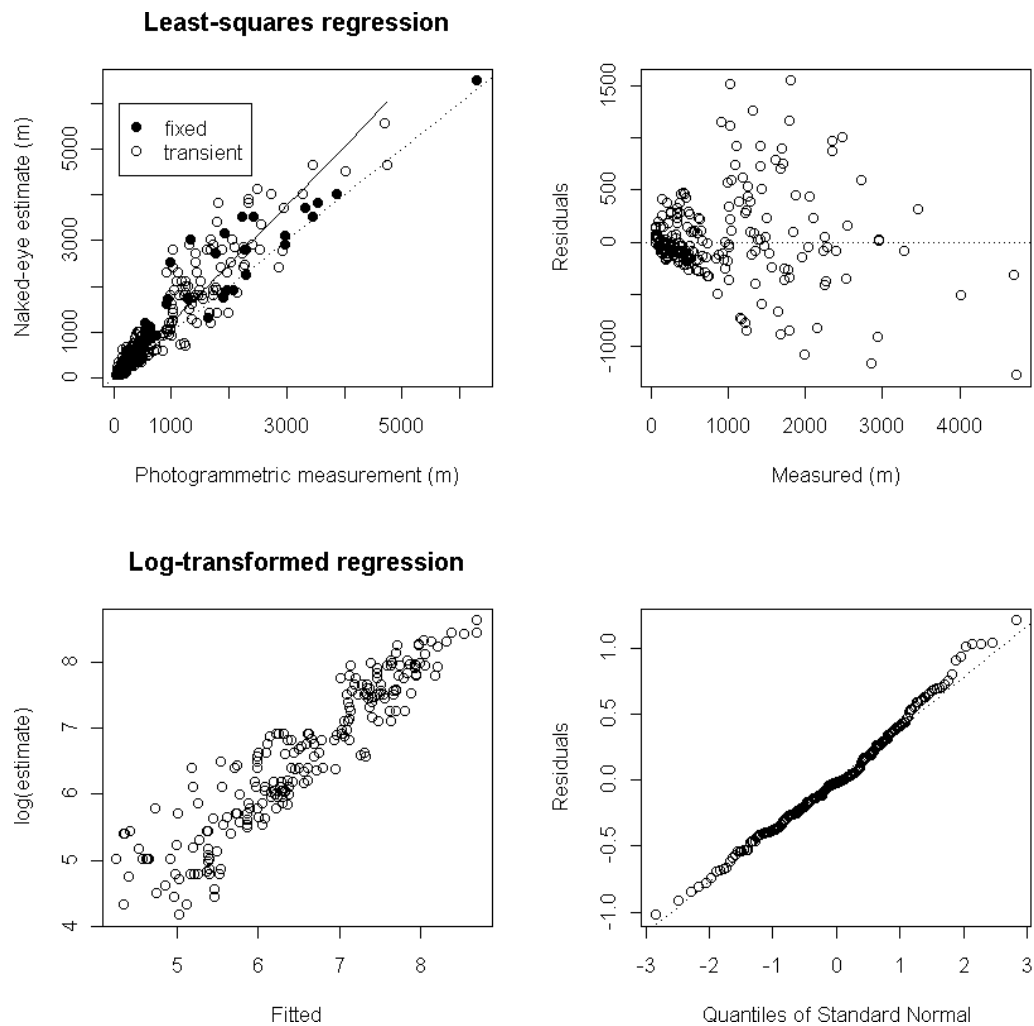
Figure 2.3. Scatterplot (upper left) showing relationship between photogrammetric measurements and naked eye estimates to fixed (closed circles) and transient (open circles) cues. A dotted line through the origin is shown with slope=1 to show an unbiased relationship. The solid line shows the fitted values of a least-squares regression applied only to transient cues at each observed value of measured range. The residuals of this least-squares model (upper right) highlight the increased variance of visual estimates at increasing range. Log-transforming x and y satisfied the constant variance assumption of least-squares regression (lower left shows log(estimate) regressed on the fitted value of a log-transformed least-squares regression). Dropping the intercept term improved the fit. The selected model, log(estimate) ~ log(measured), produced standardised residuals (lower right) that were unbiased across the range of values observed.

Plotting the results of a model where log(estimated distance) was proportional to log(measured distance) revealed a linear relationship with constant variance (Figure 2.3, lower left). The data lent support for stratifying by cue type: when cue type was introduced as a covariate, $\Delta AIC=2.07$. The intercept term was not significant at the conventional (p=0.05) level (p=0.18). Dropping the intercept term increased the R^2, lowered the AIC, and the model remained highly significant. The selected model was:

log(estimate) = 1.0282 * log(measured)

where R^2 = 0.9964, the standard error of the coefficient 1.0282 was 0.0040 (t_{220}=245.8, p< 0.00001). The model fit the data well across the range of observed values (Figure 2.3, lower right), suggesting that log transformation addressed adequately the problem of heteroscedasticity.

The relationship between measured and estimated ranges to fixed cues showed a similar relationship:

log(estimate) = 1.0422 * log(measured)

where R^2 = 0.9975, the standard error of the coefficient 1.0422 is 0.0068, t_{58}=152.2, p< 0.00001. Comparing the two regression coefficients provided some evidence that the two slopes differed from one another (t_{277}=1.752, 0.05<p<0.10). Range estimates to fixed cues were omitted from subsequent analyses because the primary aim of the study was to develop a suitable factor to correct range estimates to cetaceans.

Further efforts to explore non-linearity or other mean-variance relationships failed to produce a better-fitting model than this one. Similarly, the additional explanatory power gained by including information about sea state was insufficient to justify including additional variables in the model in terms of AIC.

This equation was rearranged to calculate a correction factor for visual estimates of radial distance to whales, where:

$$\text{corrected distance} = e^{\log(\text{estimated distance})/(\mu+0.5(\sigma^2))}$$

(Mood *et al.*, 1974). This equation was used to correct radial distance estimates in the primary platform sightings for minke and humpback whales during the 2000-1 and 2001-2 field seasons. The effects of correcting radial distances on estimates of effective strip width and school density are summarised for these species in Table 2.2, and the detection functions are shown in Figure 2.4.

	ESW(m)	CV(ESW)	D_s	CV(D_s)
Minke				
Uncorrected	798.6	(0.10)	0.0046	(0.26)
Corrected	657.6	(0.10)	0.0055	(0.26)
Humpback				
Uncorrected	1314.2	(0.075)	0.0046	(0.27)
Corrected	1068.6	(0.075)	0.0057	(0.27)

Table 2.2. Effect of correcting radial distances on estimates of effective strip width (ESW) and school density (D_s in schools·km^{-2}) for minke and humpback whales.

Correcting radial distance estimates reduced point estimates of effective strip width by approximately 20% (Table 2.2), which increased point estimates of school density by the same amount.
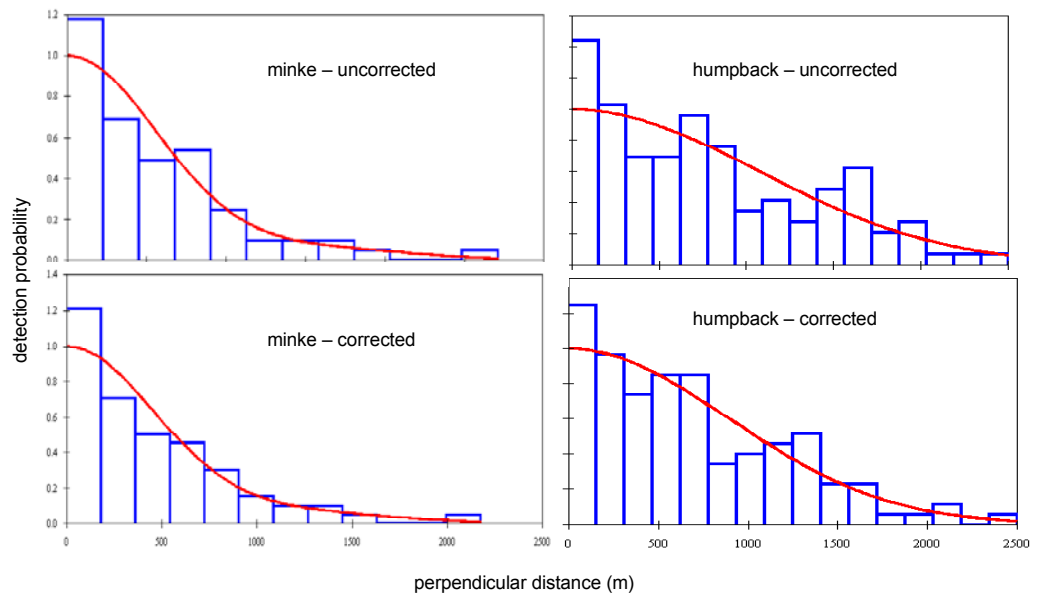
Figure 2.4. Detection functions for uncorrected (upper) and corrected (lower) radial distance estimates. The detection functions were based on 72 sightings of minke whales and on 121 sightings of humpback whales.

2.3.2 Study 2

Study 2 indicated that the six observers varied widely in the way that they estimated distance to 22 fixed objects (Figure 2.5, upper left), but that on average, observers tended to overestimate range by approximately 14% (estimate ~ 1.137 * measured; model fit was improved by dropping the intercept term). Like Study 1, the data from Study 2 showed evidence of heteroscedasticity (Figure 2.5, upper right). While model fit was improved by log-transformation, evidence remained to suggest non-linearity in the data. A GAM fitted to the data revealed that the best smoothing spline included approximately 2df (Figure 2.5, lower left). Specifying a model with variance proportional to range provided a fit whose residuals were spread uniformly along the x- and y-axes (Figure 2.5, lower right), suggesting that this model would provide corrected radial distance estimates that were unbiased on average.
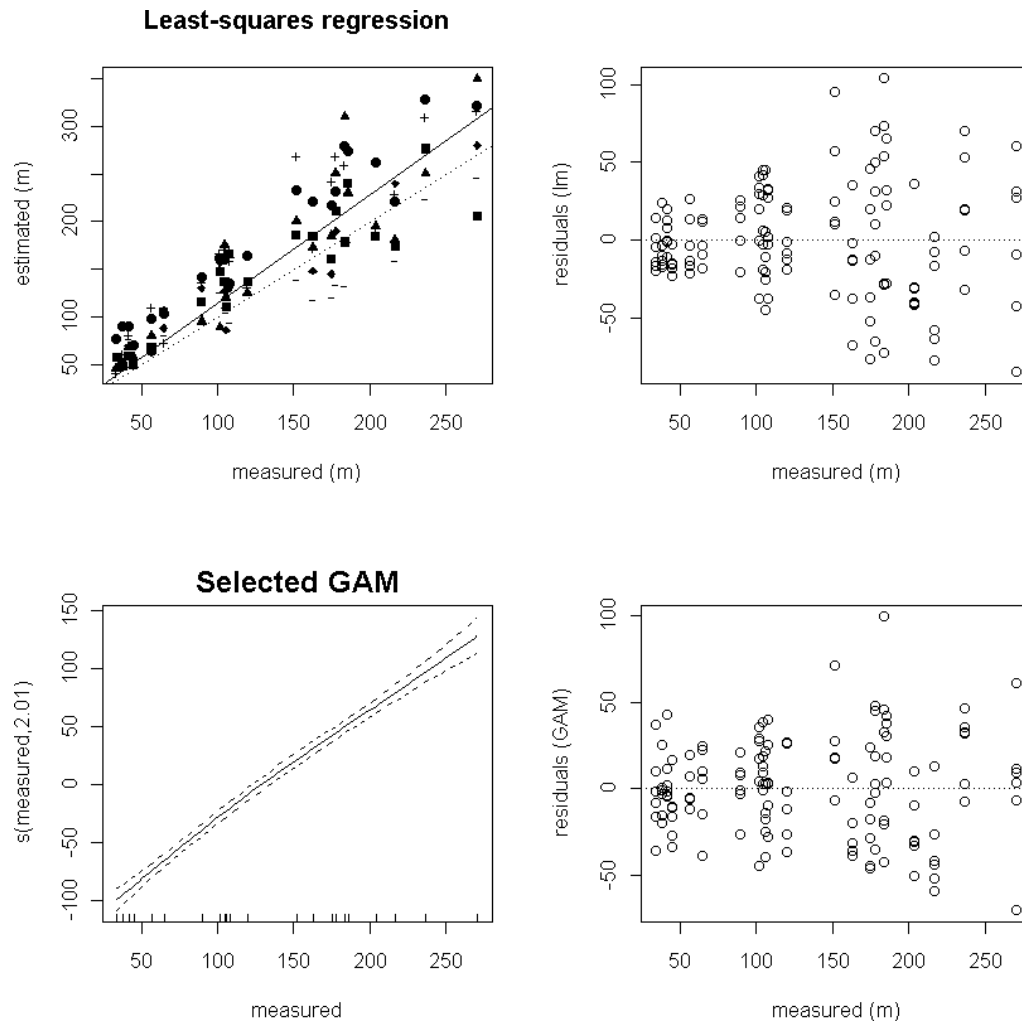
Figure 2.5. Scatterplot (upper left) showing heteroscedastic relationship between laser rangefinder measurements and naked eye estimates to fixed cues. Plot characters represent values for each of six observers. A dotted line through the origin with slope=1 is shown to illustrate an unbiased relationship. The solid line shows the fitted values of a least-squares regression averaged among all observers. The residuals of this model (upper right) illustrate the increased variance of visual estimates at increasing range. A GAM fitted to the data with variance proportional to the mean (lower left; observer included as a random factor) indicated that a smooth spline of measured distance with approximately 2df described the estimated distances best. This GAM specification produced residuals (lower right) that were unbiased across the range of values observed in Study 2, suggesting that this calibration would yield corrected distances that were unbiased on average.

The selected GAM modelled visual distance estimates as a smooth, non-linear function of measured distance, with observer as a covariate factor. The selected model is summarised in Table 2.3.

Family: Poisson. Link function: log.
Formula: estimate ~ s(measured, 10) + Observer.

Parametric coefficients:

	Estimate	std. err.	t ratio	Pr (>|t|)
(Intercept)	183.88	6.2	29.51	< 2.22e-16
ObserverB	-36.864	8.8	-4.189	5.2944e-05
ObserverC	-22.955	8.8	-2.609	0.010218
ObserverD	-35.455	8.8	-4.029	9.7364e-05
ObserverE	-6.1193	8.9	-0.687	0.49325
ObserverF	-58.273	8.8	-6.622	9.8286e-10

Approximate significance of smooth terms:

	edf	chi.sq	p-value
s(measured)	2.01	670.55	< 2.22e-16

R-squared(adj) = 0.847   Deviance explained = 85.6%   n = 131

Table 2.3. Summary of the selected model describing estimated distance as a smooth, non-linear function of distance as measured by laser rangefinders. The model formula specified in the top line indicates that the relationship between estimated and measured distances permitted a maximum of 10 knots (≈9df) of flexibility, but the optimal smoothing selected automatically in mgcv used 2.01 estimated degrees of freedom (edf). Observer was a significant covariate, and the coefficients presented can be used to calculate observer-specific correction factors. The model was highly significant, and explained approximately 85% of the variance in the observed data.

2.3.3 Study 3

Study 3 revealed a moderate discrepancy between 54 paired observations of radial distances measured by reticule binoculars and photogrammetric methods. Taking photogrammetric data as the independent variable (because those data are archived, they can be verified repeatedly), this can be interpreted as indicating bias in reticule readings. A scatterplot of reticule reading against video measurement (Figure 2.6, upper left) shows that the observer's use of reticule binoculars would have underestimated distance by approximately 20% (reticule measurement = 0.802 * photogrammetric measurement; model fit was improved by dropping the intercept term). However, the relationship was heteroscedastic (Figure 2.6, upper right), ruling out a least-squares regression of reticule reading on photogrammetric measurement. This scatterplot suggested some non-linearity in the data, however an attempt to fit a

GAM to the data in mgcv resulted in a smoothing spline with one degree of freedom (*i.e.*, a linear term).

Log-transforming the data (Figure 2.6, lower left) gave a regression, the slope of which differed only slightly from the least-squares regression. However the residuals of the log-transformed regression (Figure 2.6, lower right) indicated a superior fit to the data than the least-squares regression. Including species as a covariate improved the model fit, but resulted in a higher AIC score, so the term was dropped. The selected model was:

log(reticule range) = 0.9747 * log(photogrammetric range)

where R^2 = 0.9995, the standard error of the coefficient 0.9747 was 0.0030, p< 0.00001.
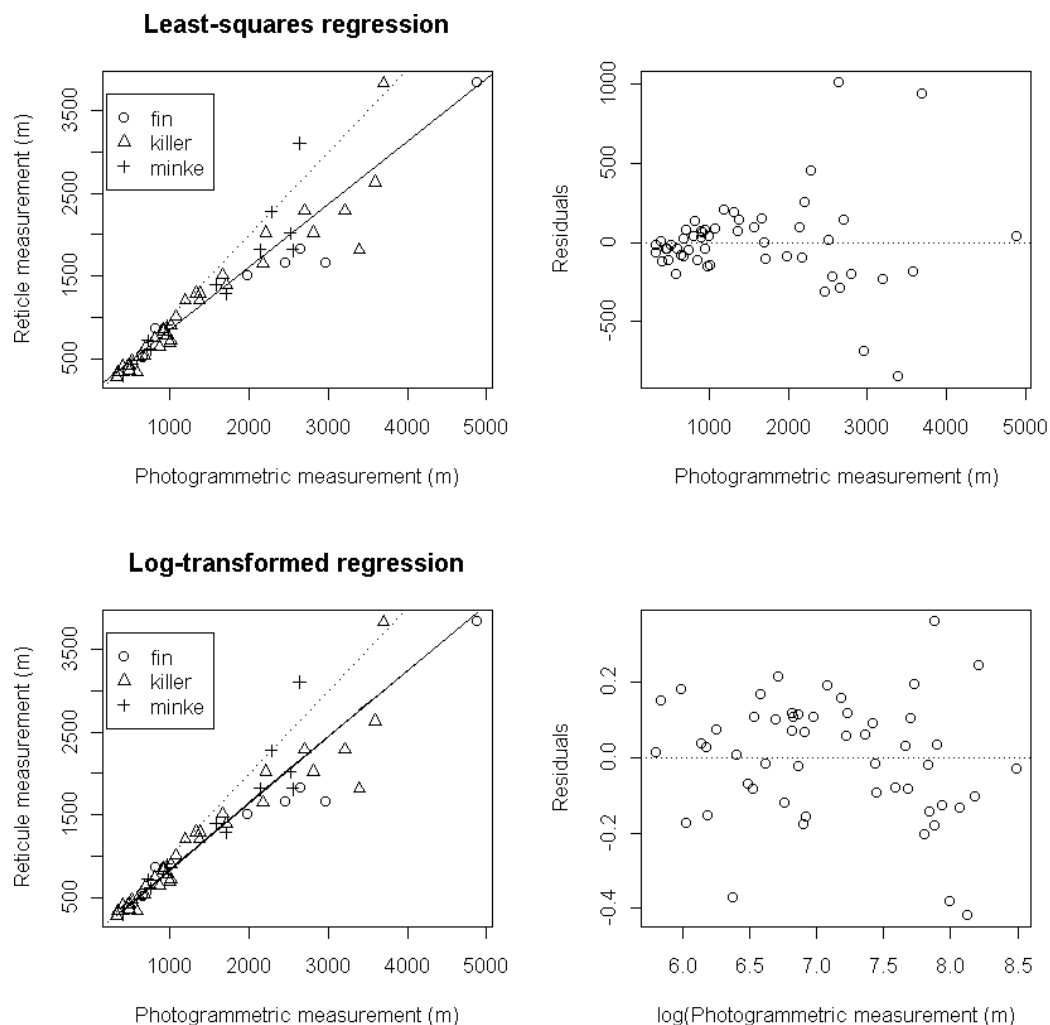
Figure 2.6. Scatterplot (upper left) showing heteroscedastic relationship between reticule and photogrammetric measurements to whales. Plot characters represent values for each of three cetacean species. A dotted line through the origin with slope=1 is shown to illustrate an unbiased relationship. The solid line shows fitted values of a least-squares regression for all three species pooled. The residuals of this model (upper right) illustrate the increased variance of visual estimates at increasing range. A regression on the log-transformed data (lower left) has a minor effect on the slope, but improves the fit (lower right).

2.3.4 Study 4

Study 4 found evidence of minor bias in reticule readings in 61 paired observations.

While the relationship between reticule and photogrammetric measurements showed

higher variance as range increased (Figure 2.7, upper left), the relationship was close

to 1:1 (reticule measurement = 0.95 * photogrammetric measurement; model fit was

improved by dropping the intercept term). Heteroscedasticity and some evidence of

non-linearity in the residuals (Figure 2.7, upper right) ruled out a least-squares regression, so a smoothing spline was explored, specifying a model with variance proportional to range. A smoothing spline with approximately 3df (Figure 2.7, lower left) was selected as the best fit by mgcv. The residuals from the model (Figure 2.7, lower right) indicated that the model fit the data reasonably well across the range of observed values, suggesting that if this GAM were used to correct radial distances, then the data would be unbiased on average.

The selected GAM modelled reticule measurements as a smooth, non-linear function of photogrammetric measurements. The selected model is summarised in Table 2.4.

Family: Poisson. Link function: log.
Formula: reticule range ~ s(video range, 10)

Parametric coefficients:

	Estimate	std. err.	t ratio	Pr (>|t|)
constant	7.4577	0.004648	1604	< 2.22e-16

Approximate significance of smooth terms:

	edf	chi.sq	p-value	
s(video range)	2.999	55253	< 2.22e-16	
R-sq.(adj) = 0.973	Deviance explained = 98.3%			n = 61

Table 2.4. Summary of the selected model describing reticule range to cetaceans as a smooth, non-linear function of distance as measured by photogrammetric methods. The model formula specified in the top line indicates that the relationship between reticule and photogrammetric measurements was permitted a maximum of 10 knots (≈9df) of flexibility, but the optimal smoothing selected automatically in mgcv used 2.99df. The model was highly significant, and explained approximately 97% of the variance in the observed data.

Least-squares regression

Selected GAM
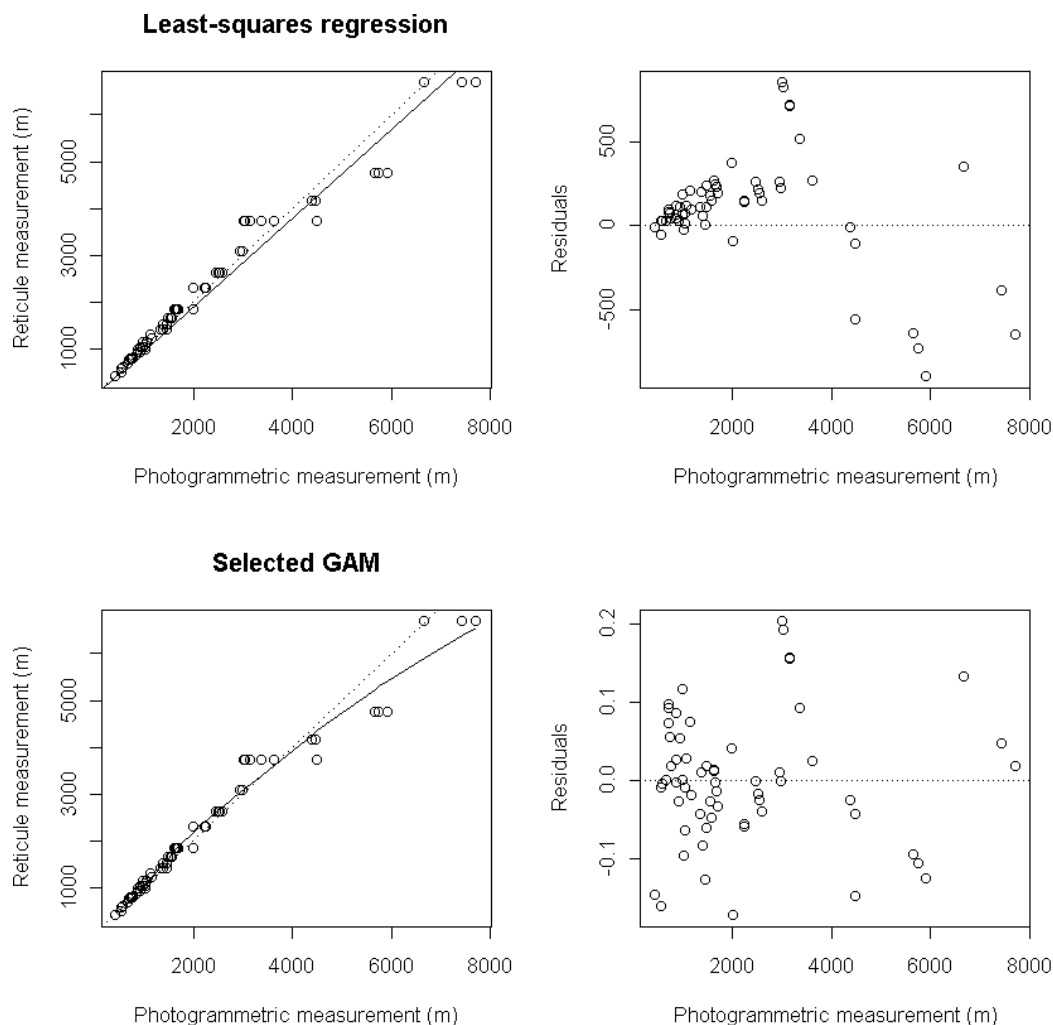
Figure 2.7. Scatterplot (upper left) showing heteroscedastic relationship between reticle and photogrammetric measurements to cetaceans. A dotted line through the origin with slope=1 is shown to illustrate an unbiased relationship. The solid line shows the fitted values of a least-squares regression. The residuals of this model (upper right) illustrate the increased variance of visual estimates at increasing range, as well as some evidence of non-linearity. Note that this model produces mostly positive residuals out to 4000m, beyond which residuals are generally negative. A GAM fitted to the data with variance proportional to the mean (lower left) indicated that a smooth spline of photogrammetric measurements with approximately 3df described the reticle measurements best. This GAM specification produced residuals (lower right) that were unbiased across the range of values observed in Study 4, suggesting that this calibration would yield corrected distances that were unbiased on average.

2.3.5 Synopsis

Bias was found to be a problem to varying degrees in all four experiments. Bias was

positive for both studies using visual estimates and negative in both studies using

reticle binoculars. All four studies found that the variance of distance estimates

increased with range. Two of the four studies indicated that the relationship between estimated and true distance might be slightly non-linear. A synopsis of the key results from the four sets of experiments is given in Table 2.5.

Study	Bias	Heteroscedasticity	Non-linearity	Comments
1	+25%	Yes	No	error differed by cue type
2	+14%	Yes	Yes	error differed among observers
3	-20%	Yes	No	
4	-5%	Yes	Yes	effect minor

Table 2.5. A summary of the key findings from the four sets of distance-estimation experiments.

2.4 DISCUSSION

2.4.1 General discussion

Measurement error was found to be a problem in all four experiments, ranging from very minor (Study 4) to substantial (Studies 1 and 3). If ignored, these larger measurement errors would have biased distance estimates downward by as much as 20% (Study 3) or upward by as much as 25% (Study 1). Note that these models considered error in radial distance, whereas detection functions are fitted to perpendicular distances, so the estimates presented impose upper limits on the extent to which bias in radial distance estimates could cause bias in abundance estimates. In the one case where radial angle measurements to sightings were available (Study 1), it was estimated that the 25% positive bias in radial distance estimates would have caused a 20% negative bias in the abundance estimates. This potential source of bias is large enough to be of general concern.

2.4.2 Reticule binoculars versus photogrammetric measurement

Reticule binoculars and video range-finding methods yielded very similar results in Study 4, but substantial bias in Study 3. Sighting conditions were excellent in Study 4

(R. Leaper, pers. comm.) and poorer (A. Zerbini, pers. comm.) in Study 3. A confounding problem is that photogrammetric methods used to measure range explicitly address refraction of light near the horizon (Leaper and Gordon, 2001). The equations of Lerczak and Hobbs (1998) ignore this, and therefore most distance range estimates using reticule measurements that are uncorrected for refraction should be considered less reliable than their photogrammetric equivalents. Study 4 corrected reticule readings for refraction and so the two are directly equivalent.

After correction for refraction, reticule measurement should be unbiased inherently (Lerczak and Hobbs, 1998). The same holds true for photogrammetric methods, but the accuracy of these methods is independent of observer training, as long as a sharp image of the target and the horizon is captured with a corresponding calibration image (Leaper and Gordon, 2001). The analyses in this study assumed that the photogrammetric measurements were more accurate than reticule readings. Under typical survey conditions (Beaufort usually 1-3, but always <7; swell no more than 1-3m) from a large oceanographic vessel (length 99m, platform height 18m), Leaper and Gordon (2001) demonstrated that measurements to fixed cues were unbiased to 5.5km, with a root mean square error of 3.5%. On the other hand, some degree of inaccuracy in reticule readings is to be expected solely from rounding to the nearest 0.1°.

The results of Studies 3 and 4 should be interpreted as evidence that observers use reticule binoculars idiosyncratically. Reticule and photogrammetric measurements are based on the same trigonometric relationships (Leaper and Gordon, 2001) and therefore, should yield the same results. However, ship movement makes reticule binoculars more difficult to use than photogrammetric methods when measuring range

to moving objects. By providing a permanent record in the form of a digital still image (in which the horizon is frozen), photogrammetric methods may provide a more reliable measurement than reticule binoculars. If the observer records in Studies 3 and 4 represent typical use of reticule binoculars on sightings surveys, then their use would generally underestimate range and overestimate abundance. The bias in reticule readings shown in Table 2.5 may suggest that observers lifted their binoculars while counting down the reticule marks. By overcounting reticules, observers underestimate range. Of course, not all observers will use reticule binoculars in the same way, but the point of photogrammetric methods is to provide an objective, repeatable, and reliable way of measuring radial distance so that this inter-observer variability can be ignored.

In both cases, making large changes to candidate models yielded relatively minor differences in the inferred underlying relationship. The difference between reticule and photogrammetric measurements was much larger in Study 3 than the difference between any candidate models. This suggests that researchers must consider accurate range estimation at the design stage of a sightings survey. The results from Study 3 suggest that asking observers to switch from one measurement type to another during a time-series of surveys could result in apparent trends in abundance due solely to measurement error.

After correction for refraction, the relationship between reticule reading and photogrammetric measurement was non-linear (Study 4). Some evidence of non-linearity was apparent in residual plots in Study 3 (Figure 2.6, upper right), although the large variance of the data would have left little power to detect non-linearity. Non-

linearity in reticule reading might be expected due to rounding to the nearest 0.1°. This will have a much larger effect on range near the horizon than it will near the observer. Indeed, much of the variance in Study 4 may be explainable from rounding error alone, and inevitably, this rounding error will introduce some non-linearity.

Photogrammetric methods may be preferable to reticule binoculars even in cases where measurement can be made to cetaceans only on some fraction of survey effort and a calibration experiment for visual estimates is required. In such cases, photogrammetric methods for correcting visual estimates of radial distance allow calibration of the process of interest directly, rather than making an untested assumption that fixed buoys are suitable proxies for cetacean cues (Figure 2.3).

The small cost of mounting a camcorder to binoculars provides data quality benefits in addition to the advantages in measuring range. Video range-finding methods provide an inexpensive and logistically practical way to make voice notes, and to archive sightings so that the data can be reanalysed as new questions emerge. For example, consider IWC's line-transect surveys that provided estimates of killer whale abundance in the Southern Ocean (Branch and Butterworth, 2001b). Recent work has identified that three ecotypes of killer whales inhabit the Southern Ocean (Pitman and Ensor, In Press). Had sightings been archived on video, one could revisit the survey data to model abundance and distributions of the three ecotypes separately, despite the fact that the data were collected when only one ecotype was thought to exist.

2.4.3 Linear on a log-log scale

It is interesting to note that the relationships between measured and perceived distance in Studies 1 and 3 were best described by log-transformation (Figures 2.3 and 2.6,

respectively).   This relationship, termed 'compression' in the psychophysical literature, may be rooted in the manner in which humans generally perceive distance. When asked to judge the sensory tasks such as brightness and loudness, human subjects often perform according to Stevens' Law, an allometric relationship between perceived sensation and stimulus intensity in which the smallest difference that observers can detect fits a logarithmic scale better than a linear one (Stevens, 1970).

Information about how humans perceive distance may yield statistical models with better explanatory power than the descriptive models presented here.   There is evidence to suggest that humans perceive range in much the same way as it is measured photogrammetrically and by reticule binoculars: by judging the angle below the horizon to the object of interest (Ooi *et al*., 2001). This may help to explain the heteroscedastic error structure observed in both visual (Studies 1 and 2) and reticule (Studies 3 and 4) experiments. Very small errors in judging declination near the horizon cause much larger errors in range estimates than similar errors do near the observer.

More importantly, note the upper right-hand graphs in Figures 2.3, 2.5 and 2.6, where the residual axis goes higher in the positive direction than in the negative direction. The errors in Studies 1, 2 and 3 showed positive skew, which suggests that visual estimates of range were overestimated to a larger degree than they were underestimated. If reticule and photogrammetric measurements yield log-normally distributed (or positively skewed) errors generally, then a least-squares regression will always overestimate the correction factor, underestimate range, and overestimate

abundance. The magnitude of this potential source of bias warrants attention in the form of simulations.

2.4.4 Fixed versus transient cues

One of the most intriguing findings to emerge from this study was that the data from Study 1 suggested different parameters for fixed cues than for transient, cetacean cues. This finding calls into question the common practice of using fixed cues as cetacean proxies in distance estimation experiments (*e.g.*, Study 2), and warrants further attention. Distance estimation experiments using fixed cues may provide the wrong correction factor because they provide observers with a longer opportunity to judge range than observers receive from transient, whale cues. Future research should identify whether this apparent difference: (1) is real; (2) represents systematic bias in fixed-cue distance estimation experiments; (3) holds true for reticule measurements; and (4) is large enough to matter in most surveys.

Clearly, if the pattern shown in Study 1 were ignored, it would have led to overestimation of correction factors and artificially increased density estimates. Consider the following example. If a cetacean were observed at a range estimated to be 100m, one would calculate a corrected distance of 82m using the relationship observed for fixed cues, and 87m using the relationship for transient cues. At an estimated distance of 1000m, the differences would be greater: 740m for the fixed-cue coefficient versus 817m for the transient-cue coefficient. At 100m, 1000m, and 5000m, the two relationships would have yielded corrected ranges that differed by 7, 10 and 13% respectively.

These radial distances and corresponding angles are converted to perpendicular distances, to which a detection function is fitted. Detection function fitting is especially sensitive to observations very near the trackline, and some models are strongly influenced by observations in the tail of the distribution of perpendicular distances (Buckland *et al.*, 2001). While distance-sampling theory appears to be robust to random errors in distance estimates (Chen and Cowling, 2001), fitting the detection function may not be robust to a source of bias that causes different measurement errors at different ranges. While truncation of distant sightings is recommended to prevent distant observations from unduly influencing the fit of the detection function in conventional distance sampling (Buckland *et al.*, 2001), model-based abundance estimation methods (Hedley *et al.*, 1999) benefit from including as many sightings as possible. A correction factor that fits the data well at small and large ranges may improve detection function fit and require less truncation. The extent to which bias in radial distance affects bias in estimated effective strip half-width will be influenced by the distribution and accuracy in angle measurements, but bias in angle measurement is minimised easily by use of angle-boards.

2.4.5 Wider Implications

The results of Study 1 illustrate a case where unmodelled measurement error would have led to an abundance estimate that was negatively biased by 20%. Study 1 also demonstrated a case where a correction factor based on a least-squares regression would have been overestimated by 7-13% if fixed cues had been used as a proxy for cetaceans. An overestimation of the correction factor would have led to an overestimate of abundance. Observers vary in their ability to judge range (Figure 2.5), so unmodelled inter-observer measurement error would reduce the ability to detect population trends, or even create the false appearance of trends as observers change

between surveys. Radial distance estimates should be measured, rather than estimated, whenever possible. This underscores the importance of proper training and distance estimation experiments on sightings surveys, and highlights the value of using simple instrumentation to measure range and bearing.

Systematic overestimation of perpendicular distances leads to underestimating animal abundance. Negatively biased estimates of cetacean abundance could have conservation implications for ecosystem modelling. Consider, for example, ecosystem approaches to managing marine resources in the Southern Ocean. Estimating sustainable levels of krill harvest will depend on accurate estimates of the total biomass of krill-eaters (Boyd, 2002), including most of the great whales that are themselves recovering from overexploitation (Laws, 1977; Mizroch, 1984; Whitehead *et al*., 1997; Gambell, 1999; Burns and Wandesford-Smith, 2002; Whitehead, 2002; Best, 2003). Negatively biased estimates of balaenopterid abundance would underestimate the krill required to sustain those populations. Conversely, systematic underestimation of perpendicular distance causes overestimation of abundance. Positively biased abundance estimates would lead to setting harvest and by-catch levels that are unduly high.

Simulations revealed that measurement error was less important when perpendicular distance data possessed a shoulder than when it did not (Borchers, 2002). In other words, distance sampling methods work best not only when $g(0)=1$, but also when $g(\text{'near 0'})=1$ (Buckland, 1985). Field methods to ensure that detection probability near the trackline is as high as it is on the trackline will eliminate much of the concern about measurement error.

2.4.6 The value of Ships of Opportunity to abundance estimation research
This study serves as an example of the value of Ships of Opportunity not only for collecting cetacean sightings data, but also as inexpensive platforms for conducting experiments that inform researchers about the sighting process itself. Distance estimation experiments do not require randomised sampling designs. Ships of Opportunity could be used for collecting data to assist existing error modelling efforts, thereby providing analysts with the opportunity to explore error in perpendicular distance measurements to cetaceans rather than, for example, golf tees (Marques, 2003). In addition, perhaps there is a role for these ships as cost-effective platforms for training observers and fine-tuning protocols prior to systematic sightings surveys. While ships of opportunity do not allow *a priori* development of an appropriate line-transect survey design, the analyst has other options. Model-based methods can be used to remove the bias associated with a non-randomised survey design, such as surveys conducted from Ships of Opportunity (Hedley, 1999; Chapter 3).

2.4.7 Synopsis
The value of measuring range to cetaceans on sightings surveys using a method that gives unbiased results is clear (Chen and Cowling, 2001). The proper approach to developing correction factors should be to plot the data, check the error distribution, test for evidence of significant covariates affecting the error, and examine the data for evidence on non-linearity. Unfortunately, there appears to be no appropriate, default method for modelling correction factors. One general recommendation is to obtain measurements in the field beyond the point at which one might expect to see the target animal (J. Laake, pers. comm.). This will allow one to look for evidence of non-linearity in the data.

However, the importance of accurate measurements, rather than those that are merely unbiased on average, cannot be overstated. Indeed, for some surveys, a correction factor may be simply not good enough. The best that one could do with a correction factor is to calculate ranges that are unbiased on average. Preliminary results of simulations suggest that the random error that remains after applying a correction factor may still cause error in detection function fitting that leads to systematic overestimation of abundance (Marques, 2003). Therefore, accurate distances will improve detection function fit, thereby reducing the variance of abundance estimates, which can be as important as bias when detecting population trends (Taylor and Gerrodette, 1993). Where possible, it is always preferable to measure range accurately in the field than to develop analytical techniques for correcting data at a later stage.

Further work is required to simulate how much bias is associated with the random errors remaining after applying a correction factor to remove bias in range estimates to cetaceans, rather than fixed cues. Additional work should explore how random error might influence detection function fitting in surveys with small sample size, or surveys that use advanced distance sampling techniques, such as duplicate sightings surveys to estimate $g(0)$, the probability of sighting an animal on the trackline, and multiple covariate distance sampling (MCDS), where detection may vary with factors in addition to perpendicular distance (Buckland *et al.*, 2001).

Leaper shared the data from Study 4. Jim Thomson helped me to build a bracket to mount the binoculars on the camera, and Kate Blowers provided training on capturing still images from digital video. Dr. Fran Allard (University of Waterloo, Canada) replied to several e-mails about depth perception. The data presented in this chapter were collected aboard m/v *Explorer* thanks to Abercrombie & Kent and the Abercrombie & Kent Global Foundation, and aboard three other ships courtesy of Patrick Shaw (Marine Expeditions and Quark Expeditions). The video camera was purchased with a grant from the Canadian Whale Institute and additional expenses covered by a grant from the McLean Foundation.

Chapter 3

Modelling distribution and abundance of Antarctic baleen whales using data obtained from ships of opportunity

ABSTRACT

Conventional distance-sampling methods assume that a survey has been designed to give every point in the study area equal probability of being sampled. It can be very expensive to obtain enough ship time to conduct a design-unbiased survey. Recently developed spatial modelling techniques allow that assumption to be relaxed, as long as survey data provide reasonable coverage across the range of explanatory variables influencing whale density. Effort and sightings data were collected along 9650km of trackline aboard ships of opportunity in the Southern Ocean during the austral summers of 2000-1 and 2001-2. Generalised additive models were used to express heterogeneity of cetacean sightings as smooth functions of spatial and environmental variables. Next, these models were used to map predicted densities and to estimate abundance of humpback, minke and fin whales in the Drake Passage and along the Antarctic Peninsula. All three species showed strong density gradients within the study area. Maps of predicted density were robust to jackknife resampling, in which each of 14 trips was removed in sequence. The best abundance estimate for humpback whales in the study area during the time of the survey was 1829 (95% CI: 978-3422). Fin whale abundance was 4487 (95% CI: 1326-15179) and minke whale abundance was 1544 (95% CI: 1221-1953). These abundance estimates seem plausible given abundance estimates reported from a designed survey conducted in the region in 1999-2000. The approach can be seen generally as an inexpensive pilot study, where areas of predicted high density could be targeted to increase efficiency of future photo-identification or biopsy surveys. Similarly, the predicted density gradient could be used to inform the design of future line-transect surveys and making them less expensive and more precise. In a spatial modelling framework, line-transect data collected from free survey platforms become much more informative than sightings alone, and the techniques are likely to have wide application to areas where financial resources are limiting and where cetacean studies are just beginning.

3.1 INTRODUCTION

Conservation of threatened species and management of exploited ones call for reliable information on abundance and/or trends in abundance. In some cases, resource managers require information on abundance of a biological population of animals. Alternatively, management may occur within a geographic area and require information on the abundance of a species in that area, regardless of whether animals encompass a fraction of a population, or several discrete populations. The United

States' Marine Mammal Protection Act (MMPA) is an example of the former approach, under which assessments are made at the level of the population, in terms of demonstrably discrete population segments or evolutionarily significant units (Pennock and Dimmick, 1997). Fishing quotas, on the other hand, are often set by geographic area. The Department of Fisheries and Oceans, Canada (DFO) adopts the latter management approach, whereby salmon harvest is allocated seasonally by area, irrespective of the number and health of natal streams (populations) targeted.

Biologists are tasked with estimating the number of animals in a population, or that inhabit a given area. One technique that cetacean biologists use commonly to answer such questions is the distance sampling method of line-transect survey (Buckland, 1985; Buckland and Turnock, 1992; Buckland *et al*., 2001; Chapters 1 and 2). Line-transect surveys can be a fast, powerful and cost-effective way to provide information on wildlife abundance and distribution.

3.1.1   Assumptions about coverage probability in distance sampling
The previous chapter considered the consequences in a line-transect framework of violating the assumption that all angles and distances to targets are measured without error**.** Satisfying that assumption, and the other distance-sampling assumptions outlined in Chapter 1, ensures that animal density is estimated accurately. This chapter is concerned with the assumption that the sample density is an unbiased, representative estimate of density within the study area. A biased sampling design, ignored at the analysis stage, will lead to biased abundance estimates, unless animals happened to be distributed uniformly throughout the study area at the time of the survey.

Bias in sampling effort is addressed best at the survey design, rather than the data collection or analysis, stage. In a conventional, design-based line-transect survey, the survey is designed in such a way that tracklines provide representative coverage of the study area. The goal of an unbiased survey design is one in which all points in the study area have equal probability of being sampled (Buckland *et al*., 2001). A variety of methods have been developed to assist researchers in achieving this goal of a design-unbiased survey (Buckland *et al*., 2001). An elegant solution to the problem was proposed by Strindberg (2001), who wrote algorithms to automate the survey design process, and to generate trackline placement configurations that give equal coverage probability throughout a study area of any shape. These automated survey design algorithms, conducted in a GIS framework, have been incorporated into DISTANCE 4.0 Release 2 (Thomas *et al*., 2002).

3.1.2 Model-based techniques allow unequal coverage probability

Surveys that appear at first glance to be well designed may provide deceptively biased coverage. A problem arises, for example, in surveys using zig-zag designs with equal angles in study areas with complex coastlines. These surveys will oversample areas inside an arc following a curvilinear coastline. Biased survey designs are surprisingly common (Buckland *et al*., 2001), and not always due to poor planning. Bad weather in one part of a study area could prevent a well-designed survey from delivering equal coverage probability. When coverage probability is unequal, but was generated by a quantifiable algorithm, coverage probability may be calculable *post-hoc* from the survey data. Mean animal density in the study area, in that case, is no longer taken to be the mean sample density. Instead, mean animal density (and hence, abundance) must be modelled from the observed data. Methods that allow for animal abundance

to be calculated from statistical models, rather than a design-unbiased survey, are termed model-based abundance estimation techniques (Buckland *et al.*, 2000).

One approach involves weighting line-transect data by including the probability of making each observation, in which coverage probability is calculated from the algorithm that generated the survey design. An unbiased abundance estimate can then be obtained using a Horvitz-Thompson (Horvitz and Thompson, 1952) abundance estimator (Borchers *et al.*, 1998a). While these estimates are unbiased, they are typically less precise than those from a designed-based survey (Buckland *et al.*, 2001).

3.1.3 Spatial modelling using line-transect survey data

A fundamentally different model-based abundance estimation technique involves describing animal density along the trackline as a function of spatial or environmental covariates, and then using that relationship to predict animal density throughout the study area. Spatial modelling methods employing line-transect survey data have been developed by Hedley *et al.* (1999) and Bravington (2000).

These spatial modelling techniques were developed in order to use descriptive models of heterogeneity in whale density to make reasonable extrapolations into unsurveyed areas. They were also designed to allow for interpolation between tracklines to compensate for tracklines missed due to poor weather. Their relevance here stems from an enticing statistical property – they make no assumptions about trackline placement. Instead, these spatial modelling techniques require only that observed data provide reasonable coverage, which is defined as a sample in which observations were made across the entire range of the explanatory variables of interest.

3.1.4 Additional advantages of spatial modelling techniques

One advantage of model-based methods over conventional distance-sampling methods is that the former allow calculation of abundance estimates for any subsets of a study area. Conversely, conventional distance sampling allows abundance estimation only over pre-defined strata (Borchers *et al*., 1998a,b; Buckland *et al*., 2001), because conventional surveys are designed to give equal coverage probability within a survey region. Surveys with overlapping but non-identical boundaries cannot be compared *post-hoc* in a conventional distance-sampling framework, but can be compared using model-based abundance estimation techniques. Suppose a species studied in an area is later found to comprise two discrete, spatially segregated stocks. A conventional distance-sampling analysis would not allow *post-hoc* stratification into two sub-areas, because the original survey was not designed to provide representative coverage to those areas. Spatial modelling techniques, on the other hand, would allow for estimating abundance in areas in which stocks were found to occupy. The techniques also allow line-transect data to be modelled across small areas where human activity is of management concern.

Relating animal distribution to habitat features is common in terrestrial studies. Butterfly distribution was strongly influenced by proximity to hedgerows (Sparks and Parish, 1995). Common toad (*Bufo bufo*) distribution, abundance and genetic diversity were correlated with proximity and number of ponds, and how humans used land adjacent to toad breeding sites (Scribner *et al*., 2001). A spatial modelling framework was used to quantify preferred habitat types for two species of large forest owls (powerful, *Ninox strenua*, and sooty, *Tyto tenebricosa*) in Australia (Loyn *et al*., 2001). The model predictions were proven in the field to perform well at discriminating areas of high and low density for the species, which occupied very

different habitat types. Ultimately, the data were used to identify priority areas to protect owl habitat.

Relationships between cetacean density and features of the animals' environment may be of similar interest. The choice of covariates in a spatial modelling framework is potentially wide. Information on distribution and density of prey species significantly improved the performance of a predictive model of Atlantic white-sided dolphin (*Lagenorhynchus acutus*) distribution in the Gulf of Maine (Summers, 2000). The relationship between minke whale distribution and sea ice is of general ecological interest (Thiele *et al*., 2002), as well as a key area of concern relating to the recent decline in Antarctic minke whale density (Branch and Butterworth, 2001a). The southern boundary of the Antarctic Circumpolar Current was linked to high productivity of the waters around the Antarctic continent (Tynan, 1998), and this feature has been shown in a spatial modelling framework to influence distribution of Antarctic cetaceans (Matsuoka *et al*., 2003b). Relating cetacean distribution to environmental variables and habitat types could allow predictions to be made about how animals will respond to environmental degradation or global climate change.

Another attractive promise of spatial modelling techniques is increased precision. If some heterogeneity in whale density observed along tracklines is real spatial variation in whale density rather than sampling error, this will allow variance estimates to be reduced because the models will explain some of that heterogeneity. One example has been provided for short-beaked common dolphins (*Delphinus delphis*) and Dall's porpoise (*Phocoenoides dalli*), in which sea surface temperature and salinity explained much of the between-year variation in encounter rate (Forney, 2000). Increased

precision of abundance estimates vastly increases the power to detect trends in abundance (Taylor and Gerrodette, 1993).

Spatial models can be used to produce maps of predicted density gradients (Hedley *et al.*, 1999; Borchers *et al.*, 2000; Hedley, 2000; Summers, 2000; Marques, 2001) whereas conventional distance sampling methods assume a flat density surface within each pre-defined stratum. Visual plots of animal density could be very useful, for example, for allocating fishing quotas spatially, so that by-catch of a species of conservation concern could be minimised (Vidal, 1995; Berggren *et al.*, 2002b). Indeed, knowing where animals are can be as important as knowing how many animals are in a population. Areas of high density could be closed to seismic surveys or naval sonar testing, and spatial modelling provides an objective way of visualising cetacean distribution. The methods are easily expandable to spatio-temporal modelling, in which seasonal or annual trends in abundance and distribution may be detected. The ability to model seasonal changes in abundance would be valuable when identifying the best time to conduct surveys.

Modelling whale density as a function of spatial or environmental covariates may be useful even in well-designed surveys. Poor weather can prevent researchers from following the planned study design. When poor sighting conditions result in excluding some transects from a proposed survey, spatial modelling can be used to guide objective interpolation of animal density between surveyed areas.

In summary, spatial modelling of line-transect survey data allows surveys to be combined to increase knowledge of how animals use their habitat, and how

populations behave over time. The techniques enable estimation of the number of animals in a spatially flexible way. And they do so without making assumptions about trackline placement, except that sampling effort provides reasonable coverage across the range of explanatory variables of interest.

3.1.5 Collecting line-transect data from Ships of Opportunity

An extreme case of surveys that fail to provide equal coverage probability is presented by those conducted from ships whose routes cannot be determined by the researcher, namely Ships of Opportunity. The high cost of dedicated sightings surveys may preclude their use for some countries and in some areas (Vidal, 1993). It would be useful to have less-expensive methods to allow some information on abundance and distribution to be obtained in cases where funds are not available for chartering a suitable ship to conduct a design-unbiased survey. Many researchers have attempted to glean information from so-called 'Platforms of Opportunity,' where the platform may be sighting logs (Braham and Dahlheim, 1982; Moore *et al*., 1999), whaling records (Mizroch, 1983, 1984; Gregr *et al*., 2000; Gregr and Trites, 2001), or ships from which both effort and sightings were recorded (Marques, 2001). On opportunistic surveys where effort is recorded, not only is coverage non-randomised, but also it is generated by other people's needs rather than a quantifiable algorithm. Consequently, coverage probability is difficult to quantify for surveys conducted from ships of opportunity, making spatial modelling techniques especially applicable.

The utility of data collected from ships of opportunity depends heavily on the coverage that the platform can provide. It is useful to draw a distinction between two broad classes of opportunistic platforms. Fixed-route platforms, such as ferries, follow a route that is inflexible. Variable-route platforms, such as tourism ships, fisheries

research vessels and fishing boats, follow itineraries that may or may not have been set ahead of time, but that vary between trips. Within the category of variable-route platforms, some will follow routes that are biased with respect to cetacean distribution (*e.g.*, whalewatching boats), but others will not. Data collected from platforms that are biased with respect to cetacean density can yield informative results. Fin and minke whale distribution were described using data collected from a whalewatch boat (Ingram *et al*., 2003). However, this chapter explores the utility of line-transect data collected from ships that provide reasonable but not systematic coverage that was not determined by distribution of whales.

Ships of opportunity may provide reasonable platforms for assessing relative abundance (*e.g.*, encounter rates per unit distance or time; lists of species in order of sighting frequency; estimates of animal density that cannot be extrapolated to a whole area). Measures of relative abundance can be informative in terms of trends over time (Forney, 2000; Best, 2003), but require data collected from the same study area, and assessment of potentially confounding factors, such as the height of a platform, the response to the survey ship, observer effort (observer experience, length and width of survey strips etc.), and sighting conditions.

One example of a study to estimate relative abundance estimates using data collected from ships of opportunity considered sightings of offshore spotted dolphins (*Stenella attenuata*) in the eastern tropical Pacific (Marques, 2001). High levels of dolphin (spotted; spinner, *S. longisrostris*; striped, *S. coeruleoalba*; and common, *Delphinus delphis*) mortality incidental to this purse seine fishery were common in the 1970s, and

negatively impacted spotted and spinner dolphin populations (Smith, 1983). The tuna-dolphin issue sparked controversy and protective legislation (Gosliner, 1999).

One management response was the placement of observers on US-registered tuna fishing vessels since 1974 to record effort and dolphin sightings, and to monitor by-catch (Marques, 2001). The use of GAMs addressed the bias inherent in this non-randomised survey design, and enabled modelling trends in relative abundance over time. Uncertainty in stock definition and data quality issues in the early part of the time-series limited the ability to detect significant trends in relative abundance, but the study serves as a useful example of the role that spatial modelling can play in detecting trends in cetacean abundance and distribution using line-transect data collected from non-randomised surveys (Marques, 2001).

If reliable estimates of absolute abundance are ever to be obtained from data collected aboard platforms of opportunity, then they must rely on model-based techniques (Buckland et al., 2000). For line-transect data collected in conjunction with JARPA, the Japanese Whale Research Program under Special Permit in the Antarctic, simulations showed that the 'count method' (Hedley et al., 1999) removed most, but not all, of the bias associated with data collected from ships actively searching for Antarctic minke whales (Clarke et al., 1998). Despite a strong relationship between sampling effort and animal density, informative results were generated from spatial models of line-transect survey data collected from these platforms.

In summary, spatial modelling techniques make no assumptions about placement of tracklines, and show some robustness to oversampling of areas of high whale density.

While the methods are still developing, these preliminary results suggest that there is valuable information on abundance and distribution to be gained by collecting accurate line-transect survey data from non-randomised surveys, especially when coverage is good and effort is not determined by distribution of whales.

3.1.6 Antarctic balaenopterids and whaling

When selecting a case study for using spatial modelling techniques to monitor absolute abundance and distribution of cetaceans using data collected aboard platforms of opportunity, an obvious region to consider is the Southern Ocean. During the last century, more than a million whales were killed there. The story is a familiar one, where the economic incentive to exploit the resource came before any perceived need to manage the hunt sustainably.

Humpback whales (*Megaptera novaeangliae*) were the first balaenopterid targets of whalers, using land-based processing plants in South Georgia. Humpback numbers began to fall, and factory ships were introduced that enabled catching of fast pelagic species and obviated the need to go back to shore for processing. Subsequently, whalers progressed through blue (*Balaenoptera musculus*), fin (*B. physalus*), and sei (*B. edeni*) whale stocks, in order of decreasing size and commercial value (Laws, 1977; Mizroch, 1984; Gambell, 1999; Best, 2003). A moratorium on commercial whaling took effect in 1985-6, and only small takes of whales, primarily Antarctic minke (*B. bonaerensis*) whales, for scientific purposes take place in Antarctic waters at present (Gambell, 1999; Burns and Wandesford-Smith, 2002).

It is difficult to know the precise fraction of whale stocks taken in Antarctic balaenopterid whaling, because historical levels of abundance can be estimated only

roughly. A common method to estimate initial stock size is to use catch data and a simple population growth model to calculate a backward population trajectory. This approach was used to determine that southern hemisphere humpback whales were reduced to a low of 1 000 animals from an initial stock of 64 000 (Findlay *et al.*, 2000). A review of the information available in 1977 suggested that blue whales were reduced to 5% and humpbacks to 3% of initial stocks (Laws, 1977). The same review indicated that Southern Ocean blue, fin, sei and humpback whales, taken as a whole, were reduced to approximately 18% of their initial population size.

This approach to estimating pre-exploitation population size is vulnerable to the assumptions it makes about population growth and catch data. Back-calculation is sensitive to poor record keeping in the early years of exploitation, and to misreporting. Soviet misreporting of Southern Ocean balaenopterid whaling was extensive (Yablokov, 1994; Zemsky *et al.*, 1995; Tormosov *et al.*, 1998). Assessment of these previously unreported catches suggested that the true number of whales taken from the southern hemisphere approached two million animals between 1904 and 1980 (Baker and Clapham, 2002). The updated estimate indicated that modern whaling in the Southern Ocean removed 80-95% of all great whales (*i.e.*, all the balaenopterids mentioned above, except minke whales, plus the sperm whale, *Physeter macrocephalus*, and the southern right whale, *Eubalaena australis*) between 1908 and 1980 (Baker and Clapham, 2002).

A second approach to estimating the fraction of whales removed by whaling is to consider changes in relative abundance during the development of the industry. Catch per unit effort (number of whales killed per boat-day of whaling effort) and rate of

sightings by spotter planes on the Durban whaling grounds indicated that blue whale abundance in the late 1950s was 2.8% of that in the early 1920s (Best, 2003). Humpbacks declined to 13.5% of 1920s levels, however whaling had already targeted humpbacks before 1920s, so this is an underestimate of removal (Best, 2003). Fin whale catch rates declined by 89.4% and sightings by 96.7% (Best, 2003).

Finally, molecular genetic techniques can be used to deduce initial population size. Genetic variability and estimated mutation rates were used to infer that the breeding populations of North Atlantic minke, fin and humpback whales were much higher than estimates from reconstructed population trajectories (Roman and Palumbi, 2003). These molecular techniques rely on assumptions that are difficult to test, and have not been applied to Antarctic balaenopterids.

By all accounts, commercial whaling in the Southern Ocean reduced abundance of this guild of predators to a small fraction of its original biomass. What remains unclear is the extent to which ecosystem-level consequences may have resulted from removing such large amounts of biomass from a high trophic level (Pauly *et al*., 1998b) of the Antarctic marine ecosystem. Great whales are a key component of their ecosystem. Baleen whales have been estimated to increase their mass by 50% or more during their summer feeding season (Lockyer, 1972). They do this primarily by feeding on krill (*Euphausia superba*), however copepods and fish are also present in the diet (Laws, 1977). A conservative estimate (*i.e*., one that ignored Soviet misreporting) assessed that the great whales of the Southern Ocean reduced annual consumption of krill by 147 million tonnes, as well as consuming 8 million tonnes less squid and 3 million tonnes less fish than their larger populations did prior to exploitation (Laws, 1977).

It seems intuitive that eliminating the vast majority of great whales from the Southern Ocean would have increased the availability of krill (*Euphausia* spp.) to other krill predators, including pinnipeds, penguins and minke whales. But the evidence either for food-limitation or for competition in Antarctic baleen whales remains scant. Insufficient data exist to assess recovery for many balaenopterid species in the Antarctic (Clapham and Brownell, 1996). It may be premature to debate factors that might be inhibiting whale recovery at least until available data are adequate to discriminate between absence of recovery and insufficient statistical power to detect recovery (Taylor and Gerrodette, 1993). Information on the status of Antarctic baleen whales is crucial. It is essential to know whether populations are recovering from commercial exploitation for basic ecological reasons. Industrial whaling can be thought of as a large-scale natural experiment that has much to teach us about the functioning of the Southern Ocean ecosystem, of marine ecosystems in general, and the resilience of whale populations.

Information on recovery of Antarctic baleen whales is needed also for management of the whale stocks themselves. The International Whaling Commission (IWC) is the authority charged by contracting nations to assess the status of whale stocks in international waters, and to regulate whaling. The Convention for the Regulation of Whaling mandates "the conservation, development, and optimum utilization of the whale resources" (IWC, 1946). Whale conservation is required to ensure the sustainability of the whaling industry: "[r]ecognizing the interest of the nations of the world in safeguarding for future generations the great natural resources represented by the whale stocks…" (IWC, 1946).

The Southern Ocean, therefore, is a good place to apply spatial modelling techniques to line-transect cetacean data collected from an inexpensive platform. The resulting information is of interest for a variety of ecological and management reasons, and the exercise may have much to teach us about how one could conduct similar surveys in areas where funding for cetacean population assessment is absent. The challenge is to collect accurate quantitative data in a climate in which research funding is sparse and the cost of dedicated ship time, especially in remote areas, is very high.

3.1.7 Antarctic tourist ships as platforms of opportunity

Environmental tourism is a large, growing and global industry (Miller, 1993; Nelson, 1994; Wallace and Pierce, 1996; Gossling, 1999; Ross and Wall, 1999; Wilson and Tisdell, 2001). Antarctic tourism is no exception (Acero and Aguirre, 1994; Cessford and Dingwall, 1994; Sanson, 1994). More than 10 000 tourists now visit Antarctica annually on expedition-style natural history cruises aboard small, ice-strengthened ships (IAATO, 2000).

As a fleet, these ships provide reasonable coverage of the Scotia Sea and Antarctic Peninsula region, straddling parts of IWC Areas I and II (Figure 3.1). Undertaking sightings surveys from a tourist ship that is already on the water is an attractive option for scientists wanting affordable access to understudied areas. The tourism industry benefits as well from trained observers who can teach passengers about the area, and provide guests with the sense that they are facilitating conservation-minded research.

An attempt has been made previously to make use of opportunistic sighting records from tourism platforms in the Scotia Sea. Southern right whales were the great whale

species most frequently reported around South Georgia, but the data lacked measures of observer effort (Moore *et al*., 1999). Without information on the width of the strip effectively searched on a survey or other measures of varying detection probabilities, rare species could be recorded more frequently than more abundant species, simply because they were detectable at greater distance or were more likely to be reported.

Antarctic tourism offers a rare chance to collect data from a platform of opportunity that is likely to satisfy assumptions of reasonable coverage (Hedley *et al*., 1999). While a wide range of itineraries may be planned, they are modified daily to adjust for weather conditions and to minimise encounters with other ships in order to maintain an impression of isolation. Clearly, such routes fail to offer systematic coverage. However, their routes are not intentionally biased with respect to distribution of whales. Cruise leaders do stop the ship opportunistically to whalewatch on occasion, but their primary goal is to take passengers from South America to the Antarctic continent. The vast majority of Antarctic wildlife-oriented tourism is land-based, targeting seabirds and pinnipeds. Taken as a whole, Antarctic tourist ships provide expansive coverage of the Antarctic Peninsula and the Scotia Sea.

This study collected line-transect survey data on cetaceans from ships of opportunity in the Southern Ocean. The primary goal was to provide a quantitative description of cetacean abundance and distribution along the Antarctic Peninsula during the 2000-2002 study period. The secondary goal was to explore the robustness of spatial modelling techniques to varying sampling effort in model-based estimates of abundance for three balaenopterid species.
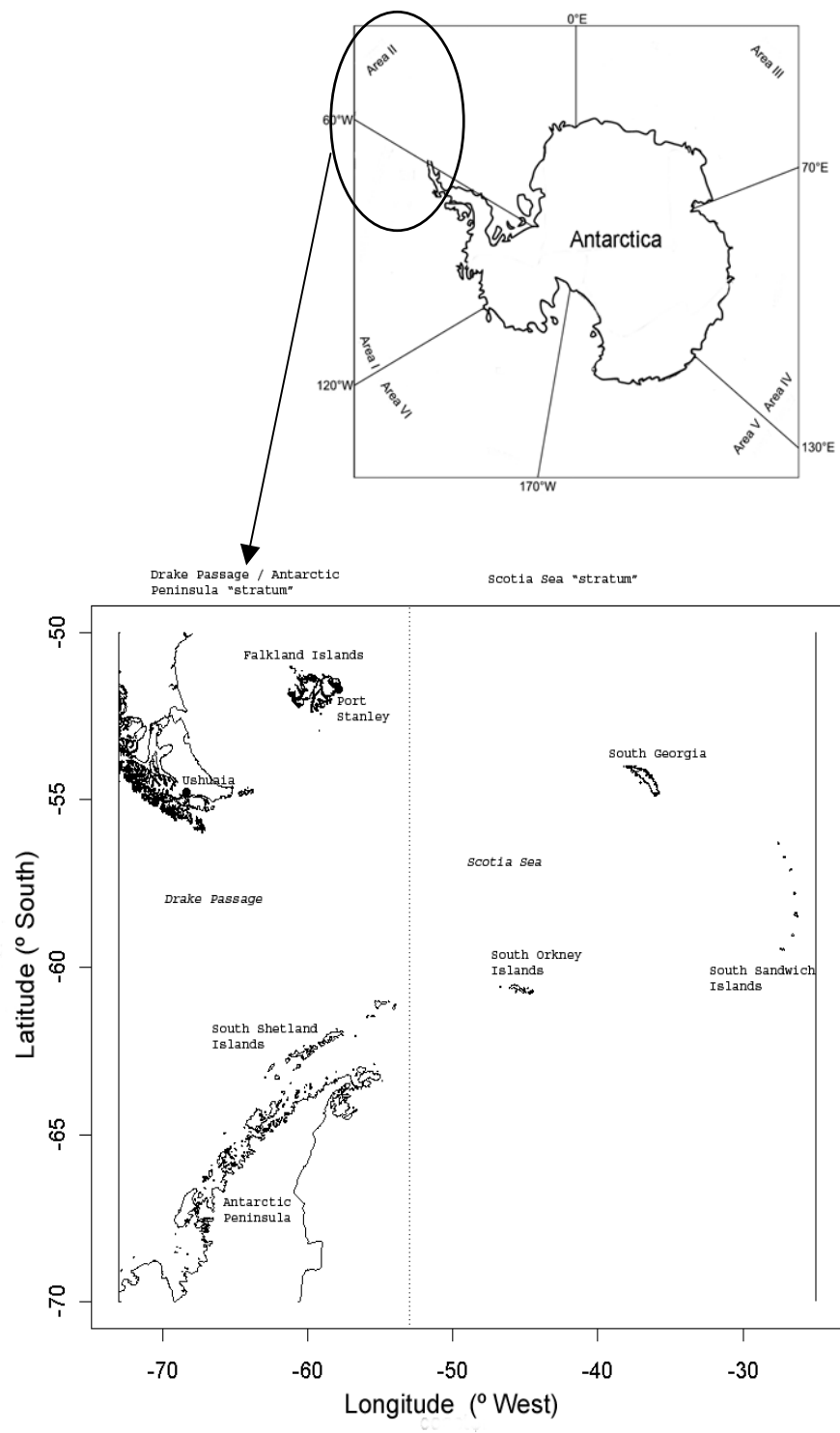
Figure 3.1. Study area in the context of IWC Antarctic baleen whale Areas. Most trips left from Ushuaia, Argentina or Port Stanley, Falkland Islands [Islas Malvinas]. Trips to the Antarctic Peninsula were more common than those to South Georgia, necessitating a post-hoc designation of an Antarctic Peninsula/Drake Passage stratum (left) and a Scotia Sea (right) stratum.

3.2 METHODS

3.2.1 Primary platform data collection

Data were collected on eight trips between 3 December 2000 and 14 March 2001, and

on 6 trips between 5 December 2001 and 12 February 2002 (Table 3.1). All trips

started or ended in Ushuaia, Argentina (Figure 3.1), and lasted from 6 to 24 days.

Two ships were used in the first season, and a third ship for the second season.

3.2.1.1 Effort

Data were collected from the highest accessible point on each of the three ships used

in this study (Table 3.1). A data collection session was initiated whenever the ship

was underway, sea state was less than 6, and when no other duties (lecturing, patching

Zodiacs, writing reports etc.) were assigned by the tour's expedition leader. At the

beginning and end of each data session, a Magellan 2000XL handheld GPS was used

for recording start time, location (latitude and longitude) and ship's course and speed.

Information was recorded on factors that could affect sighting conditions, including

sea state, cloud cover and precipitation, and a subjective visibility code that estimated

the range at which a minke whale might be visible (<500m, 500-1000m, 1000-2000m

and >2000m). In addition, information was collected on environmental conditions,

such as water depth and sea surface temperature (relayed from the bridge) and the

estimated proportion of sea surface that was covered with ice. These effort data were

collected every 30 minutes thereafter, or more frequently if sighting conditions

changed, or if the ship made a marked change in course or speed. All primary

platform data were collected by the same observer (Rob Williams).

	Platform height (m)	
Ship	Primary	Secondary
Mariya Yermolova	14	12
Lyubov Orlova	14	12
Explorer	12	10

Table 3.1. Height of the primary observation and secondary (duplicate tracking) platforms aboard three ships of opportunity used in this study.

The observer searched ahead of the ship, that is, a sector from the trackline to 90˚ abeam the ship, while concentrating primarily on the trackline. During approximately 5% of the search effort, an additional observer volunteered to help with data collection. On those occasions, each observer would search a sector spanning from 10˚ on one side of the trackline to 90˚ on the other side.

3.2.1.2 Sightings

Whenever a cetacean or school of cetaceans was spotted, it was assigned a sighting number. An angle board mounted on the deck railing was used to measure radial angle to the school, and a visual estimate was made of the range to the first sighting. Radial distance estimates were corrected subsequently using the observer-specific method described in Chapter 2. Ship location and the time of the sighting were recorded, and Pentax 8X42 binoculars were used to confirm species and school size. Additional information was recorded on cue type (*inter alia* body, blow, seabird activity), the whale's behaviour, and its heading relative to the ship.

Occasionally, the expedition leader would decide to 'close' on a sighting. As soon as the ship diverted from the trackline to whalewatch, searching effort for that data collection session was terminated. These opportunities were used to collect

identification photographs of humpback whales, and to obtain more accurate estimates of school size. When the whalewatch session ended, search effort was resumed once the ship reached cruising speed.

3.2.2 Double-platform data collection

In order to assess the validity of the assumption that detection was certain on the trackline, the so-called g(0)=1 assumption, double-platform data were collected when sufficient observers volunteered to assist. On the 10% of data collection sessions when this was feasible, three observers worked from the tracking platform from the bridge level while the primary observer searched from the usual observation deck above the bridge (Hammond *et al*., 2002).

The tracking team comprised a data recorder, and two observers scanning from the trackline to approximately 45˚ on either side of the ship. The trackers scanned with binoculars, and informed the data recorder whenever a sighting was made. Each sighting by the trackers can be considered as setting up a trial, which the primary platform would subsequently duplicate (a success), or miss (a failure). Trackers were instructed to continue observing a whale until it passed 90˚ abeam the ship, rather than searching for additional sightings. When a sighting was made by the observer on the primary platform during double-platform mode, that sighting was reported to the data recorder also, using two-way radios. The data recorder decided whether the primary observer's sighting duplicated one that was being tracked by the observers on the tracking platform. If so, the data recorder scored it as a duplicate sighting, the trackers were informed, and resumed searching to set up a new trial. If not, then the trackers continued to track their whale until it passed abeam the ship. At that point, the data recorder scored the trackers' trial as a missed sighting, and then the trackers could

resume searching for a new trial. The data recorder consulted with the tracker about certainty of duplication, and scored all 'definite' and 'probable' sightings as duplicates. All 'possible' (*i.e.*, unlikely, but not impossible) duplicates were scored as sightings missed by the primary observer. This led to an implied level of certainty whose aptness could not be evaluated. The primary observer was not informed about sightings made by the trackers.

3.2.3 Primary platform data analysis

Primary platform data were entered in DISTANCE 4.0 Release 2 (Thomas *et al.*, 2002). Detection probability for each species was modelled as smooth functions of perpendicular distance, (*x*). DISTANCE was used for exploratory data analysis and to produce diagnostic plots to assess how well the model fitted the data. Candidate forms for the detection function were the hazard-rate and half-normal models (Chapter 1). Model selection was guided by Akaike's Information Criterion (AIC; Akaike, 1973).

Detection function fit is improved often by truncating the 5-10% most distant sightings (Buckland *et al.*, 2001). However, spatial modelling performs best when the number of sightings is high (Hedley, 1999). DISTANCE was used to assess need for truncation, by testing whether removing the 5 and 10% farthest sightings had a marked effect on $\hat{f}(0)$. If the difference between 5% and no truncation was small, then no truncation was made. If the difference was large, then data were truncated at 10%. If the difference between truncating at 5 and 10% was large, then 10% was chosen as the truncation distance, *w*. If small, 5% was chosen as *w*. No attempt was made to look for truncation distances at which more than 10% of the data were truncated, unless there was evidence for heaping or poor model fit in the tail of the distance data.

DISTANCE was also used to detect evidence of school size (*s*) bias, the tendency for a large school to be more detectible at long ranges than a small school would be at that range (IWC, 1994b; Borchers and Burt, 2002; Bravington, 2003). The default method for estimating mean school size in DISTANCE was used (Thomas *et al*., 2002). This approach fits a least-squares regression of log(s) on the distance at which each school was seen, (x_i), which yields a positive slope when size bias is present (Buckland *et al*., 2001). The value at zero distance (where detection probability is assumed to be 1) is used in that case to estimate mean school size. In this study, the intercept was used as the mean school size when the slope of this line was positive. If the slope was negative, the mean value of schools close to the trackline (0 to 0.5nm) was used.

All other things being equal, whales are more easily spotted in calm seas than in rough conditions. DISTANCE allows the use of covariates, such as sea state, in fitting the detection function (Borchers *et al*., 1998a), incorporating methods developed by Marques (2001). *Beaufort* was included as a candidate covariate in the Multiple Covariate Distance Sampling (MCDS) analysis engine in DISTANCE, and the decision to include or exclude it as a term in the model was guided by AIC.

3.2.4 Spatial modelling from line-transect survey data
3.2.4.1 Compiling datasets for building descriptive models
The primary platform effort and sightings data were modelled using the "count" method developed (Hedley *et al*., 1999). The count method was found to be more robust in simulations (Clarke *et al.*, 1998) to the non-randomised survey design used by Japan's sampling vessels in Antarctic waters (JARPA) than the "waiting area" or "waiting times" methods (Hedley *et al*., 1999). Tracklines from each data collection session were divided into 2nm segments, for which start and end locations were

calculated using the GEOFUNC add-in for EXCEL 2000. In simulations, it has been shown that the count method is robust to choice of segment length (Hedley *et al*., 1999; Hedley, 2000; Hedley and Buckland, in prep.). A segment length of 2nm was found to perform well, and satisfied the assumption that the value of each explanatory variable was relatively constant across the length of the segment. The length of the last segment was constrained to fall between 1 and 3nm, to avoid very short segments. Unequal segment length is addressed by including segment length when compiling the offset term, described below.

The location of the midpoint of each segment (latitude, *LatMid*, and longitude, *LonMid*) was calculated, along with three additional candidate explanatory variables. The first of these, *depth*, was calculated in ARCINFO. A digital bathymetric database for the study area, DBDB-V Database, was downloaded from http://pdas.navo.navy.mil/data/DBDBV/dbdbv_def.html. It provided a grid of ocean floor depths at a resolution of 5 minutes of latitude. This 5-min point coverage depth data was converted to a raster grid in ARCINFO, which can be thought of as a two-dimensional smooth surface of depth. The effort segments were superimposed on this grid, and joined based on spatial location in ARCMAP. This joined table was exported as a matrix with three columns, namely the interpolated depth value at the midpoint (*LonMid* by *LatMid*) of each segment.

The second candidate explanatory variable considered was called *mindist*, the distance from each segment to the nearest coastline. A high-resolution ASCII (*x, y*) text file of the coastline throughout the region was downloaded from http://ingrid.ldgo.columbia.edu/SOURCES/.WORLDBATH/.bath/. A function was

written in S-PLUS 2000, based on the spherical trigonometric equations given in GEOFUNC, to calculate the great circle distance from the midpoint of each segment to all points in the *x,y* coastline file for South America, Falkland Islands [Islas Malvinas], South Georgia, South Orkneys, South Shetlands and the Antarctic Peninsula. The minimum of these values for each segment was stored as a vector of values in nautical miles of the shortest distance from the midpoint of a segment to any shoreline in the study area.

The last term to be included in the model is an *offset* term that describes the area effectively searched in each segment. Spatial models do not model density directly largely due to problems linking density to an appropriate distributional form of the response variable. A solution to this problem was developed by Hedley *et al.* (1999), who included the area searched as an offset term in the model. School density in a segment, $\hat{d}_s$, is given by:

$$\hat{d}_s = \frac{\hat{n}_s \cdot \hat{f}(0)}{2l} \qquad \text{[Equation 3.1]}$$

where n_s is number of detected schools in the segment, l is the length of the segment, and $\hat{f}(0)$ is the probability density function evaluated at zero distance. By including area as an offset term in the model, $offset = \dfrac{\hat{f}(0)}{2l}$, one reduces the response variable to $\hat{n}_s$, which can be modelled as count data drawn from an inhomogeneous Poisson distribution.

3.2.4.2   Modelling heterogeneity in whale density along the trackline
Generalised additive models (GAMs) were fitted in package mgcv for program R (Wood, 2001). This approach uses thin-plate regression splines (Wood, 2003) for the

smooth terms of each explanatory variable, but each spline carries a penalty for excessive flexibility (Wood, 2000). Flexibility is determined by the number of 'knots' (approximately one higher than the estimated degrees of freedom, df) for each model term. (Knots are values in the range of x between which the non-linear relationships are modelled (Wood, 2003).) Smoothing splines are fitted using multiple generalised cross-validation (mgcv). The amount of flexibility given to a model term is determined in a maximum likelihood framework by minimising the GCV score of the whole model, rather than each component score.

The model framework was of the form:

$$E(n_i) = \exp\left[\ln(2l_i w_i \hat{p}_i) + \beta_0 + \sum_k f_k(z_{ik})\right] \qquad \text{[Equation 3.2]}$$

where: n_i is the number of detected schools in the ith segment;
l_i is the length of the ith segment;
w_i is the truncation distance of the ith segment;
$\hat{p}_i$ is the estimated probability of detection of a school in the ith segment;
β_0 is a parameter to be estimated; and
z_{ik} represents the value of the kth explanatory spatial variable in the ith segment, which is a smooth function, f_k, of the explanatory variable.

The explanatory variables can be multi-dimensional. One can evaluate, for example, whether a two-dimensional smooth surface of latitude and longitude performs better than two one-dimensional smooths (or linear functions) of latitude and longitude. The default smoothing value used for one-dimensional splines was the default value set by package mgcv, 10 knots in each spline, corresponding to 9df, while the default value for a two-dimensional smoother was 20 knots (Wood, 2001). Models were fitted using the quasi-likelihood family, a log link (the natural canonical link when the response variable is drawn from the Poisson distribution (Hastie and Tibshirani, 1990)), and with variance assumed proportional to the mean. Previous work has

shown this error structure to be most robust to the over-dispersion common to clustered sightings (Clarke *et al.*, 2000; Forney, 2000; Hedley, 2000; Marques 2001).

While determination of the optimal amount of smoothing is automated by mgcv, the decision whether to include or drop a model term is not. Potential explanatory variables considered for inclusion in the model were *LatMid, LonMid, LonMid*LatMid, depth* and *mindist*. The following summarises the model specification procedure adopted for each species during this study, using the structure proposed by Wood (2001):

1. Two saturated models were fitted: {$y \sim$ s(*LatMid*) + s(*LonMid*) + s(*depth*) + s(*mindist*) + offset} and {$y \sim$ s(*LonMid, LatMid*) + s(*depth*) + s(*mindist*) + offset} with the default degree of smoothing.

2. If any model term used approached the maximum flexibility allowed (9df for a one-dimensional term), then the number of knots allowed that term was increased to 20, and the models refitted.

3. Model fit was assessed using the summary.gam and plot.gam functions in mgcv, which showed coefficients, GCV score, explanatory power (deviance explained) and fit (residual plots).

4. The model with the lower GCV score (i.e., s(*LatMid*)+s(*LonMid*) vs. s(*LonMid,LatMid*)) was chosen.

5. For each model term, the estimated number of degrees of freedom was examined to see if it was near 1. The 95% confidence intervals for that term were examined to see if they included zero across the range of observations. If so, the term was dropped temporarily, to see if the GCV score dropped.

6. A term was dropped from the final model if it satisfied all three of the conditions in step 5. If the first criterion was met, but not the other two, then the smooth term was replaced by a linear term.

A function was written in R to combine the detection function fitting, size bias regression, and spatial modelling steps outlined above in one command.

3.2.2.3. Defining the study area

In a conventional sightings survey, one defines a study area *a priori*, and allocates search effort to ensure that every point in the study area has equal probability of being sampled. Conversely, in a spatial model-based estimation study, no assumption is made about placement of tracklines, and study area is difficult to define *a priori* for surveys conducted from ships of opportunity. In this study, the tracklines themselves were used for post-hoc definition of the study area. A function was written in R to fit a convex hull (Strindberg, 2001) around the tracklines in the Antarctic Peninsula/Drake Passage stratum (Figure 3.1), where the bulk of the search effort occurred and within which area coverage appeared reasonable. This defined the area across which whale density would be predicted, however sightings and effort data from the Scotia Sea stratum (Figure 3.1) were included in the descriptive model-fitting exercise. Including effort beyond the study area provides good model structure, and tames the tendency for flexible models to extrapolate unrealistic high-density at the peripheries of study areas where coverage is poor – a so-called 'edge effect' (Clarke *et al*., 2000; Bravington, 2003; M. Bravington and S. Hedley, pers. comm.).

3.2.4.3 Predicting whale density throughout the study area

After fitting a descriptive model and defining a study area, the next step was to produce a gridded dataset in which a value was known in every grid cell for each explanatory variable in the model. A 5km square grid size was chosen for prediction. This was arbitrary, but constrained by two requirements: the resolution had to be coarser than the segment length (2nm), but not large enough for values of the explanatory variables to vary much within the cell.

The ARCINFO project used to estimate depth at the midpoint of each effort segment was used again to produce the gridded dataset. The convex hull defining the study area was superimposed on the bathymetry grid. A table was produced to show the latitude and longitude of the midpoint of each cell, as well as the depth at the midpoint, and the table was exported as an ASCII text file with these three columns. The table was imported to S-Plus 2000, and distance to the nearest coastline was calculated for each cell in the grid using the same methods as those used to calculate distance from each segment to the nearest coastline.

The prediction grid data were passed to the descriptive model selected for each species using the predict.gam function in mgcv. The output of the model was an estimate of the predicted number of whale schools in each grid cell, based on each cell's latitude, longitude, distance offshore, depth, and area (a constant at 25km^2). This predicted count was converted to density for mapping purposes by dividing the count by the area of each cell. School abundance of each species in the study area was calculated by summing the predictions for all grid cells. Individual abundance was calculated by multiplying school abundance by mean school size. A function, methods, was written in R to combine the detection function fitting, size bias regression, spatial modelling, model prediction and abundance estimation steps outlined above.

3.2.4.4 Estimating variance of abundance estimates
Variance cannot be estimated from the spatial model directly. For example, predicted and observed density values in grid cells that were not searched cannot be compared. In addition, neither adjacent segments of effort nor adjacent grid cells are likely to be statistically independent. In conventional distance-sampling surveys, variance may be estimated from the sample variance of the transects (Buckland *et al.*, 2001), however,

it is difficult to identify transects from data collected aboard ships of opportunity (Marques, 2001). Buckland *et al.,* (2001) recommended resampling the effort and sightings data to obtain variance estimates in such cases.

Two methods were used to estimate the variance of abundance estimates for minke, humpback and fin whales. First, a non-parametric bootstrap (Efron, 1979; Efron and Tibshirani, 1986) estimate of variance was made using *day* as the resampling unit. A function was written in R to sample the days of effort and sightings data, randomly and with replacement, until the total segment length, *L*, in the bootstrap resample approached *L* from the original survey. The decision to include or exclude the last day of sampling effort was based on the option that brought *L* in the resample closer to the total effort in the original survey. The resample dataset was passed to the methods function in R; the shape and truncation distance chosen for the original detection function and the terms specified in the original spatial model were fixed. The degree of smoothing of each model term was chosen by mgcv. The output (estimated degrees of freedom of each model term, estimate of mean group size, sample size and individual abundance) was stored in a text file. Then, a new bootstrap resample was made, and the process was repeated 300 times, which is higher than the minimum value of 200 recommended for generating 95% confidence intervals of abundance from nonparametric bootstrapping (Buckland *et al*., 2001). The values of the 2.5 and 97.5 percentiles were interpolated using the quantile command in R. This process was repeated using *Trip* as the resampling unit.

The second method used to estimate variance was the jackknife (Miller, 1974; Efron, 1979; Efron and Stein, 1981). Jackknife estimates of variance were made by

removing one day of effort and sightings data in turn, and analysing the remaining data to predict abundance using the methods function in R. The 95% confidence intervals were calculated based on a log-normal distribution, because the distribution of abundance estimates is positively skewed and cannot be negative (Buckland *et al*., 2001). Jackknife estimates of abundance were made also using each trip as the independent resampling unit. Jackknife estimation of variance also allowed visual assessment of the effects of removing data, one trip at a time, on the predicted density maps. Jackknife estimates of variance have been shown to perform well in spatial modelling exercises (Hedley, 2000).

In this study, the resampling unit was either each day's effort or each trip's effort. If adjacent days of sampling effort were independent, then the bootstrap estimates of variance would be roughly similar to those when trip was used as the resampling unit. If adjacent days were autocorrelated, then the 95% confidence intervals would be narrower than if trips were used as the resampling unit (Efron and Tibshirani, 1986). Confidence intervals were compared for humpback whale abundance based on the two resampling units. If using day as the resampling unit yielded more precise variance estimates than trips, then this was taken to mean that adjacent days were not independent, at which point trip would be used as the resampling unit.

3.2.5 Estimating g(0)

Double-platform data for each species were analysed in S-PLUS 2000 using the methods described by Borchers *et al*. (1998a). Data were modelled as a set of trials set up by the tracking team, where the probability of duplicate detection for each species was regressed on perpendicular distance and school size using generalized linear models (McCullagh and Nelder, 1989). The response variable was binary, so the

"logit" link function was used – 1 if the primary observer detected the whale in that trial, and 0 if he missed it. The value of this regression evaluated at zero distance is the point estimate of g(0). Variance was estimated using a non-parametric bootstrap resampling of trials that refitted the duplicate detection function in 999 iterations.

3.3 RESULTS

3.3.1 Primary platform search effort

Primary platform effort totalled approximately 10,000 km (Table 3.2.) Ship speed averaged 12.6kn (±0.08SE) or 23.4km/h (±0.15SE) during the survey. Search effort was carried out in Beaufort 4 conditions or better along 78% of the trackline. Visibility was excellent (>2km) in 94% of the search effort.

Trip	Season	Ship	Start	Date	Search effort (km) Primary	Secondary	Sightings Primary	Duplicate
1	2001	*Yermolova*	3 Dec	17 Dec	926	0	26	0
2	2001	*Yermolova*	20 Dec	27 Dec	411	0	11	0
3	2001	*Yermolova*	30 Dec	22 Jan	1298	462	87	40
4	2001	*Orlova*	24 Jan	30 Jan	180	0	1	0
5	2001	*Orlova*	2 Feb	9 Feb	342	0	11	0
6	2001	*Orlova*	11 Feb	16 Feb	297	0	2	0
7	2001	*Orlova*	19 Feb	26 Feb	680	0	27	0
8	2001	*Orlova*	1 March	14 March	1013	46	34	10
9	2002	*Explorer*	5 Dec	11 Dec	341	0	17	0
10	2002	*Explorer*	14 Dec	20 Dec	257	0	2	0
11	2002	*Explorer*	26 Dec	2 Jan	244	134	11	6
12	2002	*Explorer*	9 Jan	17 Jan	920	66	26	3
13	2002	*Explorer*	20 Jan	1 Feb	1745	171	80	9
14	2002	*Explorer*	4 Feb	12 Feb	1329	230	29	5
				Total:	9981	1109	364	73

Table 3.2. Search effort and sightings of cetacean schools. Trackline location and sightings of humpback, fin and minke whales are shown in Figures 3.5, 3.10 and 3.15, respectively.

3.3.1.2 Comparison of primary and secondary platform search effort

Double-platform search effort was conducted along 10% of the trackline, but was found to be difficult to implement successfully on an opportunistic survey without dedicated assistants. The double-platform search effort showed roughly similar

distribution across the range of sea states observed in the study (Figure 3.2), however a slight tendency for volunteers to prefer good sighting conditions (Beaufort 1-3) over potentially poor (and less comfortable) sighting conditions (Beaufort 5+) is apparent. Double-platform data collection was similarly biased toward areas of high cetacean density, which is unlikely to be a concern as long as sighting conditions are representative of the primary survey.

Unfortunately, data collection from the secondary platform was marred by rounding radial distances in nautical miles to the nearest integer, and observers' visual estimates of range could not be calibrated. Point estimates of $g(0)$ and associated bootstrap estimates of variance (CV and 95% confidence intervals) are presented below for each species, however, they should be interpreted with caution. The estimates were likely to be subject to a small degree of positive bias, because the effort was biased toward good sighting conditions. However, the tendency for observers to overestimate range (Chapter 2) would cause these estimates to be negatively biased.
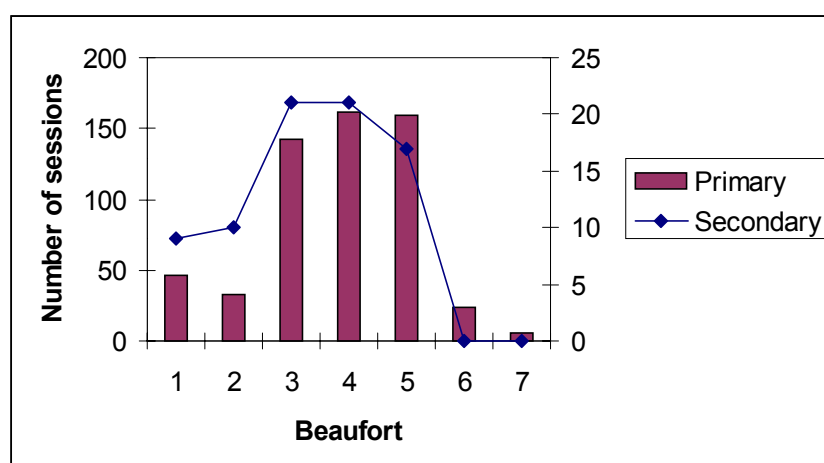
Figure 3.2. Distribution of search effort with respect to sighting conditions. Sample size refers to number of data collection sessions. The y-axis on the left-hand side refers to sessions where only primary platform effort was recorded. The right-hand y-axis refers to sessions when passengers and crew agreed to record double-platform data.

3.3.1.3   Primary platform sightings

The total number of sightings of cetacean schools observed by the primary platform

was 364. These are summarised by species in Table 3.3. Only humpback, fin and

minke whales were seen sufficiently frequently to be in the range recommended as the

minimum number of detections (60-80) necessary for modelling detection probability

(Buckland *et al.*, 2001). Results of spatial models predicting distribution and

abundance of each of these species are discussed in turn in the following sections.

Species	Schools	Indiv.
humpback whale	129	232
fin whale	80	207
minke whale	75	119
hourglass dolphin	19	86
killer whale	14	61
southern bottlenose whale	14	34
Peale's dolphin	9	46
dusky dolphin	4	15
southern right whale	4	7
sei whale	4	11
long-finned pilot whale	2	38
Cuvier's beaked whale	2	4
sperm whale	2	6
strap-toothed whale	1	1
unidentified cetacean spp.	5	9

Table 3.3. Summary of sightings of cetacean schools and individual (Indiv.).

3.3.2.   Modelling distribution and abundance of humpback whales
3.3.2.1.   Primary platform data analysis

The detection function that fitted the humpback sightings data best, as determined by

AIC, was a hazard-rate key function with no adjustment terms. Model fit was

improved by truncating at 2500m (c. 1.6nm), which eliminated only the four most

distant sightings from the spatial model. There was no support for including Beaufort

as a covariate in terms of AIC. Mean group size was estimated by a size-biased

regression to be 1.83 (±0.07SE). The distribution of perpendicular distances and the

selected model are shown in Figure 3.3. Table 3.4 provides a summary of the fitted

model parameters, encounter rate, school size and mean school and animal density in the sample.
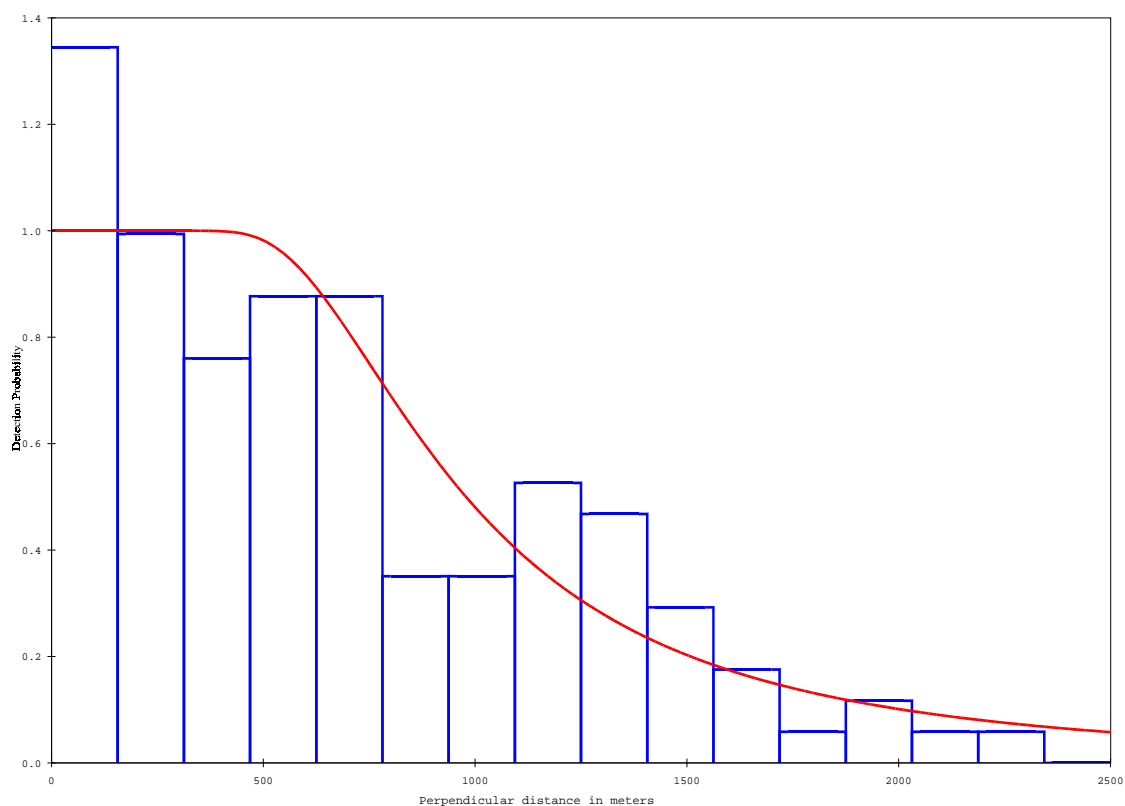
Figure 3.3. Detection probability (y-axis) of 125 sightings of humpback whale schools as a hazard-rate function of perpendicular distance (x-axis). Effective strip half-width was estimated at 1142m (±105SE).

Parameter	Point Estimate	Standard Error	% CV	95% CI Lower	95% CI Upper
f(0)	8.76E-04	8.1E-05	9.23	7.30E-04	1.05E-03
ESW	1142	105	9.23	952	1370
n/L	0.0237	0.0060	25.66	0.0142	0.0386
DS	0.0055	0.0015	27.27	0.0033	0.0094
E(S)	1.827	0.071	3.91	1.691	1.974
D	0.0101	0.0028	27.55	0.0059	0.0172

Table 3.4. Fitted model parameters, encounter rate, school size and mean school and animal density in the sample, for 125 humpback whale sightings. Note: f(0) is unitless; effective strip half-width (ESW) is in meters; encounter rate (n/L) in number of schools per kilometer; school density and animal density (DS and D, respectively) in numbers per km^2; and estimated school size (E(S)) is the intercept of the regression of group size on perpendicular distance.

The components contributing to the overall variance in the animal density estimate are of particular interest. Detection probability accounted for 11.2% of the variance, and the regression of group size on perpendicular distance accounted for an additional 2.0%. The remaining 86.8% of the variance was attributable to heterogeneity in encounter rate.

3.3.2.2. Spatial modelling from line-transect survey data

3.3.2.2.1. Modelling heterogeneity in humpback whale density along the trackline

The selected model was:

$$\hat{n}_s = \text{s}(\textit{LatMid}, 1.467) + \text{s}(\textit{mindist}, 4) + \text{s}(\textit{depth}, 4) + \text{s}(\textit{LonMid}, 3.87) + \text{offset}$$

where all four candidate variables were selected as explanatory variables in Equation 3.2. Latitude was estimated to have 1.467 degrees of freedom, distance offshore and depth each had 4edf, and longitude was estimated to have 3.87df.

Details for each variable are shown in Figure 3.4, which can be thought of as illustrating the shape of the smooth functions, f_k, of Equation 3.2. Humpback density was high south of 60ºS, with bimodal longitudinal peaks around 40ºW and 60ºW. The explanatory power of the model was moderate; the adjusted R-square score for the model was 0.129, and deviance explained was 36.1%.
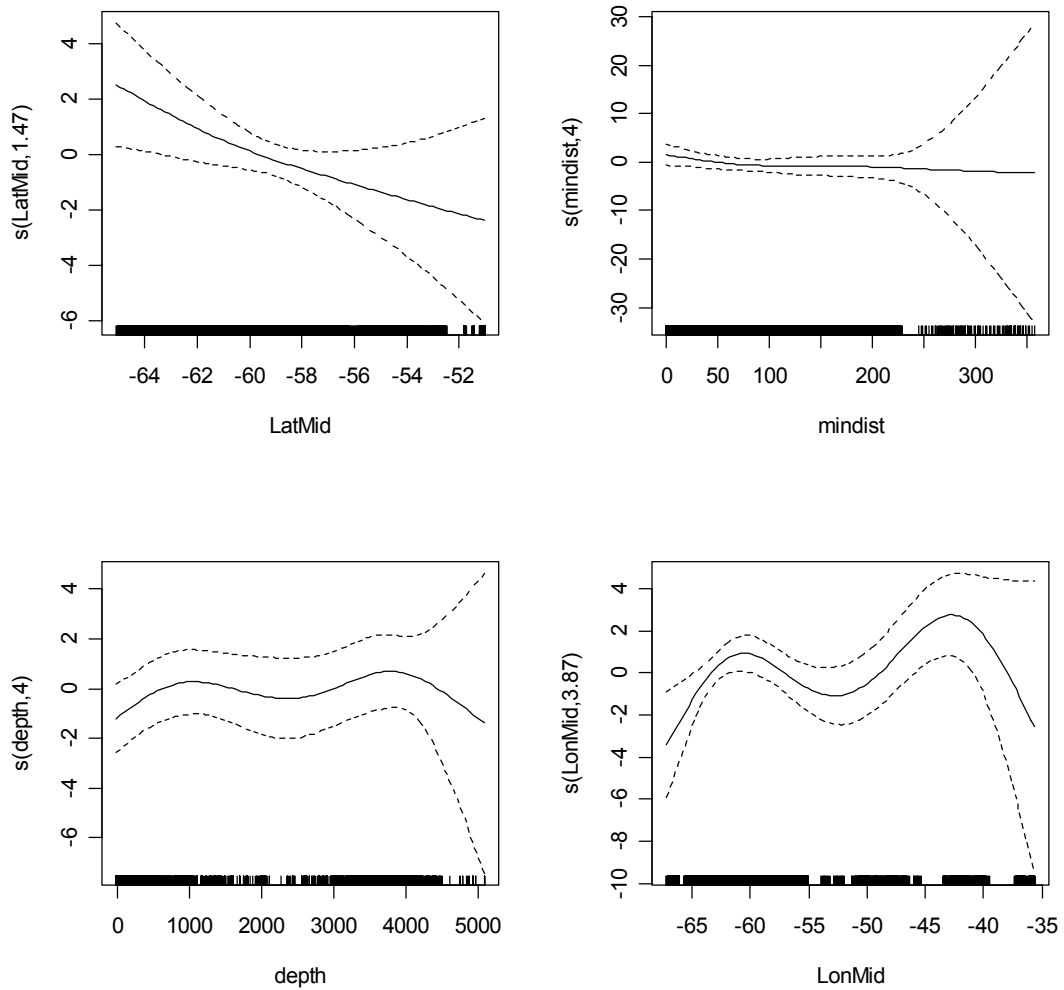
Figure 3.4. Smoothed components (solid line) of four explanatory variables (x-axes) used in the fitted GAM and the response variable, density of humpback whale schools. Each explanatory variable was allowed up to 9df and degree of smoothing was automated by mgcv. Each x-axis contains a rugplot, where small ticks mark locations of observations. Regions of high whale density are identified by values above zero on the y-axis. Note the different scale of each y-axis, which is labelled s(covariate name, estimated degrees of freedom). The dashed lines represent ±2 standard errors, or roughly 95% confidence intervals.

3.3.2.2.2 Humpback whale density and abundance across the prediction grid

The model predicted a very strong density gradient with the highest-density region predicted along the west side of the Antarctic Peninsula (Figure 3.5). Humpback whale abundance in the best-covered region of the study area was estimated to be 1829 animals.

Figure 3.5. Predicted density gradient of humpback whale schools in the best-covered region of the study area. The scale bar on the right is in units of schools per nm^2. Tracklines are shown as solid black lines, and humpback sightings shown as red circles with radius proportional to school size.

3.3.2.2.3 *Variance of humpback whale abundance estimate*

Variance estimates from jackknifing and non-parametric bootstrapping, each using Trip and Day as resampling units, are shown in Table 3.5. Non-parametric bootstraps failed in approximately 10% of iterations, however, no convergence failure was observed during jackknife variance estimation. Confidence intervals were narrower when day was used as the resampling unit, suggesting that the assumption of independence was violated. Future analyses considered only trip as the resampling unit.

Bootstrap estimates of variance, even when trip was used as the resampling unit, showed substantial positive bias. While humpback abundance was estimated to be 1829 animals, the median of 300 bootstraps was 3598 and the mean was 4569.

Maps were created during each jackknife iteration when Trip was used as the resampling unit. Predicted density gradients of humpback whale schools at each jackknife iteration are shown in Figure 3.6. Note that the area predicted to have the highest density of humpback schools, the western Antarctic Peninsula region, was identified consistently in each iteration.

	log-normal 95% CI	
Resampling method	lower	upper
Jackknife trips	978	3422
Jackknife days	1511	2215
Bootstrap trips	1521	11290
Bootstrap days	1719	12803

Table 3.5. Estimates of variance (95% confidence intervals) of humpback abundance using two resampling units for jackknifing and non-parametric bootstrapping (300 iterations).
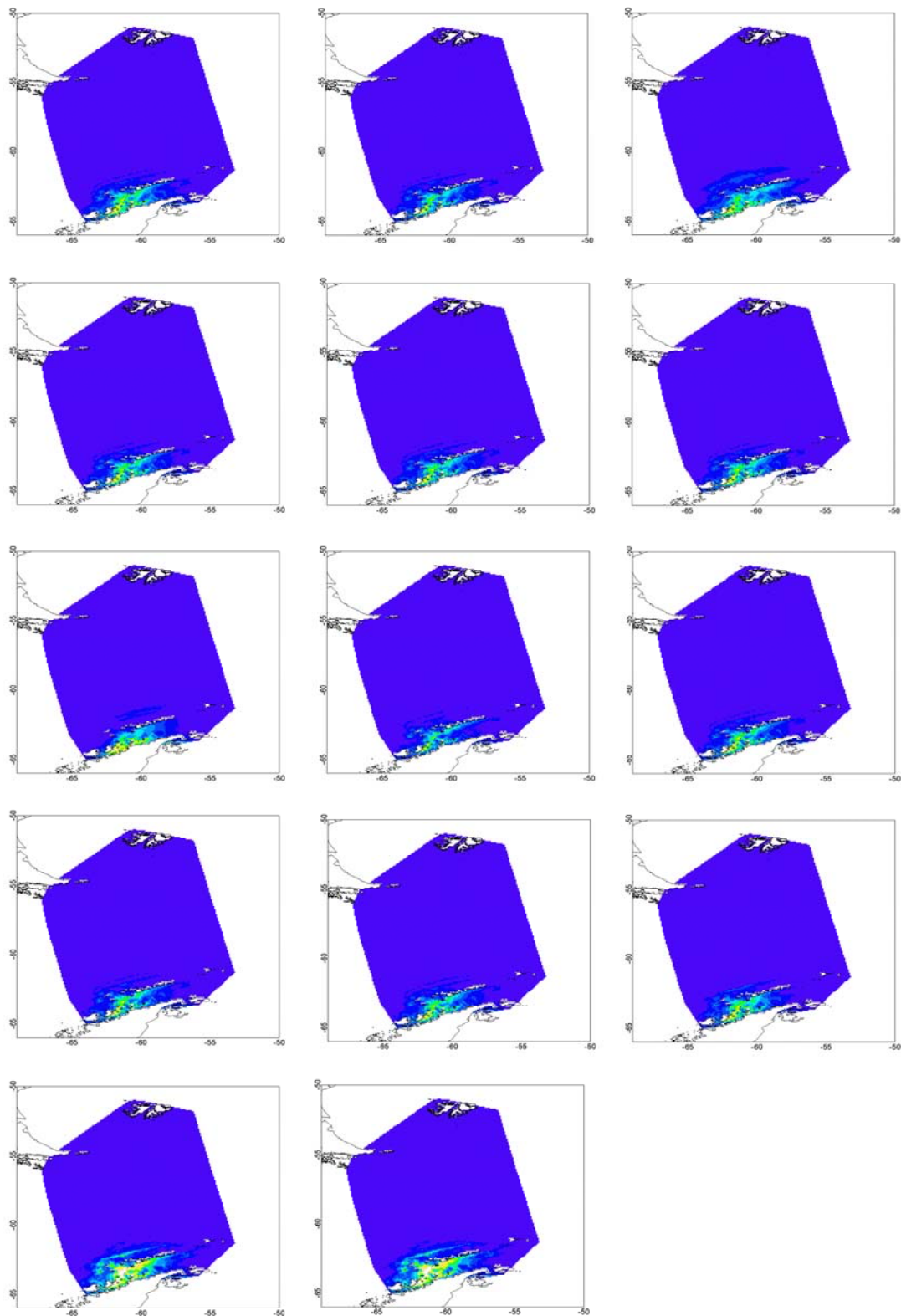
Figure 3.6. Maps of predicted density of humpback schools with each trip's effort and sightings removed in sequence, with replacement. From left to right, by row, the maps reflect predicted density with the first trip removed; then with the first trip replaced and the second removed, and so on. Note that the model was not unduly influenced by removing a given trip, and that in all cases, the model predicted that the region of highest humpback density was along the western coast of the Antarctic Peninsula.

3.3.2.3 Double-platform data
3.3.2.3.1. Estimate of g(0) for humpback whales
The logistic glm-based regression of duplicate sighting probability on perpendicular

distance is shown in Figure 3.7. Duplicate detection probability on the trackline (g(0))

for humpback whales was estimated to be 0.984. Non-parametric bootstrapping of this

function provided an estimate of 0.023 for the CV, and 95% confidence intervals of

0.918-1.
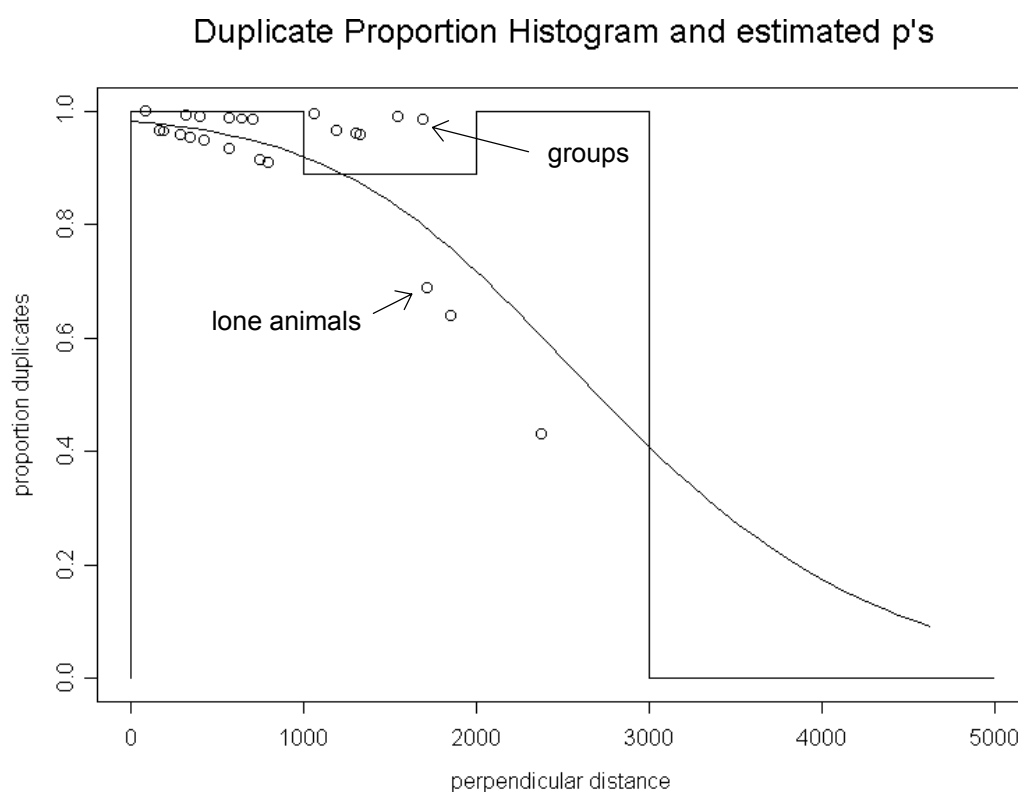
Figure 3.7. Probability of duplicate detection as a function of perpendicular distance and group size. School size was a significant term in the final model. The lower series of dots represent duplicate detections of lone animals, and the upper series represent duplicate sightings of schools of size >1. The mean estimate of g(0) was 0.984 (CV=0.023; 95% CI=0.918-1).

3.3.3 Modelling distribution and abundance of fin whales

3.3.3.1 Primary platform data analysis

The detection function that fit the fin whale sightings data best, as determined by AIC, was a hazard-rate key function with no adjustment terms. Model fit was improved by truncating at 2000m (c. 1.06nm), which eliminated the seven most distance sightings from the spatial model. There was insufficient support from the data (as indicated by AIC) to justify including Beaufort as a covariate in the detection function. Regression-based estimate of school size was 2.44 ($\pm$0.20SE). The distribution of perpendicular distances and the selected model are shown in Figure 3.8. Effective strip half-width was estimated to be 816m ($\pm$108SE). Table 3.6 provides a summary of the fitted model parameters, encounter rate, school size and mean school and animal density in the sample.

The component percentages of the variance in animal density were qualitatively similar to those found with humpback whales. Detection probability accounted for 14.0% of the variance, and the regression of group size on perpendicular distance accounted for an additional 5.4%. The remaining 80.6% of the variance was attributable to heterogeneity in encounter rate.
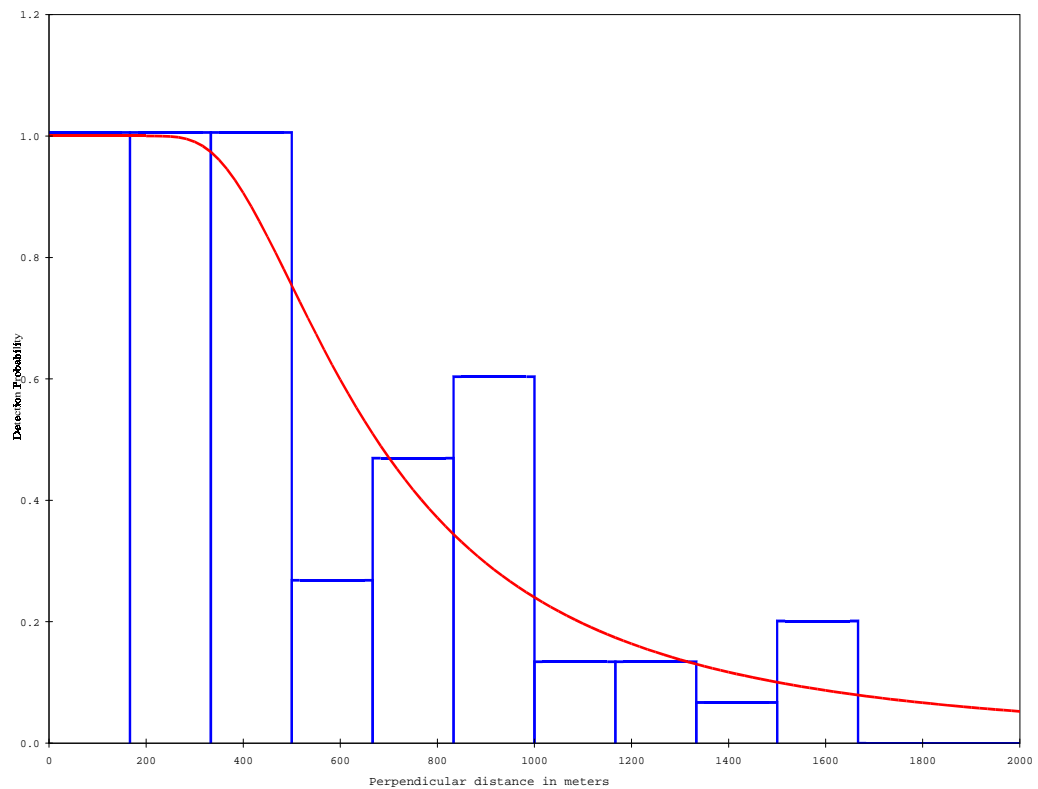
Figure 3.8. Detection probability of 73 sightings of fin whale schools as a hazard-rate function of perpendicular distance. Effective strip half-width was estimated to be 816m (±108SE).

Parameter	Point Estimate	Standard Error	Percent coef. of variation	95% Confidence Interval Lower	Upper
f(0)	1.23E-03	1.63E-04	13.28	9.42E-04	1.60E-03
ESW	816	108	13.28	627	1370
n/L	0.0137	0.0043	31.85	0.0074	0.0252
DS	0.0045	0.0016	34.51	0.0023	0.0088
E(S)	2.44	0.20	8.24	2.07	2.87
D	0.0110	0.0039	35.48	0.0056	0.0217

Table 3.6. A summary of the fitted model parameters, encounter rate, school size and mean school and animal density in the sample, for 73 fin whale sightings. Note that: f(0) is unitless; effective strip half-width (ESW) is in meters; encounter rate (n/L) in number of schools per kilometer; school density and animal density (DS and D, respectively) in numbers per km^2; and estimated school size (E(S)) is the intercept of the regression of group size on perpendicular distance.

3.3.3.2   Spatial modelling from line-transect survey data
3.3.2.2.1   Modelling heterogeneity in fin whale density along the trackline
The selected model was:

$$\hat{n}_s = \text{s}(\textit{LonMid, LatMid}, 3.789) + \text{s}(\textit{depth}, 3.797) + \text{s}(\textit{mindist}, 3.931) + \text{offset}$$

The three splines in the selected model are the f_k's in Equation 3.2, where the two-dimensional smooth of latitude and longitude was estimated to have 3.789 degrees of freedom, depth had 3.797edf and distance offshore had 3.931edf.

The selected model is shown in Figure 3.9, which can be thought of as illustrating the shape of the functions, f_k, in Equation 3.2.   Fin whale density increased generally toward the southeast.   Fin density tended to be low in water depths below 1000m, and within 40nm from the nearest coastline.   Explanatory power of the model was moderate.   The adjusted R-square score for the model was 0.103, and deviance explained was 37.9%.
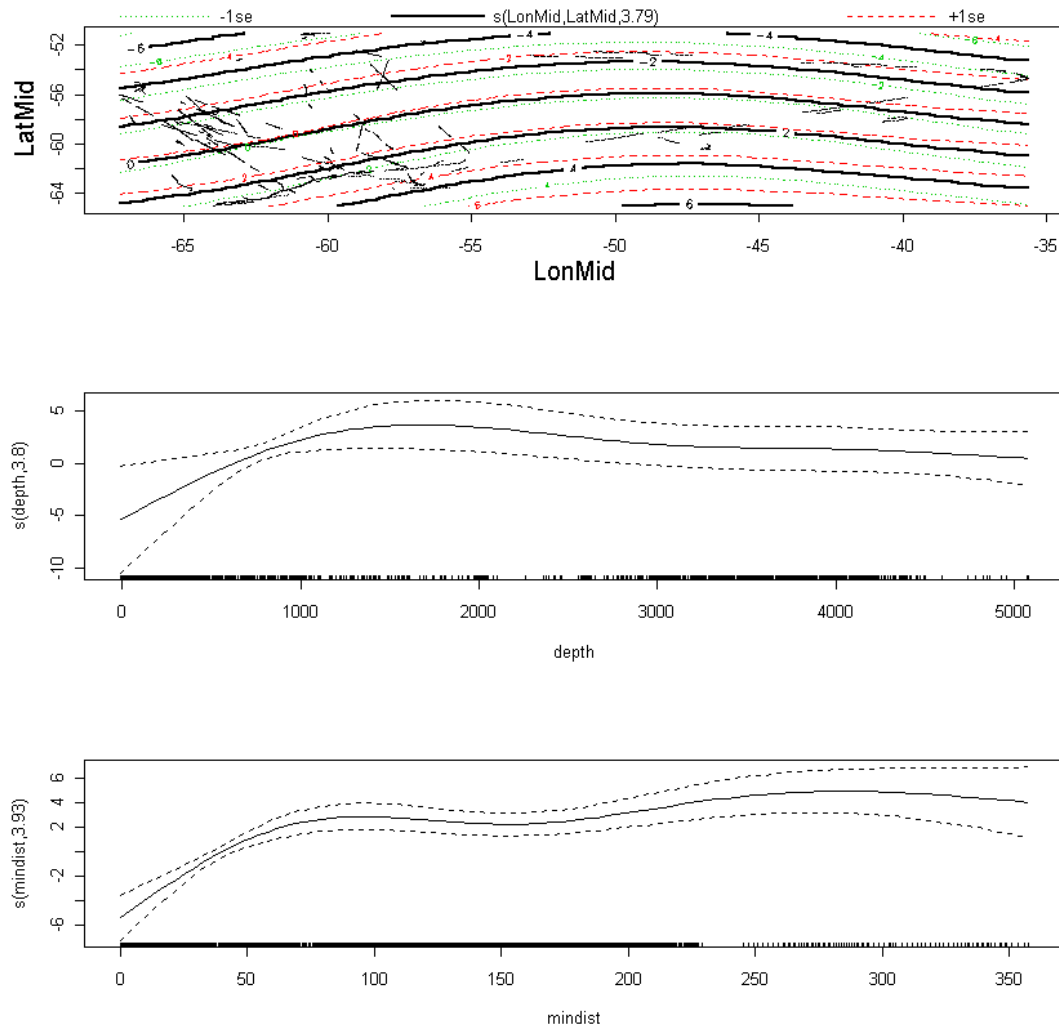
Figure 3.9. One two-dimensional (*LonMid*, *LatMid*) and two one-dimensional (*depth* + *mindist*) smoothing splines (solid line) of the fitted GAM (x-axes) and the response variable, density of fin whale schools. Each explanatory variable was allowed up to 9df and degree of smoothing was automated by mgcv. Each x-axis contains a rugplot, where small ticks mark observed values. Regions of high whale density are identified by values above zero on the y-axis. Note the different scale of each y-axis, which is labelled s(covariate name, estimated degrees of freedom). The dashed lines represent ±2 standard errors, or roughly 95% confidence intervals.

3.3.3.2.2 *Fin whale density and abundance*

The model predicted a strong density gradient with the highest-density region predicted in the Scotia Sea (Figure 3.10). Fin whale abundance in the best-covered region of the study area was estimated to be 4487 animals.
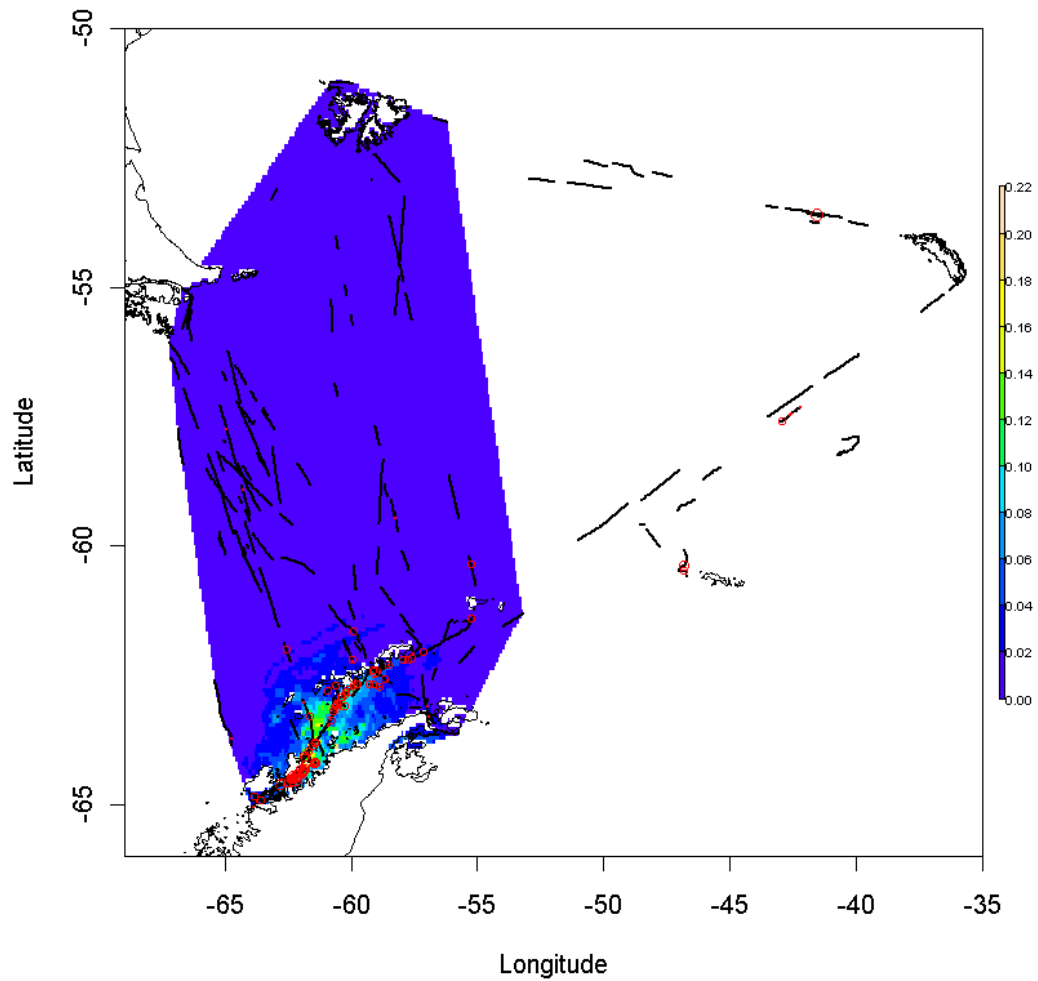
Figure 3.10. Predicted density gradient of fin whale schools in the best-covered region of the study area. The scale bar on the right is in units of schools per nm^2. Tracklines are shown as solid black lines, and fin whale sightings shown as red circles with radius proportional to school size.

3.3.3.2 *Variance of abundance estimate*

Variance estimates from jackknifing and non-parametric bootstrapping using Trip as the resampling unit are shown in Table 3.7. Day was not considered as a resampling unit, because results from resampling humpback density suggested that adjacent days of sampling effort were not independent. Non-parametric bootstraps failed in approximately 8% of iterations, however no convergence failure was observed during jackknife variance estimation. Bootstrap estimates of variance showed substantial positive bias. While fin whale abundance was estimated to be 4487 animals, the median value of 300 bootstraps was 8982 and the mean value was 16269.

Maps were created during each jackknife iteration and these predicted density
gradients are shown in Figure 3.11. Note that the area predicted to have the highest
density of fin whale schools showed more variability than was seen in humpback
whales (Figure 3.6), but was always predicted to be in offshore waters, running
parallel to the Antarctic Peninsula region.

Resampling method	log-normal 95% CI	
	lower	upper
Jackknife by trip	1326	15179
Bootstrap by trip	1475	65935

Table 3.7. Estimates of variance (95% confidence intervals) of fin whale abundance using
two methods.
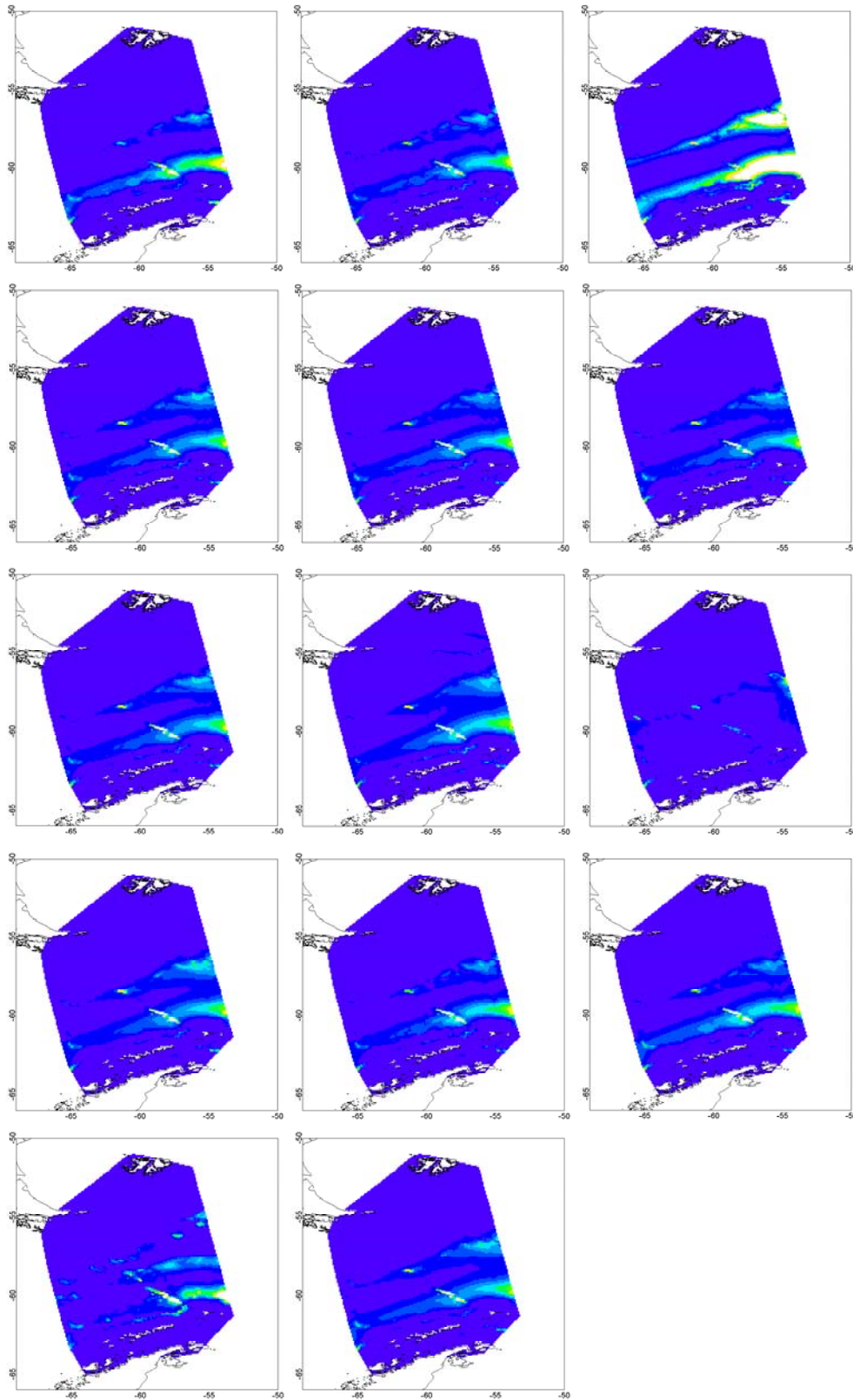
Figure 3.11. Maps of predicted density of fin whale schools with each trip's effort and sightings removed in sequence, with replacement. From left to right, by row, the maps reflect predicted density with the first trip removed; then with the first trip replaced and the second removed, and so on. The large white areas in the middle of the high-density regions in the third map reflect predicted densities greater than 0.22 schools per nm^2. Note that removing a given trip affected the scale of the predicted density gradient, but had relatively minor influence on predicted location of the high-density area.

3.3.3.3 Double-platform data collection
3.3.2.3.1 Estimate of g(0)for fin whales

The logistic glm-based regression of duplicate sighting probability on perpendicular

distance is shown in Figure 3.12. Duplicate detection probability on the trackline

(g(0)) for fin whales was estimated to be 0.999. Non-parametric bootstrapping of this

function provided an estimate of 0.045 for the CV, and 95% confidence intervals of

0.893-1.
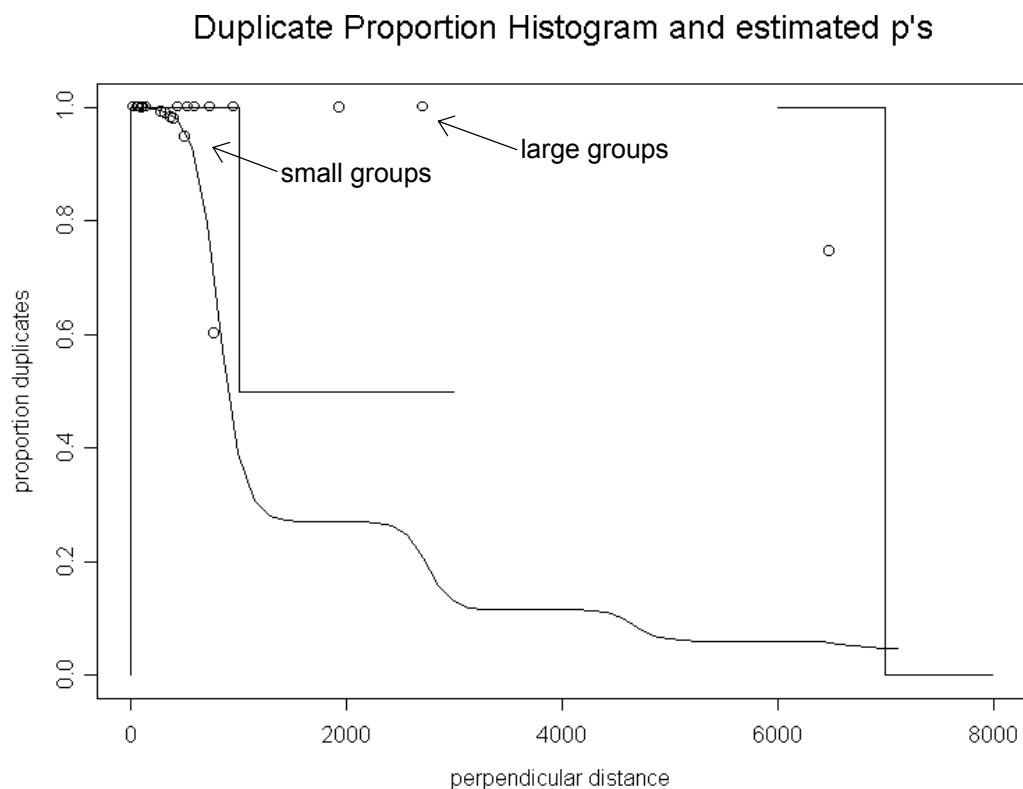
Figure 3.12. Probability of duplicate detection of fin whales as a function of perpendicular distance and group size. The selected model was glm(formula = seen ~ x + size, family = binomial(link = logit)). School size was a significant term in the final model. The lower series of dots represent duplicate detections of schools of size 1 or 2, and the upper series represent duplicate sightings of schools of size >2. The mean estimate of g(0) was 0.999 (CV=0.045; 95% CI=0.893-1).

3.3.4 Modelling distribution and abundance of minke whales

3.3.4.1 Primary platform data analysis

The detection function that fit the minke whale sightings data best, as determined by AIC, was a hazard-rate key function with no adjustment terms. Truncation failed to improve model fit, so no sightings were excluded from the spatial model. There was insufficient support from the data (as indicated by AIC) to justify including Beaufort as a covariate in the detection function. Regression-based estimate of school size was 1.209 (±0.064SE). The distribution of perpendicular distances and the selected model are shown in Figure 3.13. Effective strip half-width was estimated to be 663m (±91SE). Table 3.8 provides a summary of the fitted model parameters, encounter rate, school size and mean school and animal density in the sample.
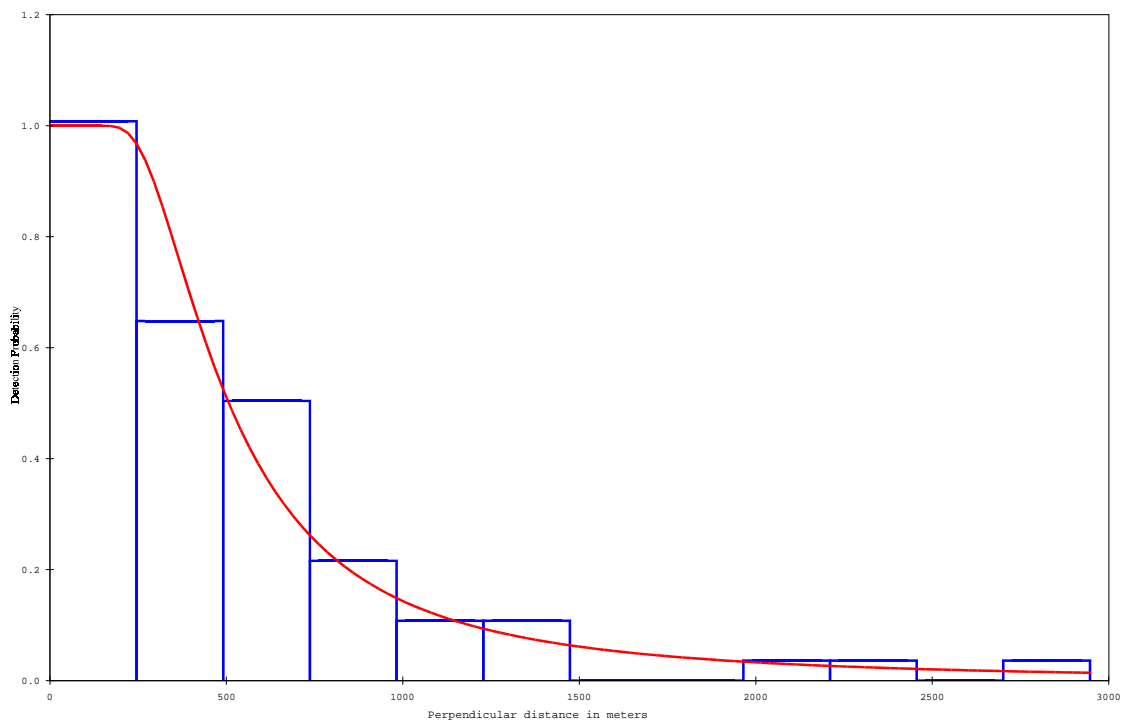
Figure 3.13. Detection probability (y-axis) of 75 sightings of minke whale schools as a hazard-rate function of perpendicular distance (x-axis). Effective strip half-width was estimated to be 663m (±91SE).

Parameter	Point Estimate	Standard Error	% CV of variation	95% CI Lower	95% CI Upper
f(0)	1.51E-03	2.07E-04	13.72	1.15E-03	1.98E-03
ESW	663	91	13.72	505	871
n/L	0.0140	0.0034	24.24	0.0087	0.0225
DS	0.0057	0.0016	27.85	0.0033	0.0098
E(S)	1.209	0.064	5.27	1.089	1.343
D	0.0069	0.0020	28.35	0.0040	0.0120

Table 3.8. A summary of the fitted model parameters, encounter rate, school size and mean school and animal density in the sample, for 75 minke whale sightings. Note that: f(0) is unitless; effective strip half-width (ESW) is in meters; encounter rate (n/L) in number of schools per kilometer; school density and animal density (DS and D, respectively) in numbers per km^2; and estimated school size (E(S)) is the intercept of the regression of group size on perpendicular distance.

The component percentages of the variance in minke whale density were qualitatively similar to those found with humpback and fin whales.   Detection probability accounted for 23.4% of the variance, and the regression of group size on perpendicular distance accounted for an additional 3.5%. The remaining 73.1% of the variance was attributable to heterogeneity in encounter rate.

3.3.4.2. Spatial modelling from line-transect survey data
3.3.3.4.1. Modelling heterogeneity in minke whale density along the trackline
The selected model was:

$$\hat{n}_s = s(depth, 2.01) + s(LonMid, 3.42) + s(mindist, 3.03) + LatMid + \text{offset}$$

Depth, longitude and distance offshore were selected as smooth functions, f_k, in Equation 3.2. Depth was estimated to have 2.01 degrees of freedom, longitude had 3.42edf and distance offshore had 3.03edf. Latitude entered the model as a linear term (which has 1 degree of freedom).

The selected model is shown in Figure 3.14, which can be thought of as illustrating the shape of the functions, f_k, of Equation 3.2. Minke whale density showed bimodal longitudinal peaks near 45ºW and 65ºW. The linear term of *LatMid* had a slope of − 0.30 (±0.12SE, p=0.011), indicating that density increased linearly in a southward direction. Explanatory power of the model was moderate. The adjusted R-square score for the model was 0.105, and deviance explained was 23.4%.
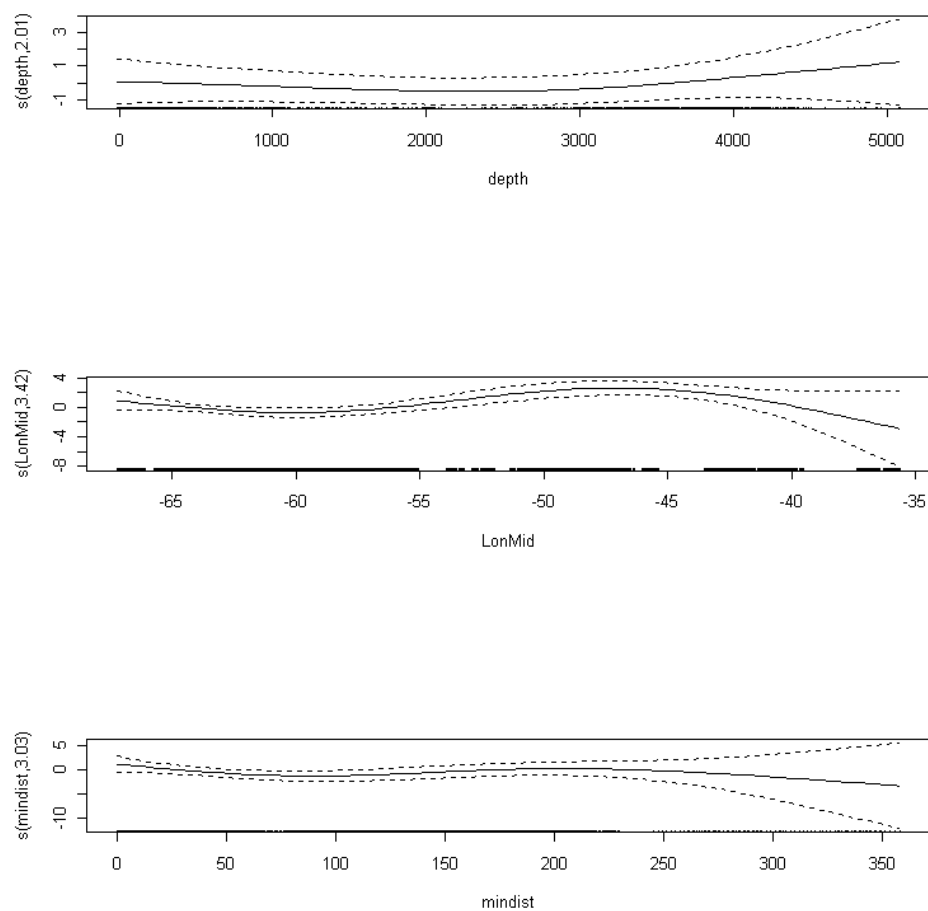
Figure 3.14. Smoothed components (solid line) of three explanatory variables (x-axes) used in the fitted GAM and the response variable, density of minke whale schools. Each explanatory variable was allowed up to 9df and degree of smoothing was automated by mgcv. Each x-axis contains a rugplot, where small ticks mark locations of observations. Regions of high whale density are identified by values above zero on the y-axis. Note the different scale of each y-axis, which is labelled s(covariate name, estimated degrees of freedom). The dashed lines represent ±2 standard errors, or roughly 95% confidence intervals.

3.3.3.4.2 Minke whale density and abundance

The model predicted a strong density gradient with a predicted high-density region

spread along the Antarctic Peninsula (Figure 3.15). Minke whale abundance in the

best-covered region of the study area was estimated to be 1544 animals.
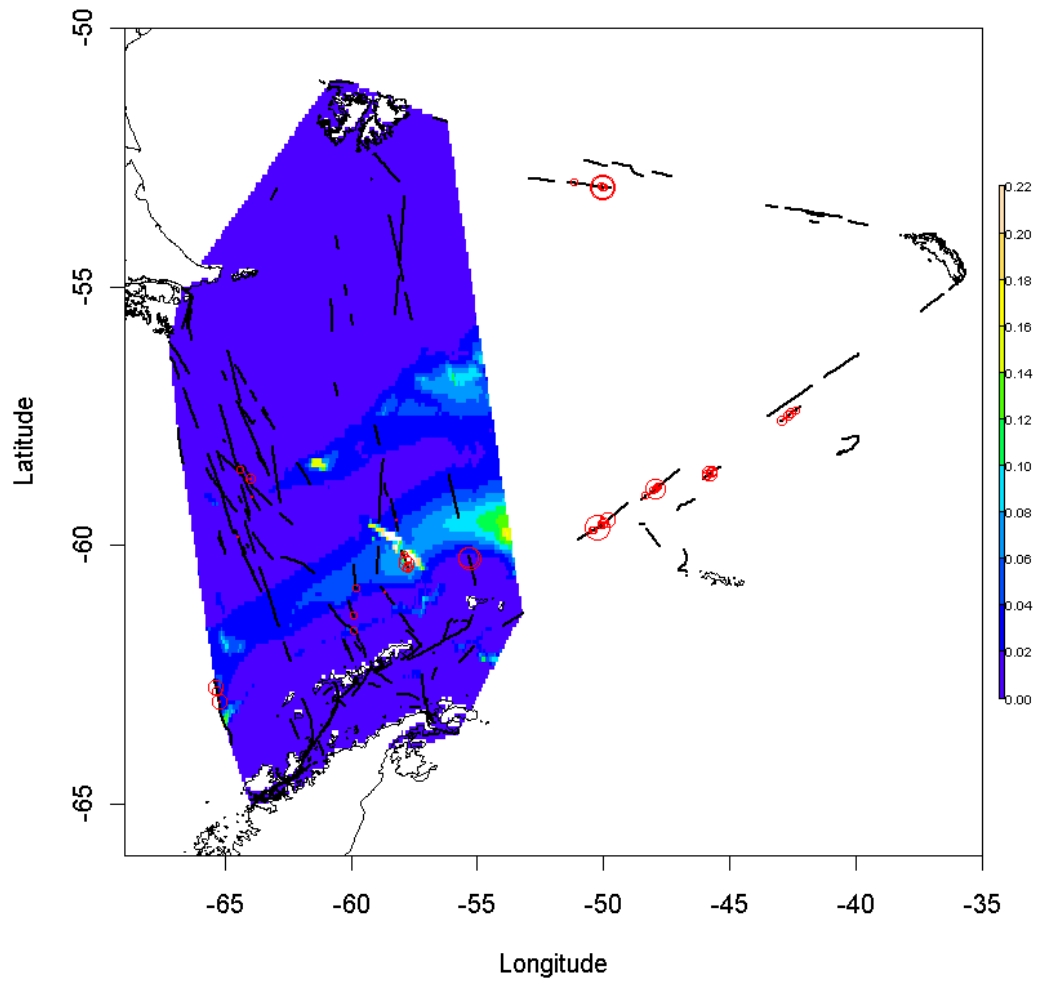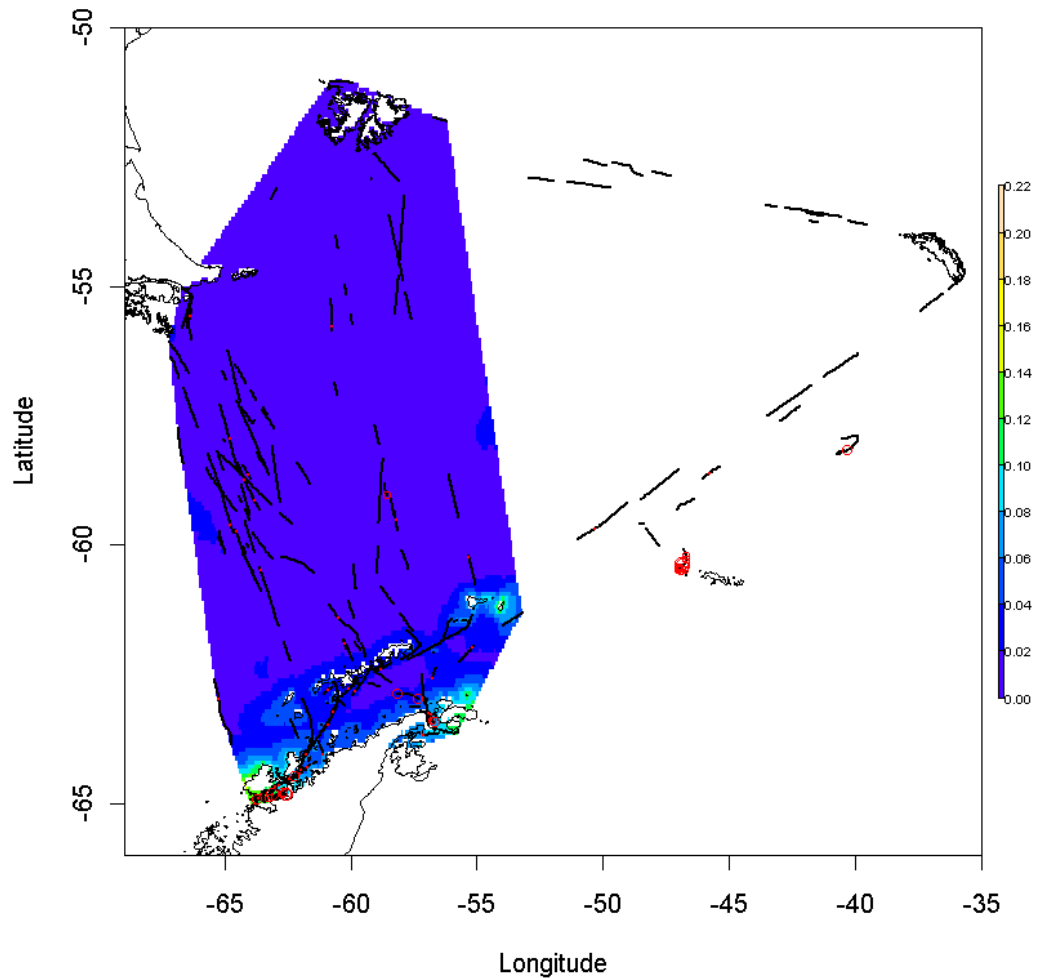

Figure 3.15. Predicted density gradient of minke whale schools in the best-covered region of the study area. The scale bar on the right is in units of schools per nm^2. Tracklines are shown as solid black lines, and minke sightings shown as red circles with radius proportional to school size.

3.3.3.4.3   Variance of minke whale abundance estimate

Variance estimates from jackknifing and non-parametric bootstrapping using Trip as

the resampling unit are shown in Table 3.9.   Non-parametric bootstraps failed in

approximately 5% of iterations, however no convergence failure was observed during

jackknife variance estimation.   Bootstrap estimates of variance showed substantial

positive bias.   While minke whale abundance was estimated to be 1544 animals, the

median value of 300 bootstraps was 3343 and the mean value was 3826 whales.

Maps were created during each jackknife iteration and these predicted density

gradients are shown in Figure 3.16.   Note that the area predicted to have the highest

density of minke whale schools, along the Antarctic Peninsula and associated island

chains, was identified consistently in each iteration.

	log-normal 95% CI	
Resampling method	lower	upper
Jackknife by trip	1221	1953
Bootstrap by trip	1495	6484

Table 3.9.   Estimates of variance (95% confidence intervals) of minke whale abundance using two methods.
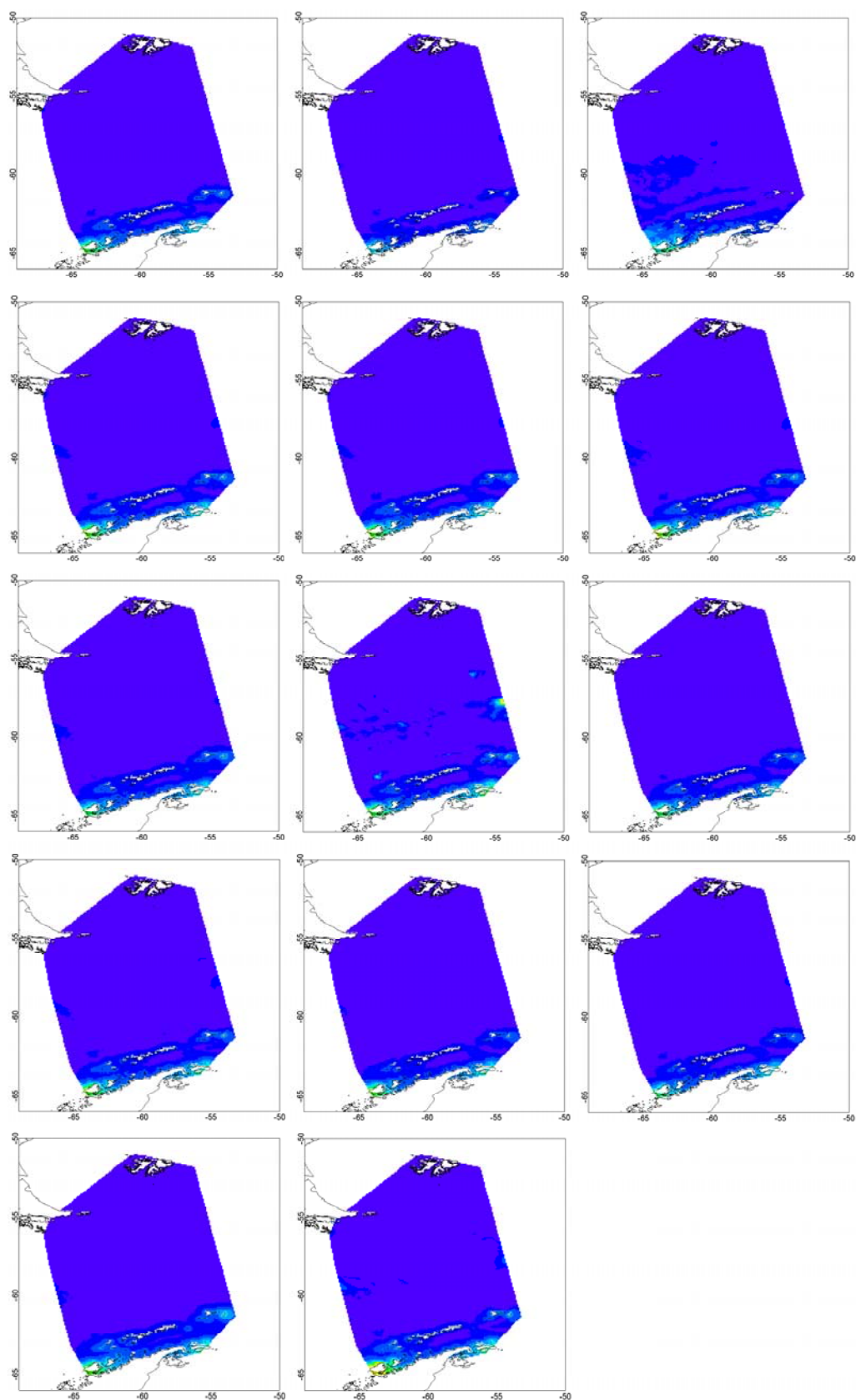
Figure 3.16. Maps of predicted density of minke whale schools with each trip's effort and sightings removed in sequence, with replacement. From left to right, by row, the maps reflect predicted density with the first trip removed; then with the first trip replaced and the second removed, and so on. Note that removing a given trip affected the scale of the density gradient, but had relatively minor influence on the predicted location of the high density area.

3.3.4.3 Double-platform data collection
3.3.3.3.4. *Estimate of g(0)for minke whales*

The logistic glm-based regression of duplicate sighting probability on perpendicular

distance is shown in Figure 3.17. Model fit was improved by dropping the school size

term as a covariate. Duplicate detection probability on the trackline ($g(0)$) for minke

whales was estimated to be 0.923. Non-parametric bootstrapping of this function

provided an estimate of 0.046 for the CV, and 95% confidence intervals of 0.865-1.
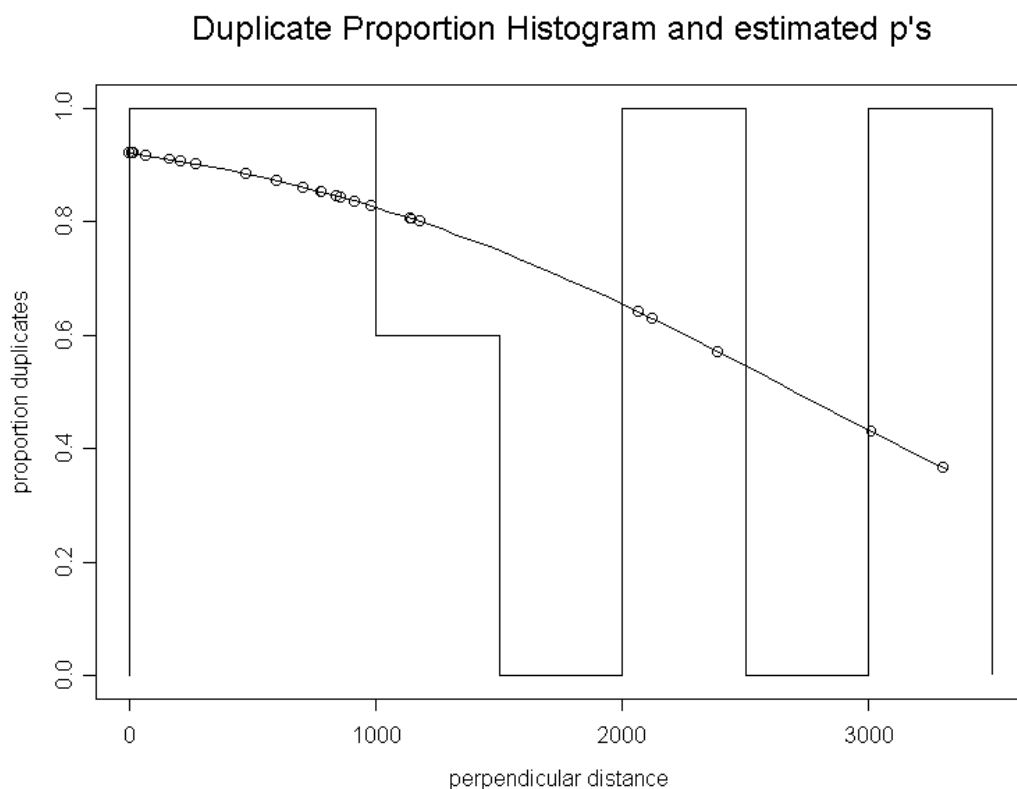
Figure 3.17. Probability of duplicate detection of minke whales as a function of perpendicular distance. The selected model was glm(formula = seen ~ x, family = binomial(link = logit)). The mean estimate of g(0) was 0.923 (CV=0.046; 95% CI=0.865-1).

3.4 DISCUSSION

### 3.4.1 Modelling cetacean line-transect data from a non-randomised survey

Spatial modelling of line-transect survey data collected from ships of opportunity

yielded predicted density maps and abundance estimates for three baleen whale

species in the Antarctic. The approach used shows promise in utilising inexpensive

platforms for conducting pilot studies in understudied areas. This study demonstrated

that there is merit in collecting reliable distance-sampling data from a non-randomised

survey with reasonable coverage, modelling heterogeneity along the trackline, and

using the model to predict density throughout the study area. The framework outlined

here is an appropriate way to gain useful information on frequently seen cetacean

species in other areas from expedition-style cruise ships, fishing boats, freighters or

other ships of opportunity. Free ship time that provides reasonable, but not systematic,

coverage of a study area may be used for pilot studies to quantify distribution and

abundance roughly, for training, and for trying out new methods inexpensively.

3.4.2 Distribution of Antarctic balaenopterids

Maps of cetacean distribution can be very useful for guiding future research. The

smooth density surfaces predicted for humpback, fin and minke whales (Figures 3.5,

3.10 and 3.15, respectively) could be used in a variety of ways, providing that they

accurately reflect mean animal distribution during the survey. Sequential exclusion of

each of the 14 trips (approximately 7% of the effort on average) affected the scale of

the density gradient, but not its placement (Figures 3.6, 3.11 and 3.16).   As a result,

the maps may be considered accurate representations of whale distribution at the

midpoint of the surveys.

Studies that do not require a randomised sampling design will benefit from identifying high-density areas that can be targeted in future to increase the efficiency of photo-identification and biopsy studies. Identifying core areas, and directing research effort within them, were important contributions to studies of resident killer whale populations of the northeast Pacific (Baird and Whitehead, 2000; Ford *et al*., 2000), because the questions asked about acoustics (Ford, 1989), social structure (Bigg *et al*., 1990) and diet (Ford *et al*., 1998) for example, did not require randomised sampling. Similarly, studies on spatial and temporal distribution (Hooker *et al*., 1999) and association patterns (Gowans *et al*., 2001) in the northern bottlenose whale (*Hyperoodon ampullatus*) benefited from finding and targeting a high-density area off Nova Scotia, Canada. Spatial modelling can be thought of as an objective means of identifying potential hotspots, like Johnstone and Haro Straits are for the resident killer whales and the Gully is for northern bottlenose whales.

High-density areas can be incorporated into future line-transect surveys as well. Spatial modelling of line-transect data collected from a ship of opportunity may be a useful way to identify the boundary between high- and low-density strata for future surveys. If the density gradient is strong, then allocating more effort in the region where most of the sightings will be made will yield a more precise abundance estimate than a single-stratum survey (Buckland *et al*., 2001). Even if the density gradient is weak, ensuring that tracklines are placed perpendicular to it will avoid real heterogeneity in animal density being interpreted as sampling error and, therefore, reduce variance estimates.

Information on whale distribution can play a role also in management and conservation. Visual plots of whale density in this region could be used to allocate krill fishing quotas spatially. This would allow harvest to be allocated in a way that minimises any local competition between commercial krill harvest and krill-eating predators (Boyd, 2002). Similarly, identifying areas where the majority of whales are found could assist efforts to minimise by-catch of a threatened species, or to set aside a protected area that satisfies the energy requirements of the population (Hooker *et al.*, 1999).

The predicted distributions of humpback, minke and fin whales were discrete and showed little overlap (Figures 3.5, 3.10 and 3.15, respectively). This may well reflect different prey preference (Laws, 1977), which in turn may represent a form of ecological niche partitioning to reduce interspecific competition (Clapham and Brownell, 1996). However, from the standpoint of designing future surveys, it is clear that high-density strata would be drawn in different areas for each species. This limits the potential for optimal design of cost-effective multispecies surveys. In fact, IWC surveys designed to estimate abundance of minke whales (*e.g.*, Branch and Butterworth, 2001a) could be thought of as platforms of opportunity surveys for non-target species (Branch and Butterworth, 2001b). In particular, substantial fin whale density was predicted north of 60ºS (as recognised by Rice, 1995 and Branch and Butterworth, 2001b), suggesting that IWC abundance estimates for this species are substantial underestimates. Fin whale abundance estimates must be made during the austral winter (Best, 2003) in addition to Antarctic circumpolar cruises, because not all whales are being monitored during summer surveys.

3.4.3 Abundance of Antarctic balaenopterids

It is important to know, but difficult to assess, whether the abundance estimates predicted by the spatial models were accurate. Two subjective approaches were used to gauge the accuracy of the point estimates of abundance. The first was a series of internal checks. The model specification procedure described previously in this chapter allowed a variety of models to be fitted to the data. A coarse indication that the abundance estimates were robust was that point estimates of abundance varied by only 10-20% when adding and dropping terms, considering two-dimensional versus one-dimensional smooths, or increasing model flexibility.

The second, external approach to gauging accuracy of these abundance estimates was to consider estimates from designed surveys. There is no 'ground-truth' against which these estimates could be judged, because the study area was defined *post-hoc* from the search effort (and therefore was not designed to be comparable with other surveys), and because true abundance is never known. An interesting approach would be to contrast data from this and a design-unbiased survey, and to model abundance for the region of overlap. While this would be informative, it would require finding and gaining access to relevant data.

The most suitable dataset for comparison might be the one collected on the CCAMLR-IWC Krill Synoptic Survey in January-February 2000, the season prior to the start of this study. The CCAMLR-IWC cetacean data were collected along a grid of systematically placed tracklines across a much larger section of the South Atlantic sector of the Southern Ocean, and with less effort in the northern part of this study area. A spatial model was developed to model humpback, fin and minke whale distribution from the CCAMLR-IWC data (Hedley *et al*., 2001). Abundance of these

species in a study area a few times the size of the one in this study was predicted to be a few times the size of those presented here (Hedley *et al*., 2001). Without access to the raw data, a more quantitative comparison is not possible, but in the interim, the abundance estimates presented here were on the expected order of magnitude.

3.4.5 Variance of abundance estimates

Estimating variance of spatially modelled abundance estimates are the most problematic aspect of these methods (Hedley *et al.*, 1999; Forney, 2000; Marques, 2001; Bravington, 2003), and this study was no exception. Two methods of estimating variance yielded 95% confidence intervals that differed by an order of magnitude (Tables 3.5, 3.7 and 3.9). In addition, the bootstrap estimates of variance showed substantial positive bias. For each species, the median value of the 300 bootstrap iterations was about twice, and the mean value of the bootstrap samples was 2.5-4 times, the best estimate of abundance. This warrants closer attention.

It is difficult to define an independent resampling unit in the context of studies conducted from ships of opportunity (Marques, 2001). Resampling methods require that the resampling unit be independent (Buckland *et al.*, 2001), while spatial modelling requires that models be fit to data that provide reasonable coverage across the range of explanatory variables (Hedley *et al.*, 1999). In an opportunistic data collection setting such as this one, these requirements may be in conflict. Resampling each day's effort with replacement may address this problem in a designed survey, where the night spent steaming between transects reduced the dependence of one day's sampling effort on another's. However neither 'Trip' nor 'Day' in this study were equivalent to a transect line. The ships used in this study typically steamed overnight

between landing sites, but some nights were spent at anchor, and these occurred most often along the Peninsula, an area of high density for minke and humpback whales.

Transect lines in designed surveys are placed to give good spatial coverage of a study area. In this study, the placement of transect lines and the extent of search effort were determined by the ship's itinerary and the expedition leader, not from ensuring equal coverage of the study area. Restrictions on the time spent collecting data from one trip to the next, meant that some trips yielded data primarily from low-density areas, while others yielded data primarily from high-density areas.

Trips were no doubt independent of one another, but random combinations of trips, with replacement, can yield iterations of search effort that violated the assumption of reasonable coverage. Random combinations of relatively few samples in this study provided markedly poorer coverage than the original sample. While this is true to some extent of any non-parametric bootstrap, the effect was exacerbated in this platform, because data collection could not be standardised across trips.

Non-parametric bootstrapping may generate positively biased variance estimates in data collected from ships of opportunity simply because no attempt can be made to sample across a density gradient. Consequently, real spatial variation in whale density was expressed in non-parametric bootstrapping as sampling error, an outcome that is unsatisfactory.

This tendency for non-parametric bootstrapping to produce positively biased variance estimates might have been anticipated. One study has been designed to simulate

JARPA search effort that was biased toward high-density minke whale habitat (Clarke *et al.*, 2000). While the count method performed well in passing mode, two warnings emerged clearly from the data. First, GAMs performed poorly in areas with no search effort. Secondly, in a highly clustered population, abundance estimates increased as the number of degrees of freedom increased in the model. This has obvious implications for this study, in which each bootstrap iteration involved an automated smoothing algorithm in mgcv. At any iteration of the bootstrap, the models were given the option to use up to nine degrees of freedom for each term, even though the model selected for the entire dataset used generally fewer than 4edf. Coupled with random combinations of trips that sampled within a density gradient in a non-systematic way, this approach extrapolates implausible density levels due to the inherent flexibility of GAMs. The alternative, conditioning on the smoothness selected for the complete dataset to tame this flexibility, would underestimate the variance by excluding model selection uncertainty from the variance.

A parametric bootstrap could be used, but would require extensive analytical and programming advances in order to incorporate the spatial auto-correlation among segments along the trackline. Efforts to incorporate parametric bootstrapping in future versions of program DISTANCE are underway, although these methods do not consider spatial auto-correlation (L. Thomas, pers. comm.).

Given the competing interests of independence (resampling methods) and good spatial coverage (spatial modelling), the best compromise for this study is the jackknife estimator using each trip as the resampling unit. This provided the most reasonable estimates of variance (not the smallest, which used each day's effort as the resampling

unit, but the most reasonable). This finding echoes previous recommendations, which found the jackknife to perform well in a spatial modelling framework (Hedley, 2000; Marques, 2001). Jackknife estimators perform relatively poorly when sample size is small, but they are unbiased (Miller, 1974; Efron, 1979; Efron and Stein, 1981). The substantial bias in bootstrap estimates in this study lends further support for relying on jackknife estimates of variance in the abundance estimates presented for minke, humpback and fin whales.

It may seem ungrateful to bemoan inconsistent performance of variance estimates from a survey in which the ship time was free. Nevertheless, accurate estimates of variance (even when they are large) are crucial to conservation efforts and resource management. A default method for establishing acceptable levels of anthropogenic mortality in marine mammal populations has been established that uses knowledge of minimum population size calculated from a mean value and some measure of its variance (Wade, 1998). Quantitative risk assessments similarly require information on abundance and variance (Harwood, 2000).

In summary, these data indicate that the best abundance estimate available for humpback whales in the study area during the time of the survey was 1829 (95% CI: 978-3422). Fin whale abundance was 4487 (95% CI: 1326-15179) and minke whale abundance was 1544 (95% CI: 1221-1953).

3.4.6 Developments in variance- and abundance-estimation techniques
One obvious reason for the large variance in these abundance estimates stems from limited data. However, analytical limitations were also to blame for the discrepancy between bootstrap and jackknife estimates of variance. The spatial modelling methods

used here are relatively new, and are still being developed. A new approach being pursued expands the mgcv package to allow variance to be estimated directly from the model-fitting process in a maximum-likelihood framework (M. Bravington, S. Hedley and S. Wood, pers. comm.). This analytical solution alone would solve many of the problems encountered in this study. This emerging approach will allow school size to vary spatially, and allows estimation of g(0) from a single platform by relaxing some of the conditions of certain detection on the trackline.

Current methods exist that allow school size to vary between strata (*e.g.*, Borchers *et al.*, 1998a) and for g(0) to be less than one (*e.g.*, Buckland and Turnock, 1992; Borchers *et al.*, 1998b). But these methods require calculating a conventional distance sampling abundance estimate (by stratum, if appropriate) and summing the variances of the various steps using the delta method (Seber, 2002). Incorporating the variance estimation procedure into the modelling process will no doubt reduce the variance as well as integrate all of the other advantages of spatial modelling techniques over conventional distance sampling. In any event, it will provide better variance estimates than current methods allow, because resampling effort and sightings will always produce poorer coverage than in the original survey.

Ongoing work is also exploring more objective means of determining the appropriate spatial scale at which to model heterogeneity in whale density (M. Bravington, S. Hedley and S. Wood, pers. comm.). Initial simulations suggest that the 'count method' is robust to varying segment length, as long as segments are short enough to ensure relatively constant whale density along the segment (Hedley, 2000; Hedley and Buckland, in prep.). While better methods are developing, the results presented here

still provide useful descriptions of whale distribution, rough estimates of abundance, and unbiased estimates of variance.

3.4.7 The importance of monitoring Antarctic balaenopterids

It is the international nature of the current moratorium on commercial whaling that makes monitoring recovery of Antarctic baleen whales so important. The 1985-6 pause in commercial whaling was an early example of truly global conservation initiatives. Monitoring the success and failure of this action will inform other multinational efforts to reduce greenhouse gas emissions, reduce overfishing and bycatch, save rainforests of global importance, and to save other endangered species.

On a more tangible note, it is plausible that removal of large baleen whales has caused a major shift in the species composition of krill-consumers in the Southern Ocean ecosystem (Laws, 1977). The existing evidence for competition among balaenopterids to limit recovery from depletion is equivocal at present (Clapham and Brownell, 1996). A simplistic model, though, of interactions among krill, blue and minke whales in the Southern Ocean indicated that when krill is limiting, minke whale population growth rate should fall faster than that of blue whales (Mori and Butterworth, 2003).

More complex considerations of multi-species interactions are currently exploring whether switching of prey species by killer whales after removal of the majority of great whales from the Southern Ocean ecosystem could account for decline of sea lions, elephant seals and minke whales (Branch and Williams, 2003). It could not. The magnitude of Antarctic minke whale decline (Branch and Butterworth, 2001a) was larger than could be accounted for by prey switching of killer whales. In addition, large whales seem to be relatively unimportant in the diet of killer whales (Clapham,

2001) and prey switching has not been documented in nearly 30 years of studies in the northeast Pacific (Ford *et al*., 1998).

Much of our knowledge of balaenopterid response to removal of the great whales from the Southern Ocean is hindered by variance in abundance estimates that is greater than any trend we could expect to measure (Taylor and Gerrodette, 1993). The blue whale provides a good example. While some estimates placed reduction of the Southern Ocean blue whale population at 0.1% of its initial biomass, recent modelling suggests that that Antarctic blue whale stocks may now number 0.9% of their pre-exploitation size (Branch *et al*., 2003). Put another way, a very rare animal is now slightly less rare than it was in recent decades, but measuring that change is difficult and the species is still rare. In this study, no blue whales were seen along 10,000km of trackline.

If, however, the Southern Ocean ecosystem responded to industrial whaling with a shift toward increased fur seal and penguin populations (Laws, 1977), then it becomes important to decide whether one should protect the current ecosystem (Mangel and Hofman, 1999) or to manage with the goal of restoring the balance of the original one (Laws, 1977). If the ecosystem responded with a shift toward higher species diversity of the whale community (Kasamatsu, 2000), then this might have much to teach us about how marine ecosystems would respond to other perturbations. Perhaps the uncontrolled experiment of commercial whaling in the Antarctic is best viewed as an unintended cull. Culling marine mammals to aid commercial fisheries plays an undeniable, if controversial role in marine resource management globally (Johnston *et al*., 2000; Yurk and Trites, 2000; Lunneryd, 2001; Clapham *et al*., 2002). At the very least, any suggestion that Antarctic balaenopterids are food-limited would lend support

to managing Antarctic krill harvest under an ecosystem approach that minimises impact on cetacean populations recovering from overexploitation (Boyd, 2002). Such efforts are underway elsewhere to ensure that the energetic needs of higher predators are considered empirically before harvest is allocated in commercial fisheries (Read and Brownstein, 2003).

Monitoring recovery or lack thereof of Antarctic baleen whale populations is an essential part of evaluating the effectiveness of marine resource management. In order to manage ecosystems sustainably (Larkin, 1996), it is important to have a set of quantitative rules, procedures, which govern allocation of quotas. It is equally important though, to simulate the anticipated outcome of such actions, and to monitor whether the implementation had the expected effect (Butterworth and Punt, 1999).

3.4.8 Using ships of opportunity for collecting and modelling cetacean line-transect data

As a first attempt to collect and model cetacean line-transect survey data from Antarctic tourism ships, the lessons learned from this study may assist similar studies in future. The key distinction between a platform of opportunity and an opportunistic dataset is that in the former, the platform is opportunistic, but the study design and data collection are rigorous and dedicated. The same may or may not be true of the latter. To that end, studies that require multiple observers should not rely on assistance from passengers or crew. If this study were typical, then perhaps one could count on eliciting additional observers 10% of the time.

Relying on haphazard assistance for double-platform data collection has implications in terms of data quality and quantity. The ability to spot Antarctic minke whales

showed strong correlation with observer experience (Mori *et al*., 2003), so inexperienced volunteers may contribute little and may confound trend analysis. Similarly, simply waiting for volunteers may reduce sample size to a point that compromises data analysis (Buckland *et al*., 2001). A cost-benefit analysis might reveal whether it is better to conduct a free study 10% of the time, or to pay for cabin space to bring additional, dedicated observers on board. The same holds true for the primary observer, because time spent on passenger-related duties cannot be spent on data collection. Researchers using these platforms must be prepared to be flexible, because what one gains financially and logistically, may be lost in terms of control over study design.

Spatial modelling techniques require large gridded datasets. Many of the datasets used in this study took days to compile using inefficient programming in S-Plus, but could have been created in minutes in a GIS framework. A strong recommendation, then, is that researchers interested in pursuing these methods become comfortable not only with a statistical programming package like R or S-Plus, but also with a GIS package.

The number of candidate environmental covariates in a spatial modelling framework is potentially large. These methods are easily expandable, and should be expanded, to include variables of direct relevance to whales, such as temperature, ice cover and prey density. In one study, however, no relationship was found between krill and whale density that could not be better described using simpler, spatial covariates (Borchers *et al*., 2000). In addition to identifying how many animals are in an area, and how they are distributed, spatial modelling methods can generate correlations to tell us why whales are found where they are, or at least testable hypotheses about distribution.

3.4.9   Sophisticated analyses are not a substitute for good survey design

Hedley *et al*. (1999) were correct in predicting that GAM-based techniques could be used to model abundance and distribution from data collected using a non-randomised survey design. But just because one can model abundance and distribution does not mean that one necessarily should do so. The suitability of modelling must be assessed on a case-by-case basis. Abundance and distribution estimates should be undertaken only when the key assumptions underlying these techniques have been met, namely that one has obtained good coverage across the range of explanatory variables, and that the selected model is appropriate.

Having said that, it must be borne in mind that even abundance estimates from conventional distance sampling surveys rely on a simple spatial model: the sample mean. Conventional distance-sampling methods fit a flat density surface throughout a study area at the level specified by the mean density from all tracklines. Abundance estimates from these surveys should be interpreted with an equally critical eye in terms of coverage probability, to ensure that the mean density of tracklines is truly representative of the study area.   When poor weather, for example, prevents completing a design-unbiased survey in an area with strong gradients in cetacean density, cautious use of statistical models would be preferable to taking the mean density observed in tracklines from an unintentionally biased survey design.

3.4.10   Synopsis

Most importantly, spatial modelling of line-transect data will allow surveys to be undertaken from ships of opportunity in regions where abundance and distribution data currently do not exist. Funding for systematic sightings surveys is lacking in

many developing countries (Vidal, 1993). As tourism expands globally to target currently untouched regions, it will be important to gain as much information from those platforms as possible. GAM-based models enable estimation of the number of animals in a spatially flexible way, which will increase our ability to combine disparate surveys to increase knowledge on changes in distribution and abundance over time.

These data were collected, and some insight gained in the process, using minimal funds, and the volunteer efforts of people on a ship heading to Antarctica, with or without a scientist on board. Future work should consider the use of these ships to collect data that allows modelling of variables of biological relevance that influence heterogeneity in whale density. Habitat variables that may affect whales such as temperature, ice cover, density, salinity and prey density, can be explored in a spatial modelling framework. When these data can be collected from a ship of opportunity, they should be. The results presented in this chapter suggest that in understudied areas, a ship of opportunity that provides reasonable coverage is a valuable platform for pilot studies on abundance and distribution.

Chapter 4

Behavioural responses of male killer whales to a 'leapfrogging' vessel

ABSTRACT

The research and whalewatching communities of Johnstone Strait, British Columbia, Canada have worked closely together to identify whalewatching practices that minimise disturbance to northern resident killer whales. Local guidelines request that boaters approach whales no closer than 100m. Additionally, boaters are requested not to speed up when close to whales in order to place their boat in a whale's predicted path: a practice known as 'leapfrogging.' We designed a land-based study to test for behavioural responses of killer whales to an experimental vessel that leapfrogged a whale's predicted path at distances greater than 100m. We repeatedly approached 10 male killer whales and found that animals responded on average to experimental approaches by adopting paths that were significantly less smooth and less straight than during preceding, control conditions. This adoption of a less 'predictable' path is consistent with animals attempting to evade the approaching boat, which may have negative energetic consequences for killer whales. Our results support local consensus that leapfrogging is a disruptive style of whalewatching, and should be discouraged. Similarly, as the experimental boat increased speed to overtake the whale's path, the source level of engine noise increased by 14dB. Assuming a standard spherical transmission loss model, the fast-moving boat would need to be 500m from the whale for the received sound level to be the same as that received from a slow-moving boat at 100m. We recommend that whalewatching guidelines encourage boaters to slow down around whales, and not to resume full speed while whales are within 500m.

4.1 INTRODUCTION

In 1993, the International Whaling Commission resolved "to encourage the further development of whalewatching as a sustainable use of cetacean resources" (IWC, 1994). Tourism based on whalewatching has become a vital component of the

economies of many coastal communities and shows potential to assist many more (Hoyt, 1997). Such tourism also affects attitudes toward protecting critical whale habitat and threatened populations (Barstow, 1986; Duffus & Dearden, 1993). However, a growing number of studies link vessel traffic with behavioural changes for whales, which may lead to increased energetic costs (Au and Green, 2000; Erbe, 2002; Williams *et al.*, 2002). As a result, resource managers are now tasked with balancing the economic and educational benefits of whalewatching with the habitat needs of whales.

Researchers have identified four distinct populations of killer whales (*Orcinus orca*) on the coast of British Columbia, Canada. Despite having overlapping ranges, each population is socially and ecologically isolated (Ford et al., 2000). Whalewatch operators here tend to focus on the *northern* and *southern* communities of *resident* killer whales, the fish-eating type, since these whales are found more reliably than *offshores* or the marine-mammal-eating *transients*. A core summer area for northern resident killer whales and whalewatching activity is Johnstone Strait, off northeastern Vancouver Island, BC (Figure 4.1). Northern resident killer whales return each year to socialise and to feed on migrating salmon (Nichol & Shackleton, 1996). A similar core whale and whalewatching area for southern residents is in Haro Strait between British Columbia and Washington State (Heimlich-Boran, 1986), where proximity to urban areas makes whalewatching a much larger industry than in Johnstone Strait.

The first whalewatching company to focus on killer whales began operation in 1980 in Johnstone Strait. The whalewatching and research communities of Johnstone Strait work together closely to identify whalewatching practices that minimise disturbance to

whales. Local guidelines request that boaters parallel whales no closer than 100m; approach animals slowly, from the side; and not place boats in the path of a whale – a practice referred to in the guidelines as 'leapfrogging.' Leapfrogging is a way of achieving a closest approach to a whale that is substantially closer than 100m. It complies with the letter of the distance guideline, but not its spirit.

In 1995 and 1996, Williams *et al.* (2002) experimentally approached killer whales to test the biological significance of the 100m parallel guideline. Results showed that killer whales used a suite of subtle tactics to evade a boat even at that distance, and that these avoidance patterns became more pronounced as boats approached closer (Williams *et al.*, 2002). Some boaters see leapfrogging as a benign means of getting close to whales without violating the 100m guideline. This has the added advantage from the tourists' perspective of making it seem that whales are approaching the boat, which is the only way for boaters to watch whales closely without violating local guidelines. Other community members view leapfrogging as a potentially disruptive style of whalewatching.
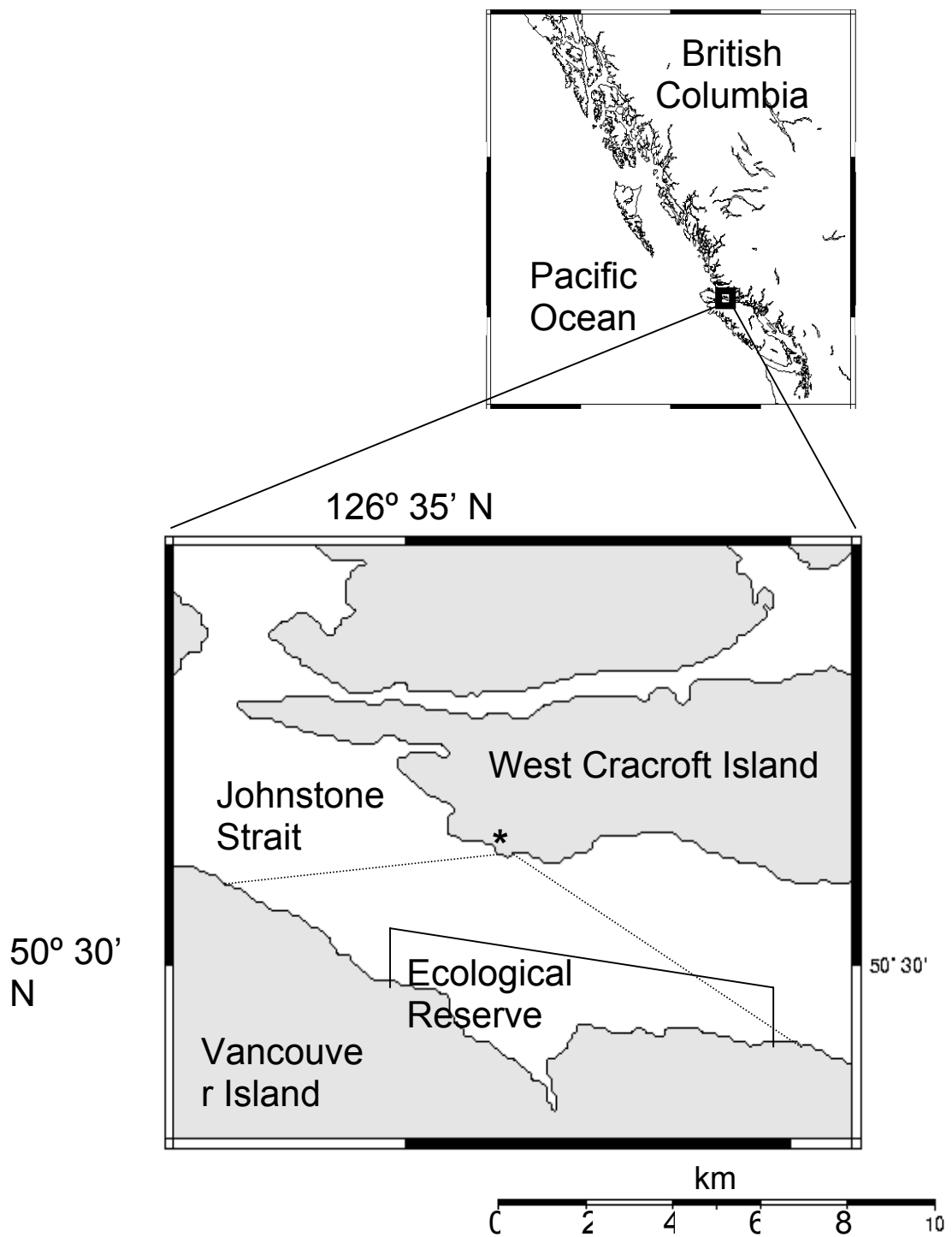
Figure 4.1. Study area in Johnstone Strait, BC, Canada, showing lines of sight (- - -), position of theodolite (*), and boundaries of Robson Bight - Michael Bigg Ecological Reserve.

Leapfrogging may be at least as disruptive as parallel approaches. When speeding up to leapfrog, boat noise generally becomes more intense and higher in frequency

(Richardson *et al*., 1995), which offers greater potential to mask killer whale communication (Bain and Dahlheim, 1994) than slower, parallel approaches. Leapfrogging involves paralleling whales for some distance, at a faster speed than that of the whale, and then turning 90° to place the boat in the whale's predicted path. At this point, the leapfrogging manoeuvre places the noise source directly ahead of the whale, which is the position where masking effects may be greatest (Bain and Dahlheim, 1994).

The people who live and work with killer whales in Johnstone Strait want whalewatching guidelines to be biologically relevant. To that end, they have endorsed a policy of experimental testing of various components of the guidelines. Northern resident killer whales generally used horizontal avoidance tactics to evade an experimental vessel that attempted to travel in parallel with them at 100m (Williams *et al*., 2002) by adopting a more erratic surfacing pattern than they were following prior to the boat's approach. The present study hypothesised that whales might respond to more intense whalewatching pressure by similar horizontal avoidance tactics; by the other horizontal avoidance tactic of swimming faster at the surface; or by vertical avoidance in the form of diving longer than during preceding, no-boat conditions. Whales might also display surface-active behaviours, such as slapping flukes or pectoral fins on the surface of the water. A more extensive study would be required to determine whether leapfrogging elicits stronger behavioural responses than other forms of whalewatching. Since commercial operators have agreed that leapfrogging is an inappropriate style of whalewatching, it should be necessary only to demonstrate that the technique is sufficiently disturbing to justify requesting that non-commercial whalewatchers also avoid leapfrogging.

The following outlines the result of a study designed to test whether a vessel that speeds up to leapfrog a whale's path, at a distance greater than 100m, alters the behaviour of northern resident killer whales that summer in Johnstone Strait.

4.2   MATERIALS AND METHODS

4.2.1 Study area

Data were collected between 28 July and 10 September 1998, from a land-based observation site on the south shore of West Cracroft Island in Johnstone Strait, British Columbia (50° 30' N, 126° 30' W; Figure 4.1).   Data were collected under permit from BC Parks, in conjunction with a contract to provide land-based spotting for boats violating the boundaries of the Ecological Reserve.

Data were collected using an electronic theodolite (Pentax ETH-10D with a precision of ±10 seconds of arc) connected to a laptop computer equipped with custom software (THEOPROG: available from D.E. Bain, dbain@u.washington.edu). Cliff height and reliability of distance measurements were measured using methods described by Davis *et al*. (1981) and Williams *et al.* (2002).   The theodolite was located approximately 50m above mean sea level. The theodolite-computer apparatus measured the length of a 30m rope to be 28.93m (n=20, SE=0.18) at a distance of 3.79km. This translates to a measurement error of approximately 3.5% in terms of accuracy, and <1% in terms of precision. Percent errors in measuring cliff height, distance travelled and speed tend to be approximately equal (Würsig et al., 1991).

4.2.2 Selection of focal animals

Northern resident killer whales entered the study area in social units referred to as matrilines (Ford *et al.*, 2000). Matrilines were generally dispersed with individuals spaced a few hundred metres apart, which is typical while foraging, the most commonly observed activity of resident killer whales in summer in Johnstone Strait (Nichol & Shackleton, 1996). Focal animals were chosen so that they could be re-sighted consistently. A focal animal typically had a distinctive dorsal fin and saddle patch (Bigg *et al*., 1990). Only mature and subadult males were tracked in this study – they can be readily distinguished from other group members since their dorsal fins can reach twice the height of those of adult females. Animals were selected whose location within the study area made them more likely to be visible for more than 15 minutes, because earlier work has shown that tracks that are substantially shorter than 1000s tend to bias estimates of respiration rate (Kriete, 1995).

4.2.3 Tracking

The tracking team consisted of a spotter, a theodolite operator and a computer operator. The spotter announced each time that a focal animal surfaced to breathe or display surface-active behaviour, and recorded tide height approximately every 15min. The theodolite operator located the position of the whale during the surfacing. Events recorded by the computer operator included: breath, breach, fluke slap, pectoral fin slap, dorsal fin slap, unidentified splash, porpoising, and spy-hop (Ford *et al.*, 2000). The computer was linked to the theodolite to record the time that it retrieved the horizontal and vertical angle co-ordinates of a whale's position. After approximately 15min of no-boat, control observations, the computer operator requested (via VHF radio) that the experimental boat operator approach the focal animal.

Local whalewatch operators agreed to remain clear (>1nm) of the focal animal while whale behaviour was recorded under control, no-boat conditions. The experimental boat was a 5.2m rigid-hull Zodiac inflatable with a 90hp Mercury 2-stroke outboard engine. The boat operator was instructed to approach the focal whale slowly, from the side, and then run a course parallel to the whale at approximately 100m. THEOPROG was customised to display the distance between the last two positions as they were collected. After approximately 5-10 minutes, the computer operator asked the boat operator to speed up to overtake the whale. When the distance between boat and whale reached approximately 200m (ahead and to the side of the whale) as indicated by the theodolite-computer apparatus, the boat operator placed the boat directly in the whale's predicted path (completing the leapfrogging manoeuvre). Once the boat was in position, the operator shifted the engine into neutral and left the engine idling as the whale swam past. The boat operator made no sudden direction changes, and was in frequent VHF radio contact with the cliff-based observers. When the whale had swum approximately 500m past the experimental boat, the process was repeated twice more. After the third leapfrog, the operator shut off the engine when the whale was approximately 500m from the boat. The entire treatment period lasted approximately 20min, depending on the whale's swimming speed.

4.2.4 Acoustic monitoring of the experimental vessel

The source and received levels and frequency spectra were calculated from DAT recordings made of the experimental boat under slow (i.e., paralleling speed) and fast (i.e., leapfrogging speed) conditions. A 2m, 15-element calibrated hydrophone array and on-board recording system, both flat to 24kHz, was towed from a recording boat (Miller & Tyack, 1998). The experimental boat operator was instructed to approach the recording boat slowly, at approximately 3kn speed as indicated by a Magellan

2000XL handheld GPS. The operator then accelerated towards the recording boat at the throttle position typically used to leapfrog a whale's position. As the experimental boat approached the recording boat, parallel to the hydrophone array, the recorders measured distance to the experimental boat using Bushnell laser rangefinders. When the distance reached 100m, a 2s sample of the recording was digitised for subsequent spectral analyses.

4.2.5 Data compilation

A mean dive time (i.e. average time between surfacings) was calculated for each track. The average swimming speed of the whale was obtained by dividing the total distance travelled by the duration of the tracking session. Two measures of path predictability were calculated: a *directness index* and a *deviation index* (Fig. 2) (Williams *et al.*, 2002).

The directness index is 100 times the ratio of the distance between beginning- and end-points of a path to the cumulative surface distance covered by all dives. The directness index is the inverse of the milling index of Tyack (1982) and Kruse (1991). The directness index ranges from zero (a circular path) to 100 (a straight line).

The deviation index is the mean of all angles between adjacent dives, and can be considered an inverse measure of a path's smoothness. For each surfacing in a track, we calculated the angle between the path taken by a dive and the straight-line path predicted by the dive before it (Williams et al., 2002). The deviation index is the mean of the absolute value of each of these discrepancies, in degrees, during the entire track. A low deviation index indicates a smooth path, while a high deviation index indicates an erratic path. Indices of directness and deviation were calculated for each

track. A track that shows high deviation and high directness is erratic but directional, whereas a track with low deviation and low directness is smooth but non-directional.

We recorded each time that surface-active events such as spy-hopping or breaching took place. We scored a bout of tail-slapping or fin-slapping as one event if more than one slap took place during a surfacing.

4.2.6 Data analysis

Mean values for each dependent variable were averaged across all observations for an individual, such that each whale was represented only once. Variables recorded under control and experimental conditions were compared using two-tailed, paired t-tests. Comparisons were made only when at least 20 minutes of baseline, control observation were followed by an experimental approach of the same whale lasting at least 20 minutes.

Deviation index

$$\bar{\alpha} = \frac{|\alpha_1| + |\alpha_2|}{2}$$

Directness index

$$DI = 100 \left(\frac{T}{(d_1 + d_2 + d_3)} \right)$$
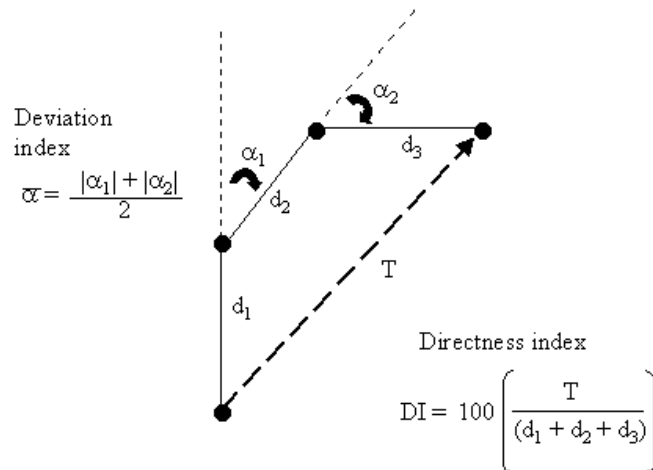
Figure 4.2. A sample swimming path with location of four surfacings (•) and three dives (d_i), showing two measures of path predictability: deviation and directness. The deviation index is the mean of all angles (α_i) between observed dives and the straight-line paths *predicted* (··) by preceding dives. The directness index is 100 times the ratio of the track diameter (T) to its perimeter.

4.3   RESULTS

4.3.1   Behavioural responses of killer whales to leapfrogging vessel

This study obtained 12 paired (control-treatment) observations of 10 male killer whales (Table 4.1). [Earlier work (Williams *et al.* 2002) demonstrated the potential for sex-based differences in boat-avoidance tactics, if not boat tolerance. Consequently, our two experimental approaches of female killer whales were excluded from the analyses.] Whales responded to a leapfrogging vessel by adopting a path that was significantly less direct (t_9=3.41, p=0.007), and the mean angle between successive surfacings became significantly greater (t_9=-5.29, p=0.001) than during the preceding, control period (Figure 3). No significant difference was observed between whale behaviour during control and leapfrog conditions in terms of mean dive time (t_9=0.42, p=0.684), swim speed (t_9=0.29, p=0.775) or rate of surface-active behaviour (t_9=-1.76, p=0.113). However, the power of these tests is low because of the small sample size. Beta probabilities (the probability of accepting a false null hypothesis) were high in the last three trials (β=0.941, 0.944 and 0.568, respectively). This suggests that if these mean and standard deviations were the true values, we would have needed sample sizes of 1408, 1978 and 33, respectively, to detect significant differences at the conventional level.
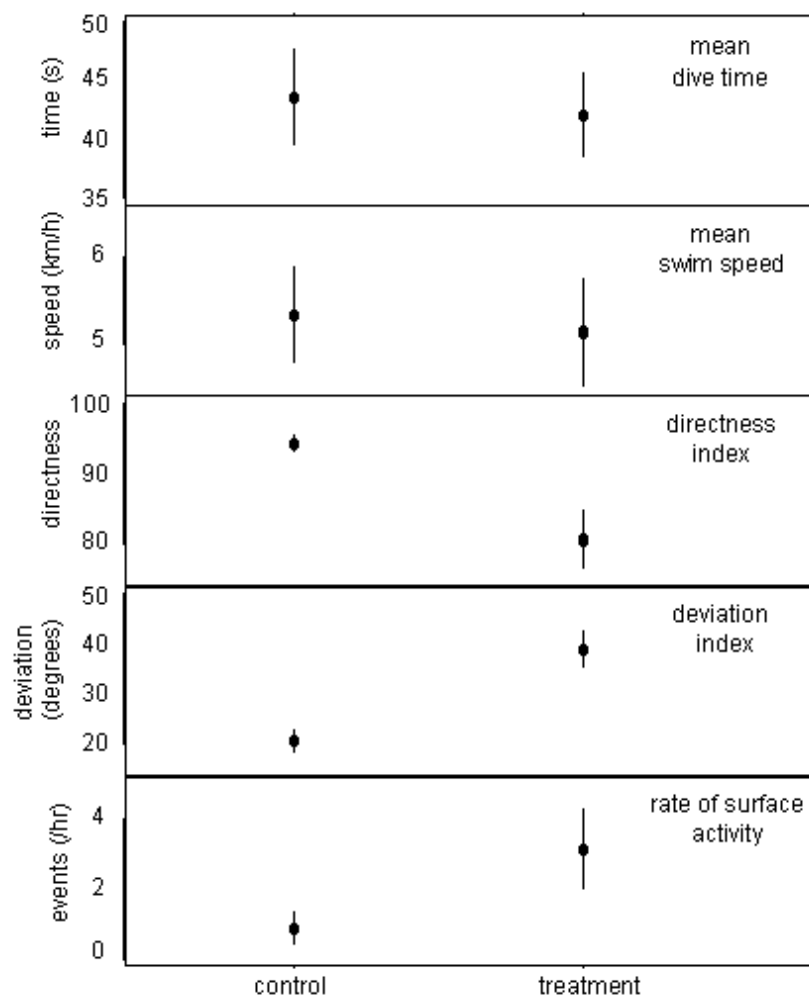
Figure 4.3 Behavioural responses (mean ± SE) of whales to experimental approach by a leapfrogging vessel.

Whale	Sub-pod	Tracks	Age
A13	A11	1	18
A33	A12	2	27
A39	A30	1	27
A46	A36	1	17
A6	A30	1	47
B10	B7	1	19
B2	B7	1	47
B8	B7	1	34
C9	C6	1	27
I41	I15	2	18

Table 4.1. Number of pairs of observations (control vs. treatment) for each focal animal. Values were averaged for animals that were approached twice, so that each subject was represented only once in the analyses. Subjects' ages calculated from presumed year of birth reported by Ford *et al*. (2000).

4.3.2 Experimental boat noise

As the experimental boat approached the recording boat at slow speed, the tracking crew recorded its position 10 times along its path. Mean speed was 5.2km/h (± 1.02 SE). This agrees roughly with the 3kn (5.6km/h) average speed as measured by the GPS. During the high-speed approach, the theodolite team recorded 16 positions, and the measured boat's speed was 23.3km/h (± 1.79 SE). Again, this is corroborated by the simultaneous GPS measure of 12-13kn (22.2-24.1km/h).

We later measured the mean speed of the experimental boat during the leapfrogging sections of theodolite tracks. On average, the experimental boat sped up to 20.7km/h (± 1.70 SE) during the leapfrog components of the 12 treatment tracks. We are confident that recordings made of the experimental boat during the high-speed approach accurately represent sound production during leapfrog approaches of whales: the mean speed of the boat did not differ significantly between samples (t_{25}= -0.99, p=0.330).

Source level of the experimental boat at slow speed was estimated to be 148dB re: 1μPa at 1m, assuming a spherical transmission loss model (Richardson et al., 1995). When the experimental boat sped up to leapfrog, the source level increased to 162dB re: 1μPa at 1m – an overall difference of +14dB. The greater sound pressure level under high speed was found across the entire frequency range of the on-board multi-channel recording equipment, and was observable to at least 24kHz (Figure 4). The *received* levels were measured at 100m, and are presented in Figure 4. At 200m, the distance at which the boat operator was instructed to leapfrog the whale's position, the received level was approximately 116dB.

If we assume that sound levels drop at 20log10(range), a leapfrogging boat would need to be approximately 500m away from the whale for the level received by the whale to be the same as that from a boat paralleling at slow speed at 100m (Richardson et al. 1995).
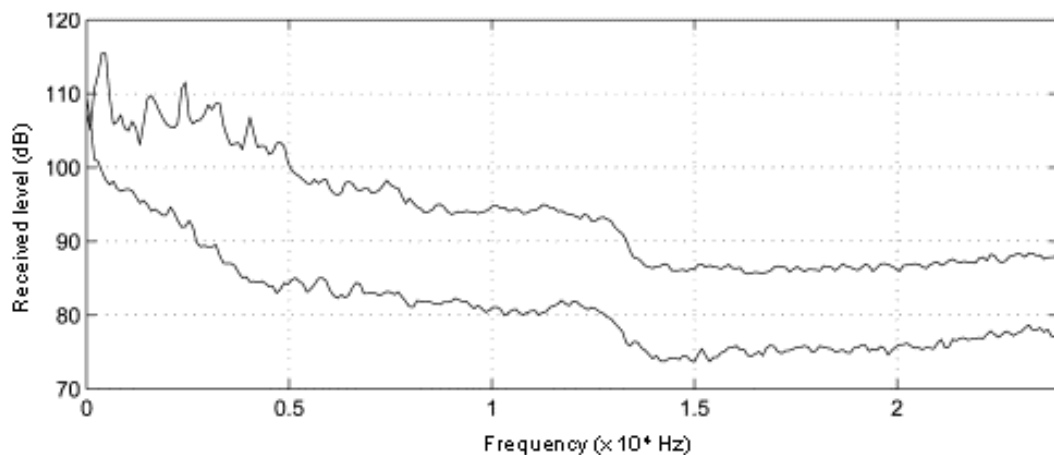
Figure 4.4 Power spectral density comparing received noise level 100m from the experimental boat under fast (upper line) and slow (lower line) operating speeds.

4.4 DISCUSSION

Northern resident killer whales evaded the leapfrogging vessel on two spatial scales (deviation and direction). Increased deviation index reflected a less predictable path on the scale of one surfacing to the next, while the reduced directness index reflected a less predictable path on the scale of an entire 20min observation session. These path predictability parameters were the same ones altered by a boat following whalewatching guidelines (Williams *et al*., 2002), and thus, these appear to be useful indices for assessing disturbance in northern resident killer whales.

There was a pronounced difference in the quality and level of sound produced by the experimental boat operating under two speeds. Whalewatching guidelines, in addition

to limiting leapfrogging and proximity, should also address speed of vessels around whales. In the absence of experimental studies to guide whalewatching activity by regulating noise level received by killer whales, reducing boat speed is a useful proxy (Richardson *et al*., 1995). More specifically, boaters should be discouraged from operating outboard engines at full speed within 500m of whales.

These findings are especially interesting in view of recent attempts to model zones of influence from boat noise (Erbe, 2002). The results from this study are consistent with Erbe's prediction that a fast-moving boat would elicit change in behaviour of killer whales at 200-250m. Her prediction was based on the assumption that a 120dB received level would cause behavioural change in 50% of cetaceans (Richardson *et al*., 1995). In fact, this study demonstrated significant behavioural responses of male resident killer whales at received levels of approximately 116dB.

Effective management of whalewatching often requires choosing between practices that maximise human benefit and those that minimise disturbance to whales (Duffus and Dearden, 1993). The gain to whalewatchers from leapfrogging, where the benefit is a closer approach than that offered by other styles of whalewatching, may not be as high as one might assume. A study in Australia tested the assumption that whalewatchers wish to get close to whales (Orams, 2000), and found that tourist satisfaction was influenced by number and behaviour of whales, numbers of fellow passengers, cruise duration, boat construction and seasickness. However, proximity of whales was not a major influence. The tendency in Johnstone Strait to discourage leapfrogging may be a case where mitigating disturbance to whales costs whalewatch operators little in terms of tourist satisfaction.

Leapfrogging in close proximity to whales is a style of whalewatching engaged in mostly by the recreational and sportfishing boaters, rather than by commercial whalewatch operators in Johnstone Strait. Thus the sample size in the present experiment was intended to test the null hypothesis that leapfrogging has no effect on behaviour. This sample was not intended to be large enough for the more stringent test of whether leapfrogging had more effect than paralleling, since this was not a particularly urgent management goal in Johnstone Strait, although it might be of interest to managers in other areas.

It is unfortunate that the experimental boat that elicited behavioural responses to a paralleling vessel at 100m in 1995 and 1996 (Williams *et al*. 2002) is no longer available for acoustic study. A concerted experiment to test both treatments simultaneously on the same subjects would be valuable. Members of the whalewatching and research communities of Johnstone Strait aim to endorse and follow biologically relevant whalewatching guidelines. It is sufficient to them to demonstrate that leapfrogging is disruptive, and unnecessary to illustrate that one whalewatching tactic is more disturbing to whales than another. Nonetheless, a qualitative comparison of whales' behavioural responses to the two types of whalewatching, paralleling and leapfrogging, may be instructive.

When a single vessel approached northern resident killer whales in 1995 and 1996 to parallel the animals at 100m, mean directness index of male killer whales declined from 83.6 to 74.1. A directness index of 83.6 is equivalent to having to travel 119.6m along a circuitous path to gain 100m of headway. The decline in directness index

while a boat parallels at 100m is equivalent to having to travel 135m to cover the same distance – an increase of 13%. During leapfrogging tracks, mean directness index declined from 94.1 to 80.5, an increase of 17% in the distance a whale would have to swim to cover 100m of straight-line distance. More telling is the fact that no significant change was noted in the deviation index, the mean angle between surfacings, when the experimental boat paralleled male whales' paths at 100m (t_{23}=0.56, p=0.58) (Williams *et al.*, 2002). When an experimental boat leapfrogged the swimming paths of the whales, the animals increased the mean angle between successive surfacings by 90%, from 20.4° to 38.7° (Figure 3). A particularly noteworthy aspect of these findings was that significant effects were apparent even with small sample sizes.

Studies that measure short-term responses of animals to human disturbance often stem from an inability to tackle directly the underlying concern that repeated disturbance may have a cumulative impact on wildlife populations. Northern resident killer whales continue to return to Johnstone Strait each year after more than 20 years of whalewatching traffic and the population increased throughout this period (Ford *et al.* 2000). Nevertheless, whalewatching has been cited as a likely contributing factor in recent population declines of southern resident killer whales (Baird, 1999).

Bain (2001) produced a model for extrapolating energetic consequences of disturbance, including those addressed in this study, to population-level effects on killer whales. Studies employing methods like these may be useful in quantifying the nature and magnitude of avoidance responses in order to model population-level costs of whalewatching across a range of traffic levels, and the benefits to whales of various

management strategies. More importantly, this study reveals an opportunity to mitigate impact. By identifying a whalewatching practice that may carry energetic costs and likely reduces foraging efficiency in the form of masking echolocation, it is hoped that members of the Johnstone Strait community continue to discourage that practice. Likewise, it is hoped that resource managers in other areas are encouraged by the Johnstone Strait model of establishing reasonable guidelines proactively, and then testing those guidelines experimentally to ensure biological relevance. Reducing short-term effects may ensure ultimately the mitigation of long-term consequences.

4.5 ACKNOWLEDGMENTS

Chapter 5

Killer whale activity in Robson Bight: the role of protected areas in cetacean conservation

ABSTRACT

This study examined usage patterns of northern resident killer whales (*Orcinus orca*) in Robson Bight – Michael Bigg Ecological Reserve (RBMBER) and an adjoining section of Johnstone Strait in July and August during eight years (1995-2002). The primary aims of the study were to test whether whales used the Reserve differently than they used the neighbouring environment; to test whether boat presence altered whales' activities; and to estimate whether behavioural responses carried energetic costs. Whales showed strong preference for RBMBER over adjacent waters. Activity budgets differed inside the Reserve from when whales were in adjoining waters, suggesting that the whales preferred RBMBER for specific activities. Boat presence in the same zone as focal whales was linked to significant changes in the probability that whales would switch from one activity state to another. Overall, this led to significantly different activity budgets for whales in the presence of boats than in their absence. Whales appeared to reduce their time spent feeding in the presence of boats, and the time spent rubbing their bodies on smooth pebble beaches (a unique behaviour that was rarely observed on beaches outside the Reserve). These were used to calculate estimates of the difference between the 12h energetic costs of meeting these budgets, which differed by only 3-4%. The most commonly observed vessel type in the study was commercial fishing boats, which suggests that the observed behavioural responses were not driven solely by vessels that were interacting with whales. The Reserve conferred some conservation benefit to whales, but would confer greater benefit if boundary compliance were required of all vessel types.

5.1 INTRODUCTION

Three killer whale (*Orcinus orca*) ecotypes are found in the coastal waters of British

Columbia (BC), Canada (Ford *et al.*, 2000): mammal-hunting *transients*; rarely seen

and poorly studied *offshores*; and northern and southern communities of fish-eating

resident killer whales. A core area for northern residents is found in Johnstone and

Queen Charlotte Straits (Figure 5.1; JSKWC, 1991).   The northern resident

community comprises 16 pods (Ford *et al.*, 2000), which are themselves comprised of

matrilines or natal groups. Many of the northern resident pods return to this area each

summer to mate and to socialise, and to rub their bodies on smooth pebble beaches. One of the area's benefits to killer whales is the tendency for narrow Johnstone Strait to concentrate migratory salmon (Nichol and Shackleton, 1996). Not surprisingly, commercial fishing vessels, freighters, cruise liners and commercial and recreational whalewatching boats also use the area heavily.

Robson Bight – Michael Bigg Ecological Reserve (RBMBER; Figure 5.1) was recognised as a sanctuary for these northern resident killer whales by the provincial government of British Columbia (BC) in 1982. The Reserve was intended to prevent boaters from approaching the gravel beaches on which the whales rub. The functional role of this activity is unknown, but beach-rubbing behaviour is rarely seen in other cetaceans. However, the marine boundaries of the Reserve are currently unrecognised by the Department of Fisheries and Oceans Canada (DFO), the federal agency that has jurisdiction over marine affairs in Canada. This leads to a management framework in which BC Parks, the provincial agency responsible for protecting the Reserve boundaries, can prevent access to the Reserve's terrestrial component (namely the rubbing beaches and the seabed), but can only request that boaters comply with their no-entry policy in the marine component. BC Parks makes these requests for voluntary compliance very strongly in the form of an on-the-water warden service; however, the marine boundaries of the reserve remain "highly permeable" (Duffus and Dearden, 1992).

Figure 5.1. The study area bounded by lines drawn from the cliff-top observation site (*). Shaded area of zones 3-6 marks the boundaries of RBMBER, and zones X and 2a-c indicate the boundaries of the study area outside the Reserve.

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) is a panel of experts from national, provincial and non-governmental agencies that identifies which wild species face threat of extinction in Canada. COSEWIC currently lists northern resident killer whales as *Threatened* (Baird, 2001). Their listing was made partly in response to lack of population growth, and more recently, a population decline observed in annual censuses (Ford *et al*., 2000). While the cause(s) of the decline remains unknown, it is generally agreed that both northern and southern resident communities face a variety of threats (Baird, 2001) in the form of reduced prey availability (Allendorf *et al*., 1997), high toxin loads (Ross *et al*., 2000), and anthropogenic disturbance (Williams *et al*., 2002). The most contentious example of human disturbance may be commercial whalewatch operators, however these represent only a small fraction of the vessels that use the same waters as northern resident killer whales in Johnstone Strait, and their compliance with the Reserve boundaries was highest of the 10 vessel types in the area (Wong and Williams, 1998).

Protected areas mitigate effects of human activities on terrestrial mammals (*e.g*., grizzly bears: Noss *et al*., 1996; African dogs: Woodroffe and Ginsburg, 1999; Eurasian badgers: Revilla *et al*., 2001). Protected areas were found to be crucial nocturnal feeding areas for dabbling ducks (Guillemain *et al*., 2002). However, protected areas (sanctuaries, reserves, preserves, parks, refuges and Marine Protected Areas (MPAs)) take on a wide range of meanings in marine management (Reeves, 2000). Sometimes, protecting small patches is the only feasible management option (Fischer and Lindenmayer, 2002). What value is there in protecting small areas that

whales use, when it is not possible to restrict human access to the entire area in which whales live?

At one extreme, marine mammals can be ignored altogether when designing MPAs to protect biodiversity (Vanderklift *et al*., 1998). At the other, MPAs can be used to protect cetaceans by designing a reserve to satisfy the population's energetic requirements (Hooker *et al*., 1999). Clearly, neither definition is applicable to the role of Robson Bight. The small reserve at Robson Bight was never intended to satisfy the energetic requirements of the northern resident community. Not all matrilines use the area, and those that do, do so primarily in summer. Any benefit to the whales of having a Reserve at Robson Bight is likely to stem from a requiem role, that is, providing whales with temporary respite from some forms of human activity. The value to whales of such a refuge is the focus of the present study.

Local whalewatch operators no longer enter the Reserve at Robson Bight, however commercial fishing vessels continue to do so. Whalewatch operators assisted the provincial government in identifying the Reserve boundaries, and began complying with them long before researchers demonstrated any effect of vessel traffic on killer whale behaviour. The decision to create a reserve proved prescient when, subsequently, studies began reporting correlations between vessel traffic and whale behaviour (*e.g.*, Briggs, 1991; Kruse, 1991). Note that even non-whale-oriented vessel traffic, such as fishing boats, altered the behaviour of killer whales (Williams *et al*., 2002), leading park managers to question whether the whales would benefit from having the Reserve closed to all vessel traffic.

BC Parks has proven willing to allow researchers to cut costs by piggybacking studies onto this land-based observation platform. The land-based observation site used by contractors to spot boaters entering the Reserve is also an excellent vantage site for studying killer whales (Williams *et al*., 2002; Chapter 4), and the logistical support (*e.g*., field camp, boats, and supply runs) required to run the warden project lend themselves to cost-sharing with opportunistic research projects. The first two opportunistic studies aimed primarily to acquire detailed observations of well-marked focal individuals (Williams *et al*., 2002; Chapter 4). Land-based theodolite tracking of killer whale responses to an approaching experimental vessel showed that focal animals attempted to evade a boat that followed (Williams *et al*., 2002) or violated (Chapter 4) local whalewatching guidelines, by adopting more circuitous paths than those observed during preceding, no-boat conditions.

At least three gaps exist in the vessel impact studies conducted to date. First, it is unclear whether the subtle avoidance responses observed in experimental studies carried energetic costs to whales. Secondly, the experimental subjects in previous impact assessments may not represent the population from which they were selected. Selection of focal animals with distinctive dorsal fins resulted in theodolite tracking datasets in which females, juveniles and calves were either underrepresented (Williams *et al*., 2002) or absent altogether (Chapter 4). Finally, it is unknown whether animals were equally vulnerable to disturbance in all activity states. Previous experimental studies targeted foraging whales only, in order to avoid confounding effects of activity state and vessel traffic on whale behaviour. No unified attempt has been made to assess whether the sensitivity of these animals to disturbance varies with initial activity state. Consequently, it is unclear whether the impact assessments

conducted to date are representative of population-level responses. An impact assessment should include subjects from all age-sex classes and span the entire repertoire of activity states.

Agencies contracted by BC Parks to provide the Robson Bight warden service have used land-based observers to inform wardens when recreational boaters were approaching the Reserve boundaries. Since 1990, BC Parks has asked contractors to record vessel traffic and coarse observations of all whales using the study area in summer months. Since 1995, contractors began collecting these data in a systematic way. This ongoing partnership between research and environmental education has proven to be a cost-effective one, since land-based observers were required already to record boat and whale activity. The partnership with researchers added very little cost, but resulted in a study design that allowed collection of rigorous data that could be used for answering questions about killer whale biology and resource management. The resulting broad-scale behavioural sampling approach provided a good opportunity to learn about the activity of all northern resident killer whales that spend the summer in Johnstone Strait. Broad-scale sampling addresses two of the gaps in current vessel impact studies: all age-sex classes in the population are equally likely to be sampled; and sampling includes all activity states.

Broad-scale sampling of whale activity could also address the third gap identified in existing vessel impact studies in this area, namely identifying whether avoiding vessels carries energetic costs to whales. The energetic requirements of two adult and two sub-adult captive resident killer whales were measured across a wide range of physical activity (Kriete, 1995). Kriete then estimated the energetic cost of traveling,

resting, socialising and feeding for free-ranging killer whales, based on curvilinear relationships between swim speed and respiration rates of both captive and wild killer whales. Thus, Kriete developed a framework that allows one conversion of observed killer whale time-activity budgets to estimates of energetic demand. That framework is used in this study to estimate energetic requirements of whales in Robson Bight.

This cliff-top and associated logistical support supplied a natural experiment to assess whether boats influenced the activities and energy requirements of whales. It provided a land-based study that could measure an effect without contributing to it. It allowed examination of two factors potentially influencing whale activity: a geographic effect that compared activity of whales inside the Reserve to that in waters immediately adjacent to the Reserve; and a vessel effect. The indifference of commercial fishermen to the Reserve boundaries ensured that one could observe whales both with and without boats, both inside and outside the Reserve. This study represents the first attempt to infer patterns from observations of every animal that used the study area during daylight hours in summer months from 1995 to 2002.

The primary goal of this study was to test the assumption that killer whales used RBMBER differently from the way they use adjacent core habitat, by testing whether whales' activity budget inside the Reserve differed from that in the waters immediately adjacent to it. A secondary goal was to assess whether the no-entry policy in the Reserve conferred conservation benefit to northern resident killer whales, by testing whether whale activity budgets differed when boats were present from activity budgets when boats were absent. The fact that time-activity budgets can be linked to energetic demands in this species (Kriete, 1995) set a third goal, to estimate

whether energetic demand of killer whales in the presence of boats was greater than in their absence. This framework, using killer whales as an example, could serve as a model linking field observations of short-term responses to human activities to energetic effects at individual and population levels. This case study illustrates the utility of integrating behavioural studies in conservation strategies for large mammals (Sutherland, 1998).

5.2 METHODS

5.2.1 Data collection

Data were collected from a cliff on West Cracroft Island (Figure 5.1) approximately 50m above mean water level, which offered an expansive view across Johnstone Strait. The study area was divided into 8 zones, 4 inside the Reserve and 4 in the waters immediately adjacent to the Reserve. These zones were readily identifiable from the cliff based on sightlines drawn to prominent landmarks.

Field season length varied among years, but the period common to all years was 1 July – 31 August. At least three observers recorded boat and whale activity from 08h00 to 20h00 daily, but for consistency, one observer (Cheryl Ciccone) collected whale data almost without exception. Every 15 min, observers scanned with 7X50 binoculars and/or a 25-40X50 spotting scope to record boat number in each zone.

Whale activity was recorded on the same 15-min schedule. Observers were often cued to approaching whales by members of the research and tourism communities of Johnstone Strait, who share information about killer whale movement patterns in the study area using VHF radio. In addition, by monitoring the signals from hydrophones

installed throughout the area by Orcalab (a land-based monitoring station on nearby Hanson Island), BC Parks and the Vancouver Aquarium Marine Science Centre, researchers knew when vocal whales were approaching the study area. Consequently, it is likely that whales spent relatively little time in the study area unobserved during daylight hours.

Whales entered the study area in matrilines and temporary groups of matrilines, but their activity was recorded at the level of individual whales or groups of individuals. The term matriline is used when indicating relatedness (Ford *et al.*, 2000), and the term group is used when referring to a collection of whales about which no assumption of relatedness is implied. Whales were recorded as being in a group if they were within approximately 10 body lengths of one another, and displaying the same behaviour at the surface. Otherwise, whale activity data were recorded for individuals.

Once whales entered the study area, observers used both visual and acoustic cues to identify individuals. Accurate identification was necessary to establish sequences of activity for focal animals over successive observations. When whales entered the study area, identity of individuals was determined by comparing natural markings to published photo-identification catalogues (Ford *et al.*, 1994; 2000). A hydrophone was used to aid in identifying groups, since each matriline has at least one distinguishing call type (Ford, 1989). The identity of poorly marked individuals in a group can be inferred sometimes through a process of elimination, based on the exceptional fidelity of individuals to their natal groups in this population. Whale identity could not always be determined, however. Any unidentified whales were given a temporary designation and monitored, with observers recording as much

information as was certain (*e.g.*, number of whales, presence of adult males in a group). Focal animals or groups were defined post-hoc from the subset of the data in which group composition remained constant across a sequence of samples.

Scan sampling was chosen over recording bout duration (Tolkamp and Kyriazakis, 1999) because *ad libitum* sampling (Altmann, 1974) proved unfeasible. The 15-minute sampling interval was chosen because initial work suggested that this was a good approximation of the time it took to locate and observe whales and to record activity when large numbers of whales were in the study area. Whale activity recorded during each 15-min scan sample was assigned to one of five discrete activity states (Table 5.1). While the use of behavioural categories involves some level of subjectivity (Janik, 1999), observers were given clear, mutually exclusive definitions. The definitions of these states were adapted from those used in other behaviour and energetics studies (Felleman, 1991; Hoelzel, 1993; Kriete, 1995; Barrett-Lennard *et al.*, 1996; Ford *et al.*, 2000). Each observer was furnished with the activity state descriptions and a data form for recording group activity and group size by zone at 15-min intervals.

Activity State (this study)	Energetic cost category (Kriete, 1995)	Probable functional role
A	1	Resting
B	1	Beach-rubbing (Socialising)
C	mean(2+3)	Traveling/Foraging
D	mean(2+3)	Feeding
E	3	Socialising

Table 5.1. List of activity state codes (A-E) used in this study with their equivalent energetic cost categories defined by Kriete (1995). Activity State B, beach rubbing, is considered equal to rest in terms of energetic cost, but probably plays a social role (Ford *et al.*, 2000). Probable functional roles for the other activity states are inferred from earlier studies of behaviour and feeding ecology in northern and southern resident killer whales (Felleman *et al.*, 1991; Ford *et al.*, 1998; Hoelzel,1993).

5.2.1. Definition of activity states

The five categories used to record activity state were defined structurally so that states

were mutually exclusive and cumulatively defined the entire activity budget of

resident killer whales. They are presented below roughly in order of increasing

energetic cost of the activity, as estimated by Kriete (1995):

> *Activity State A* refers to observations when whales were swimming at slow speed
> with highly predictable sequences of several short (30s) dives followed by a long
> dive of 3-5 minutes. This activity state was characterised by the absence of
> surface-active behaviour (*e.g.*, breaching or tail-slapping). Activity State A
> probably functioned as resting behaviour (Ford *et al.*, 2000). Solitary whales could
> exhibit behaviour that met this definition, but more commonly, all members of a
> matriline coalesced to form a resting line. When a group exhibited the above
> conditions, and when all animals were heading in the same direction, surfacing and
> diving in synchrony, the group's status was assigned to Activity State A.

> *Activity State B* was defined to indicate whale presence within 50m of a gravel
> beach; independent surfacing and diving of individuals; long periods spent
> stationary at the surface, followed by slow swim speeds toward a beach; at which
> point, bubbles or splashing could be observed in the vicinity of the beach. This
> activity was designated "beach rubbing" by Ford *et al.* (1994) and considered as a
> subset of socialising activity. It was treated as a discrete activity state in this study
> because of its importance to the mandate of the Reserve.

> *Activity State C* applied when whales surfaced and dove independently but all
> whales in the group were heading in the same general (east-west) direction. The
> dive sequences of individuals showed regular patterns of several short dives
> followed by a long one, and whales swam at moderate speeds. This category's
> function likely includes both a travel and a foraging component, that is, travelling
> between feeding sites and searching for prey *en route* (Ford *et al.*, 1994).

> *Activity State D* referred to cases when individuals were spread out across the
> Strait; individuals were surfacing and diving independently in irregular sequences
> of long and short dives; and individuals displayed fast, non-directional surfacings
> in the form of frequent directional changes. Several studies have associated the
> fast, non-directional swimming typical of this category with successful fish
> captures as evidenced by finding scales or bits of fish floating near the surface
> (Felleman *et al.*, 1991; Ford *et al.*, 1998; Hoelzel, 1993), thus its functional role
> appears to be related to feeding – prey detection, if not prey capture events. A
> degree of overlap will be perceived between Activity States C and D. Ambiguity
> in classifying activity between these states was addressed by the following rule –
> whales were classed as searching for prey (Activity State C) until evidence was
> found that prey were detected (*i.e.*, individuals deviating from the group's general

direction; fast, non-directional swim speeds; or erratic sequences of long and short dives), at which point, they were assumed to be feeding (Activity State D).

Activity State E refers to cases where animals surfaced in tight groups with individuals engaged in tactile behaviour; whales showed irregular surfacing and diving sequences and swim speeds; irregular direction of movement; and high rates of surface-active behaviour. The functional role of this activity state is probably a social one, as it is observed commonly when two matrilines meet.

5.2.2. Constructing Markov chains from scan sample data

Adjacent 15-minute observations were unlikely to be statistically independent, so the scan sample data were analysed as a series of time-discrete Markov chains (TDMC) (Caswell, 2001; Lusseau, In press). TDMC modelling quantifies the dependence of an event on events preceding it in time. Each sequence of scan samples of the activity of a focal group formed a Markov chain: say, Activity State D, followed by D, followed by A, across three 15-min scans. If group composition changed between scans, then that marked the beginning of a new chain. Modelling temporal dependence is a way to quantify the probability that a given event will follow another. It is possible to assess the difference in transition probabilities depending on the presence of a given factor (in this case, boat presence in the same zone as the whale) during the transition, and therefore, to quantify the effect of this factor. Markov-chain modelling has proven to be a useful way to detect effects of human activity on cetacean behaviour (Lusseau, In press), namely to model effects of boat traffic on bottlenose dolphins in Doubtful Sound, NZ.

Boat and whale scan samples were sorted to allow identification of behavioural sequences of focal animals or groups over time, and to associate these sequences with ancillary information on location and boat presence. The data from each day in the dataset were sorted in EXCEL by the time of the observation. Markov chains were

created only from sequences of scan samples across which identity of focal animals or groups was unambiguous. All other data were excluded from the analyses.

Two binary grouping variables were calculated. First, each scan sample of whale activity was given a value for location, either inside or outside the Reserve. A second dummy variable, traffic, was calculated for each scan, depending on the presence of boats. If no boats were present in the same zone as a focal group of animals, then that scan was identified as a control (*i.e.*, no-boat) observation, regardless of whether boats were present in other parts of the study area. Similarly, observations were scored as treatment (*i.e.* boat-present) observations only when boats were present in the same zone as the focal animal.

TDMC modelling requires a constant sampling interval (Caswell, 2001). Thus, after sub-setting the data to exclude cases of unknown individual identity or missing values, additional data censoring was conducted to remove cases where animals were seen only once (and hence, no transitions between activity states were observed) or where data were recorded at a sampling interval other than 15 minutes. At this point, the binary grouping variables were used to subset the data based on location and boat presence. Focal follows were separated into four data files: those in the presence versus absence of boats, and those inside versus outside the Reserve. No attempt was made to include analyses on a finer spatial scale than inside versus outside the Reserve, or to explore for effects of different vessel types on whale activity. Suitable sample size for each Markov-chain should be somewhere between 5 and 10 times the squared repertoire size (Fagen & Young 1978). For example, this study recorded 5 activity states in the resident killer whale repertoire, so a good sample size would fall

between 125 and 250 transitions per location/traffic category. Recall that wardens attempted to keep recreational boats out of the Reserve, so finer-scale analyses might fail quickly due to relatively few observations of whales in the Reserve with boats other than commercial fishing boats. The same concern prevented analysis by year.

5.2.3. Modelling transition probabilities

Program UNCERT (available from http://uncert.mines.edu) was used to tally the number of times one state was observed following another from these series of samples, conditional on location of the focal group and boat presence in the same zone as the whales. Four-way contingency tables were constructed with the following categories: preceding activity (5 possible states, factor labelled P in the model on Figure 5.2), succeeding activity (5 possible states, labelled S in the model), boat traffic (present or absent, labelled B) and location (inside or outside the Reserve, labelled L).

Dependence of transitions in activity states on location and boat traffic variables was tested for in SPSS 10.0 using General Log-Linear Analysis. Log-linear models are to categorical data what linear models in analysis of variance are to continuous variables (Sokal and Rohlf, 1997). The candidate independent covariates in this case were boat traffic and location, and the response variable is the observed frequency of the number of times one state was observed following another.

Unlike analysis of variance, the main effect measured by log-linear analyses is the presence of interactions between independent variables. Fitting two models is necessary to test for significance of candidate covariates: one with the term present and one with it absent. The G-statistic for goodness-of-fit is computed for each model

and the difference between the G-values is used to test the significance of the term being left out. (Sokal and Rohlf, 1997)

In this study, the goal was to understand the effect of location and boat presence on the behaviour of the animals. It was especially important to know whether the likelihood that a given activity bout followed another was dependent on these two independent variables. The number of factors to assess was therefore restricted in this four-way table. The default (null) model assumed that succeeding state was dependent on preceding state. In other words, some two-way interactions were not tested, because they are inherent assumption in the construction of first-order Markov chains (Lusseau, In press; Caswell, 2001).

If there were no effect of these factors on the probability of whales switching activity states, then these grouping variables would be equivalent to randomly sub-sampling the dataset. In that case, no differences would be seen among sub-samples. Models were constructed starting from a null model (Table 5.2) that only assumed the dependence of succeeding behaviour on preceding behaviour (included terms **PS** and **PBL**). The effect of both boat and location were then tested by adding the dependence of **S** on each of these factors (by adding the terms **xS** and **xPS** where x can be either **B** or **L**). The significance of these terms was tested by testing the significance of the difference in explanatory power (G^2) between the two models (Caswell 2001, Figure 5.2). The best fitting model was selected using Akaike's Information Criterion (AIC; Akaike, 1973), which carries a penalty for adding unnecessary parameters. This analysis therefore provided not only a way of identifying the best fitting model, but also a way of quantifying the significance of the contribution of each factor to

explaining the variance observed in the dataset. Subsequently, four matrices of state transition probabilities (*i.e.*, the likelihood that a succeeding state followed a preceding state, given the samples) were calculated; one for each category of location and boat traffic variables.

		Models compared	
Effect tested	Term tested	Initial	After adding term
Interaction between boat and location	BLS, BLPS	BPS, LPS, PBL	PSBL
Boat	BS, BPS	PS, PBL	BPS, PBL
Boat	BS, BPS	LPS, PBL	BPS, LPS, PBL
Location	LS, LPS	PS, PBL	LPS, PBL
Location	LS, LPS	BPS, PBL	BPS, LPS, PBL

Table 5.2. Steps in constructing the log-linear analysis to test the effects of location and boat presence on behavioural transitions. Models tested the effect of boat and location on the main effect, 'succeeding behaviour,' and the interaction effect, 'preceding X succeeding.' All models include all main effects and all interactions included in the ones present in the model (*e.g.*, BPS includes B, P, S, BP, BS, PS, and BPS). The null model infers that there is a significant interaction between 'preceding' and 'succeeding' (because the data are behavioural transitions). Therefore the null model includes the terms B, L, P, S, PS, BL, BP, LP, and PBL and is noted PS, PBL.

5.2.3. Activity budgets
The transition probability matrices obtained from the contingency tables were eigenanalysed to estimate the stationary distribution of each matrix, which corresponded to the left eigenvector of the dominant eigenvalue (Caswell 2001). This eigenvector possessed a value for each behavioural state (vector in 5 dimensions in this study), which corresponds to the time-activity budget of the population (Caswell, 2001; Lusseau, In Press). In other words, stationary distribution of each matrix corresponds to the proportion of time spent in each behavioural state. This eigenanalysis was conducted using the PopTools add-in for Excel, which is available from CSIRO (http://www.cse.csiro.au/CDG/poptools). Activity budgets were

calculated in the presence and absence of boats, as well as inside and outside the Reserve. Note that data presented represent the average activity budgets (by location and traffic condition) of all whales that used the study area. Data from focal and group follows of both males and females were used, and for simplicity, all follows (male and female, and individual and group) were combined to determine average activity budget. No attempt was made to test whether the activity budgets of males and females differed.

5.2.4. Estimating Energetic Requirements from Time-activity Budgets

The time-activity budgets observed with respect to boat presence were converted to rough estimates of the energetic demand of free-ranging killer whales (Kriete, 1995). Only Kriete's data from Hyak (a 4733kg adult male) and Yaka (a 2800kg adult female) were used, rather than values for both adult and sub-adult subjects, since data on the sub-adult female was thought to be unreliable (Kriete, 1995). As a result, the estimates presented illustrate the energetic demand for two hypothetical northern resident adults of the same mass as the captive adult subjects.

Energetic demand was presented in two currencies. Firstly, caloric demand was presented using the category-specific (Table 5.1) estimates of the energetic cost of each activity state (Kriete, 1995). Secondly, these were converted to units of fish known to be consumed by the resident killer whales that frequent Johnstone Strait. The resident group most frequently observed in Johnstone Strait is the A1 pod. Movements of this pod show good correlation with runs of pink (*Oncorhynchus gorbuscha*) and sockeye (*O. nerka*) salmon (Nichol and Shackleton, 1996), both of which are found in the diets of northern residents (Ford *et al.*, 1998). The mean caloric value of an adult 2.27kg sockeye salmon was 4210.8kcal (Brett, 1983), and the

digestive efficiency of a fish-eating killer whale was assumed to be 0.82, based on the three reliable estimates (0.80, 0.83 and 0.83) of net assimilation efficiency presented by Kriete (1995). Time-activity budgets were converted to rough estimates of the energetic requirements of a free-ranging 4733kg adult male and a 2800kg adult female by traffic condition. Note that male and female energy budgets were estimated using the average activity budget described above, rather than using sex-specific activity budgets.

5.3 RESULTS

This study synthesises observations from 8 seasons, during 496 days (5952 hours) of effort, including 2000 hours observing whales. All 16 pods in the northern resident community (Bigg *et al*., 1990) were recorded in the area at some point during the study. As has been documented previously (Bigg *et al*., 1990; Ford *et al*., 1994; 2000; Nichol and Shackleton, 1996), usage of the area varied widely among individuals and pods, ranging from being identified in the area only once (I31 pod) to being present in nearly 3000 15-min scan samples (A1 pod). After strict censoring, 7517 transitions of focal groups or individuals from one activity state to another were observed.

5.3.1 Log-linear analyses
The two-way interaction between location and boat presence was tested first, and the interaction was shown not to be significant (Figure 5.2). Succeeding behaviour and the interaction between preceding and succeeding behaviour therefore were not dependent on the interaction of the two independent variables.

Each variable could be tested separately, since the interaction was not significant. Both variables affected the behaviour of the whales (Figure 5.2: testing components BS, BPS for the effect of boat presence and components LS, LPS for the effect of location). The left-hand path in Figure 5.2 represents model fits when location effect was added after the boat effect. In this case, the location effect decreased substantially the AIC of the model. Adding the boat effect to a model already including location, however (right-hand side path of Figure 5.2), increased the AIC. When starting with a null model in the log-linear analyses (*i.e.*, that adjacent scans are independent, and that location and boats have no effect on whale activity), the best model in terms of lowest AIC included location only (AIC = -40, Figure 5.2). However, the model considering both location and boat factors provided a large contribution to the explanation of the variance in the dataset (AIC = -32.8, Figure 5.2). Thus, the effect of location was much stronger than the effect of boats, but in both cases, adding the boat effect (by adding the term BS and BPS) explained a significant portion of the variance (after the null model: ΔG^2_{20} = 164, p<0.0001; after model including a location effect: ΔG^2_{20} = 32.8, p = 0.035; Figure 5.2).

There was no significant interaction between boat traffic and location (tested by adding the terms BLS and BLPS to the model: ΔG^2_{20} = 7.2, p = 0.996; Figure 5.2), which meant that whale response to boats was similar inside and outside the Reserve. The selected model included boats and location, given the importance of boats to the management of the study area, and since the data lent strong support to this model when boat was added to the null model before location was added.
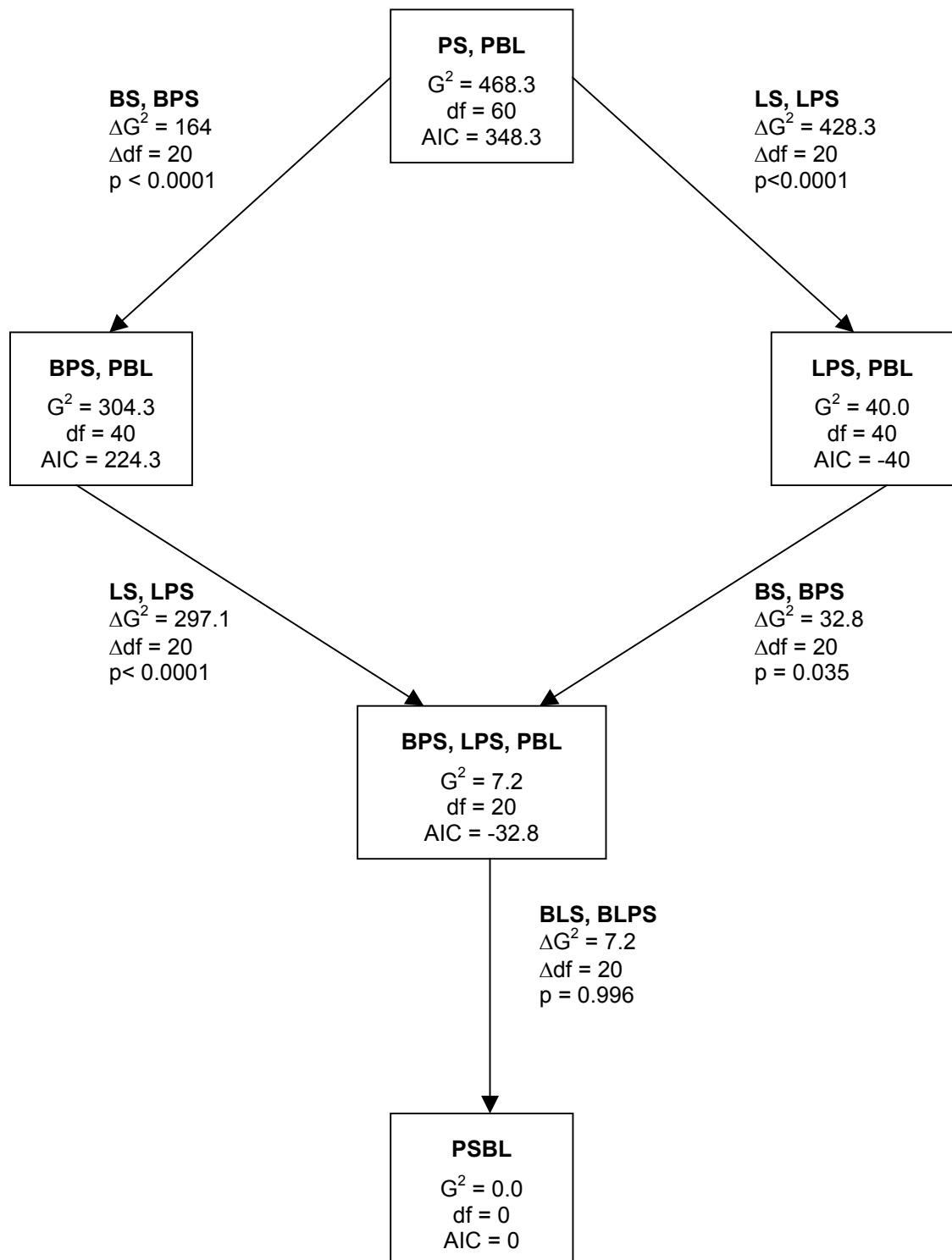
Figure 5.2. Results of the log-linear analyses. P: preceding behaviour, S: succeeding behaviour, B: boat presence, L: location. Numbers at the nodes indicate the G-values resulting from goodness-of-fit tests conducted at each iteration. Numbers along the arrows indicate the differences in fit between the model at the base of the arrow and the model at the tip of the arrow when the

corresponding model terms were added. Model selection based on AIC favoured the hypothesis that location affected significantly the behavioural transitions, however the importance of vessel traffic to management of the Reserve necessitated selection of a model that added vessel traffic before location (left-hand path). There was strong support from the data for a model that included effects of vessel traffic and location on preceding and succeeding behaviour.

5.3.2 Killer whale use of RBMBER

A total of 3508 activity transitions of focal groups of killer whales were observed in the four zones inside RBMBER, and 3770 transitions were observed in the four zones outside the Reserve. Recall that the size of the study area outside the Reserve (2491ha) was larger than the area of the marine component of the Reserve (1245ha). If all parts of the study area were equally used by the animals, one would predict that 33% (1245ha/(1245+2491ha)) of the observations of whales should have occurred inside the Reserve. The observed proportion of transitions recorded inside the Reserve was roughly 48%. Thus, killer whales were observed to spend 45% more time in the Reserve than one would expect by whales using the two locations in proportion to their sizes (proportiontest: Z=18.25, p<0.0001).

5.3.4 Effect of boat presence on transition probabilities

Boat presence showed strong effects on the probability of whales switching from one activity state to another for most initial activity states (Figure 5.3). The strongest effect of boat presence on transition probabilities was observed in Activity State B. Animals were less likely to enter Activity State B from any other state with boats present than when boats were absent.

Whales engaged in Activity State D also showed strong responses to the presence of boats. Whales were less likely to switch from Activity States C to D when boats were present than in their absence (Figure 5.3). In addition, whales observed in Activity State D were less likely to remain in that state (and more likely to switch to lower-

energy Activity States C or A) when boats were present than when boats were absent.

Whales engaged in Activity State C were more likely to remain in that state when

boats were present than when they were absent.
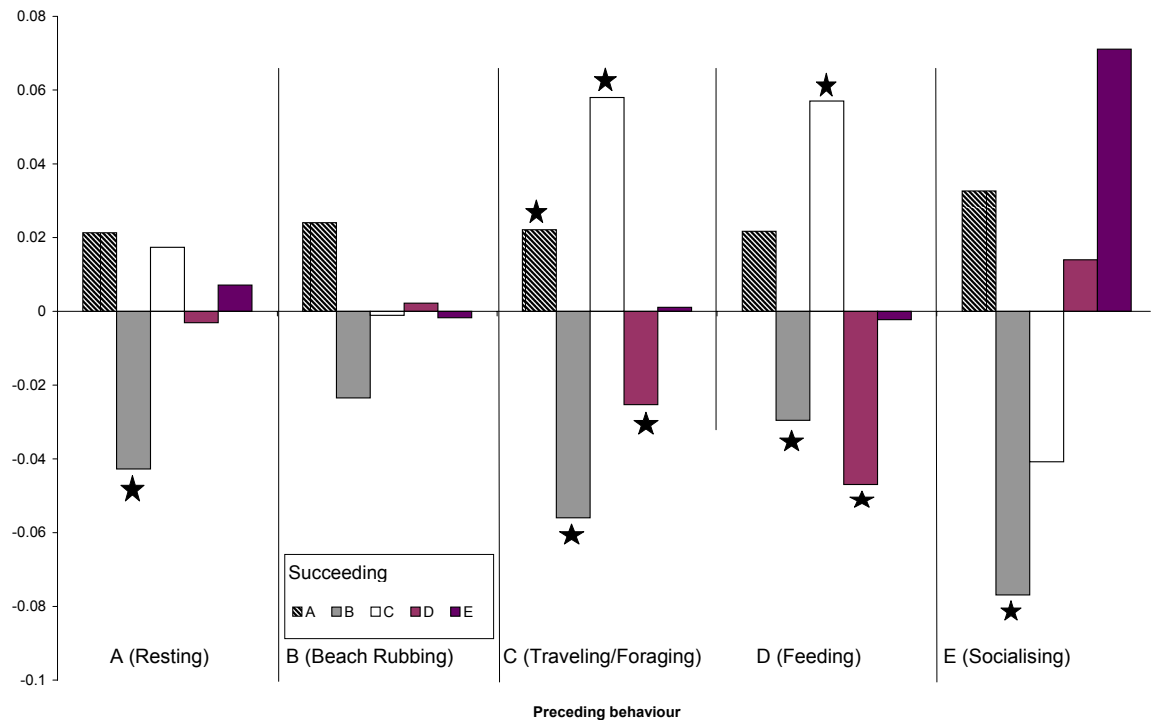
Figure 5.3. Difference between the transition probability of the no-boat chains and the boat chains. A negative value on the y-axis means that the transition probability of the impact chain is lower than the control one. The significance of the difference between two transition probability was assessed using a Z proportion test. Stars mark significant differences (p<0.05). For the p-value of any given comparison, please refer to the text.

5.3.5   Effect of location and boat presence on activity budget

Activity budgets of animals were significantly different inside the Reserve versus the

waters immediately adjacent to the Reserve (Figure 5.4). Activity State B was

observed frequently when whales were inside the Reserve (in 23.4% of 3508 focal

activity transitions), but the activity was confined essentially to the areas near two

smooth pebble beaches inside the Reserve. Activity State B was exceedingly rare

(observed twice, or 0.04% of 3770 transitions) when whales were near the two similar

beaches outside the Reserve. Activity State D was observed inside the Reserve

(13.1%) 1.5 times as often as outside (8.7%). Conversely, whales were observed in Activity States A, C and E less frequently inside the Reserve than outside. Activity State A was 1.9 times as common outside the Reserve (24.5%) as it was inside (13.2%). Similarly, Activity State E was more common outside (5.2%) than inside the Reserve (1.6%).

Boat presence showed strong effects on the overall activity budgets of whales (Figure 5.5). Whales spent, proportionally, far less time in Activity States B and D when boats were present in the same zone of the study area as focal animals than in their absence. The proportion of time spent in Activity States A, C and E was significantly greater when boats were present than in their absence.

5.3.6 Effect of boat presence on whales' energetic requirements

While activity budgets were significantly different in the presence and absence of boats, the effect of boat presence on energetic demand was relatively small after converting the time spent in each activity state (Table 5.2) to estimates of 12h energetic demand in the presence and absence of boats (Table 5.3). The relative cost of the estimated energetic demand over 12h for a free-ranging 4733kg male and a 2800kg female represented approximately 3-4% greater demand in the presence of boats than in the absence of boats. No attempt was made to test for statistical significance of these differences, since variance estimates have not been presented for the estimates of energetic costs of the different activity states (Kriete, 1995). These differences likely do not represent statistically significant differences at the conventional level ($\alpha = 0.05$), as the uncertainty at any step in these calculations was likely to be larger than the 3% differences presented in Table 5.3.

| | Cost of activity (kcal/kg/h)[1] | | Proportion of time in activity | |
Activity	Male	Female	No-boat	Boat
A	1.17	0.91	0.152	0.230
B	1.17	0.91	0.168	0.029
C	1.935	1.79	0.533	0.598
D	1.935	1.79	0.125	0.102
E	2.19	2.28	0.023	0.040
Transitions observed			3500	4017

[1] After Kriete (1995)

Table 5.2. Approximate eneregetic cost of five activity states on equivalent catagories used by Kriete (1995), and proportion of time spent in each state in the presence and absence of boats.

	No-boat	Boat
Male (4733kg)		
kcal	96356	99216
number of fish	27.9	28.7
Female (2800kg)		
kcal	51080	53138
number of fish	14.8	15.4

Table 5.3. Estimated 12h energetic demand of a free-ranging male and female killer whale in activity budgets observed in the absence and presence of boats. Energetic requirement is presented in terms of caloric demand (kcal) and in the number of sockeye salmon the whale would need to assimilate to meet that demand.

5.4 DISCUSSION

This study achieved all three of its primary aims. First, it identified that killer whales use Robson Bight differently from the way they use adjacent habitat. Secondly, it provided evidence that the way in which whales used the study area changed when boats were present. Thirdly, it offered a point estimate of the extent to which these changes in activity may carry small energetic costs to whales. These three objectives

were met using a cost-effective, environmental education platform, while addressing

two shortcomings of previous studies: this study included observations of all age-sex

classes of whales in the population, and sampled across the entire repertoire of killer

whale activity in Johnstone Strait.

5.4.1 Killer whale use of RBMBER

Within the study area, killer whales showed strong fidelity to Robson Bight. Whales

were observed in the Reserve 45% more often than one would expect if animals

showed no micro-scale habitat preference. This is unlikely to be a spurious result,

since observer effort was constant between the two areas, and whales were similarly

detectable inside and outside the Reserve. The importance of Robson Bight to

northern resident killer whales, however, was seen not only in terms of spending a

disproportionate amount of time there, but also in how whales used the Reserve and

adjacent waters.

Robson Bight – Michael Bigg Ecological Reserve was established largely to protect

the rubbing beaches and, indeed, beach-rubbing activity (Activity State B) was seen

hundreds of times more often in the Reserve than at the beaches immediately adjacent

to the Reserve (Figure 5.4). In addition, Activity State D occurred 1.5 times as often

inside the Reserve as outside. The fast, non-directional swimming characterising this

activity state was often associated with successful prey capture events (Felleman *et al*.,

1991; Hoelzel, 1993; Barrett-Lennard *et al*., 1996; Ford *et al*., 1998). Thus, Robson

Bight appeared to provide whales with good feeding habitat. This finding has

important conservation implications, given the whales' status as a threatened

population (Baird, 2001). Concern about prey availability, in terms of degradation of

salmon spawning habitat and overfishing, was a key factor in Baird's review of the status of resident killer whales.
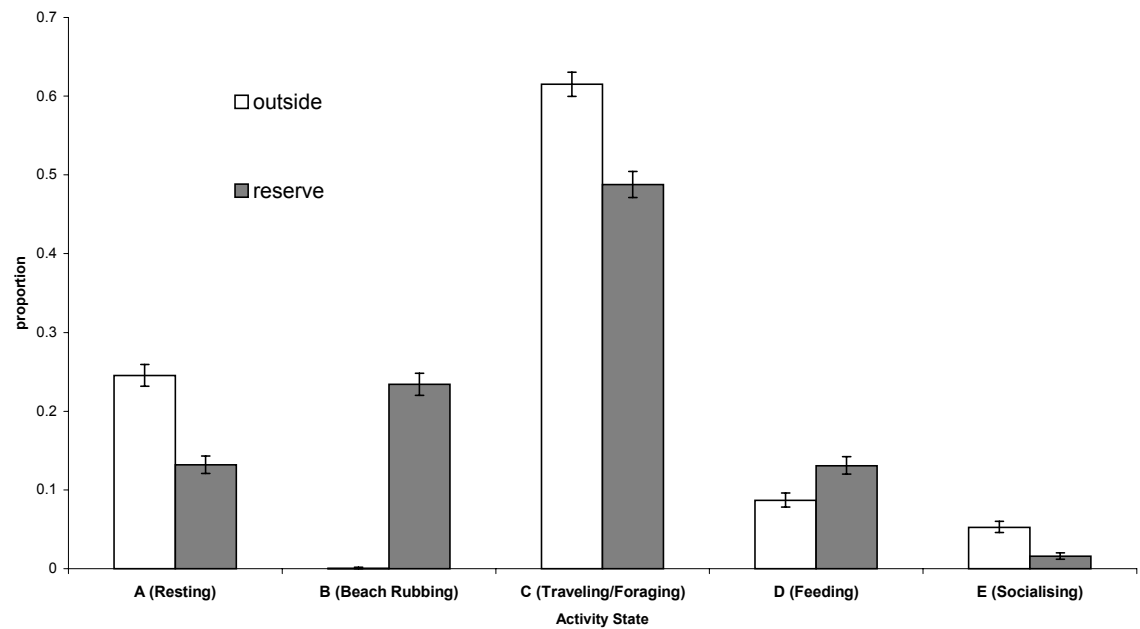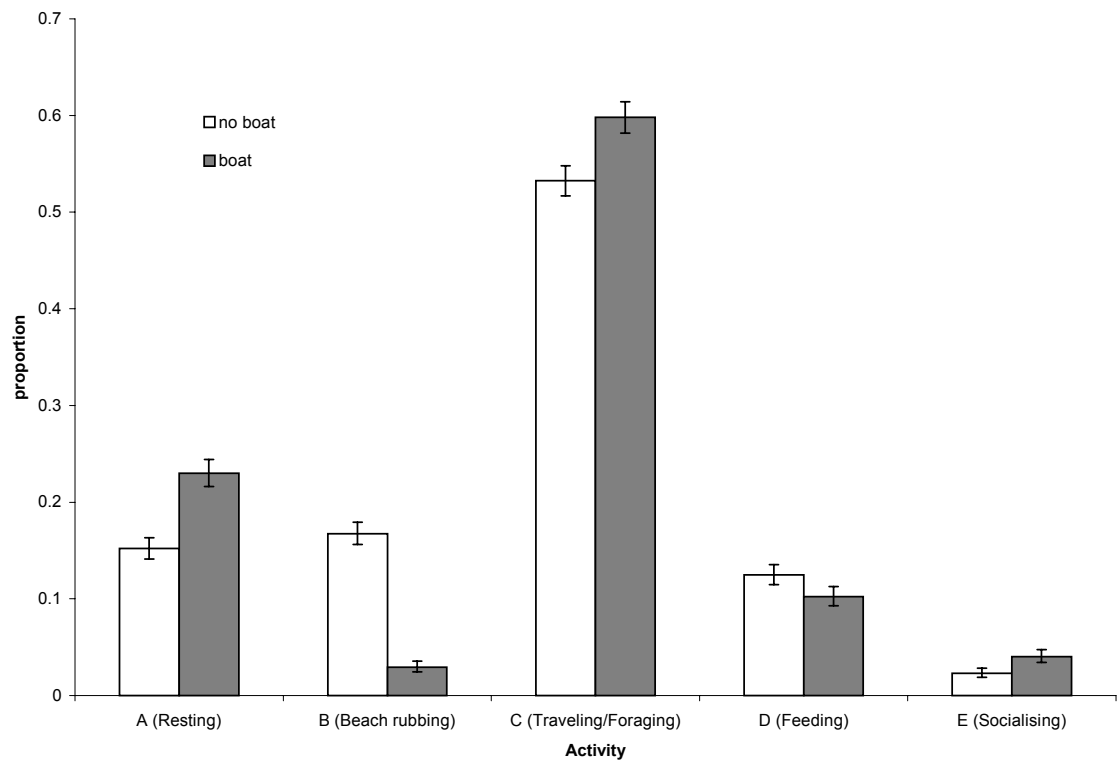
Figures 5.4 (top) and 5.5 (bottom). Effect of location (top) and boat presence (bottom) on activity budget. Bars represent 95% CIs, and all differences are significant at the conventional level (p<0.05).

Johnstone Strait is one of the narrowest points along the Inside Passage and serves as a bottleneck to concentrate salmon, which makes the Strait an important commercial fishing ground (Nichol and Shackleton, 1996). Within the Strait, Robson Bight appears to be an exceptionally good fishing spot for whales and humans. It is perhaps unsurprising that killer whales should spend so much time feeding in Robson Bight itself. Commercial seiners have made some of the largest catches of salmon in BC history in Robson Bight (David Lane, T. Buck Suzuki Foundation, pers. comm.). Lane suggests that strong tidal action washes prey fish into the Bight, and that prevailing currents make Robson Bight a good place for salmon to rest while waiting for the tide to change. When the tide flows out, so do the salmon.

As a possible requiem reserve (Duffus and Dearden, 1992) however, Robson Bight appeared to play little role in providing whales with a place of rest, since Activity State A was observed much more frequently outside the Reserve than inside (Figure 5.3). Similarly, when whales were in the waters adjacent to the Reserve, they were more likely to be engaged in Activity States E (socialising) and C (traveling/foraging) than when inside the Reserve. This suggests that the parts of Johnstone Strait outside the Bight were used for socialising and as a travel corridor to transit among good feeding grounds.

Taken as a whole, these findings support the conclusion that whales use Robson Bight differently from the way they use adjacent habitat (Figure 5.4). It is unclear whether the differences in activity budgets observed in this study warrant classification of Robson Bight as so-called 'critical habitat' (Duffus and Dearden, 1992). However, it is clear that whales spent a far greater proportion of their time in the study area inside the Reserve than would be predicted from random use of the study area. The area was important for feeding and beach-rubbing activities to the matrilines that used the area most often.

5.4.2 Effects of Boats on Killer Whale Activity Budgets

Both commercial salmon catches and whale activity in the Reserve indicated that Robson Bight offers good fishing opportunities. The ability of the Reserve to provide good feeding habitat to resident killer whales, however, may have been compromised when boats entered it. Whales spent nearly 17% of their time in the study area rubbing when boats were absent, compared with 3% when boats were present in the same zone as the whales (Figure 5.4). Overall, whales reduced their time spent

feeding from 13% to 10% when boats entered the same zone of the study area as whales. This effect was found on two levels. Focal whales or subgroups showed a lower probability of continuing feeding and a lower probability of switching from travel/forage to feeding activity (*i.e.*, initiating a feeding bout) when boats entered a given zone of the Reserve than when boats were absent (Figure 5.3). Recall that the vast majority of boats in the study area were not engaged in whalewatching, but rather were commercial fishing vessels (Wong and Williams, 1998).

Noise, rather than simple presence of the boats, seems the likeliest mechanism for boats to disturb whale behaviour. Evidence exists for killer whales evading annoying noise on fine temporal and spatial scales (Chapter 4), and harmful noise on annual and regional spatial scales (Morton and Symonds, 2002). Empirical evidence exists that boat noise can impair killer whales' ability to detect pure tones (Bain and Dahlheim, 1994) and low-frequency lateral components of calls (Miller, 2002), thereby reducing the whale's active space, the volume of water that is within acoustic range of a whale. Whalewatching vessels themselves can ensonify substantial fractions of killer whale foraging habitat (Erbe, 2002). However, these analyses are the first to indicate that vessel traffic did impact feeding activity of northern resident killer whales.

One should exercise caution when interpreting behaviour from subjective activity categories, especially in cetacean studies where behavioural observations are restricted to the surface. However, one observer collected the vast majority of whale data. And any misinterpretation of whale activity on the observer's part was unlikely to introduce systematic bias in this study. Approaches of foraging killer whales by an experimental boat (Williams *et al.*, 2002, Chapter 4) demonstrated that on average, killer whales

adopted a less direct path when the boat was present than it was following before the boat arrived. These zigzag avoidance responses, if misinterpreted, would most likely have been mistaken for feeding activity. Thus, if misinterpretation of behaviour were an issue, one would predict that whales that were traveling and foraging would initiate more apparent feeding bouts, not fewer. Thus, avoidance behaviour would have been manifested in the opposite direction to the results found here. Rubbing and resting activities, the other states in which transition probabilities were affected by boat presence, are less subjective activities to differentiate than foraging and feeding.

5.4.3 Effect of Boat Traffic on Killer Whale Energetic Demands

Table 5.3 shows point estimates of how many sockeye salmon a whale might require to meet its energetic needs for 12h in the absence and presence of boats. These are meant to be interpreted as relative, not absolute costs. Killer whale activity budgets varied markedly between absence and presence of boats, but the net energetic effect was relatively small. This reflects the tendency for whales to replace one low-energy activity (e.g. beach rubbing) with another (e.g. resting) in the presence of boats. As a result, the point estimates of the total energetic demand of 12h spent in two different activity budgets are quite similar, suggesting that at low traffic levels, northern resident killer whales may to be able to balance the energetic cost of avoiding boats.

This exercise was presented to illustrate the point that short-term behavioural responses can carry energetic costs. In fact, northern resident killer whales eat a variety of prey (Ford *et al*., 1998), and the numbers of fish presented in Table 5.3 would have been amplified had they been presented in units of a smaller salmonid, pink salmon (*O. gorbuscha*), or greatly reduced in units of the largest Pacific salmonid, chinook salmon (*O. tshawytscha*). More importantly, the point estimates of

the energetic cost of each activity state (Kriete, 1995) reflect categorisation of a continuum of energetic costs, and carry uncertainty that has not been quantified, and therefore could not be included in this exercise.

However, this is the third study to suggest that, while responding to boats may carry some energetic cost to northern resident killer whales, the upper limit of that cost is currently likely to be low (Williams *et al.*, 2002; Chapter 4). The question now becomes whether whales are able to satisfy their energetic demands under disturbed or undisturbed conditions. In the context of a conservation strategy for northern resident killer whales where prey availability is already a concern (Baird, 2001), the real issue may not be increased energy expenditure in the presence of boats so much as the potential for boats to cause a reduction in overall energy acquisition, via masking effects of boat noise or replacement of feeding activity with boat-avoidance tactics.

5.4.5 Possible Effects of Boat Traffic on Killer Whale Energy Acquisition

This study provides indirect evidence that feeding activity is disrupted by the presence of boats. In addition, killer whale populations will respond numerically in the same way to reduced prey abundance as they will to an equivalent reduction in prey detection due to masking effects of boat noise. In a food-limited population, this is one mechanism that could link short-term consequences of vessel traffic to long-term, population-level consequences. Prey availability has been cited as a concern for both the Threatened northern resident and Endangered southern resident killer whales (Baird, 2001). The difficulties inherent in assessing prey preference, prey availability and quantity of prey acquisition in free-ranging killer whales are obvious. To that extent, it may be necessary to model population-level consequences of reduced

foraging efficiency under varying degrees of masking, rather than to try to measure these costs empirically.

The activities both of whales (Figure 5.4) and fishermen suggest that the Bight provides exceptionally good fishing habitat. Assuming that the fast, non-directional swimming behaviour observed in Activity State D was associated with prey capture attempts (as observed by Felleman *et al*., (1991), Ford *et al*., (1998), and Hoelzel (1993)), it is perhaps unsurprising that killer whales near boats shortened their feeding bouts and initiated fewer of them than in the absence of boats. It has been demonstrated that many bird species respond to tourism presence by shortening feeding bouts (*e.g.* Burger et al., 1997; Galicia and Balassarre, 1997; Ronconi and St Clair, 2002). This has been found also in numerous studies of terrestrial mammals, where feeding activity is easier to observe than in free-ranging cetaceans.

Bighorn sheep (*Ovis canadensis nelsoni*) reduced food intake dramatically when approached by helicopters near the Grand Canyon (Stockwell *et al*., 1991), and woodland caribou (*Rangifer tarandus*) exposed to tourists reduced their time spent feeding in the Charlevoix Biosphere Reserve (Duchesne *et al*., 2000). Terrestrial carnivores, as well as herbivores, have been shown to reduce food intake as a consequence of increased vigilance in the presence of humans. Grizzly bears (*Ursus arctos*) spent 53% less time feeding on army cutworm moths (*Euxoa auxiliaris*) in Glacier National Park, Montana, USA after detecting the presence of climbers in the area (White *et al*., 1999). This represented a substantial reduction in the caloric value of estimated food intake. Similarly, Amur tigers (*Panthera tigris altaica*) in Krai, Russia showed strong vulnerability to human disturbance in the form of roads (Kerley

et al., 2002). Tigers at undisturbed sites spent more time at kills and consumed more of the kill than tigers disturbed by humans. Ultimately, disturbance to tigers was linked to lower reproductive success and higher adult mortality than tigers that occupied sites far from roads (Kerley *et al*., 2002). Thus, a range of disparate studies has found that feeding activity of large mammals was disrupted by human activity.

In summary, the case for boat traffic reducing energy acquisition in resident killer whales is equivocal. Fast, non-directional swimming does not always indicate prey location and capture (Wilson *et al*., 2002). Neither is the relationship between time spent searching for food and energy acquisition a straightforward one. Time spent suckling in horses showed no correlation with milk intake (Cameron *et al*., 1999). Increasing the cost of transport to foraging fur seals caused adult females to stay away from their pups longer than the control group, but animals appeared to be able to alter their diving behaviour to compensate for this cost (Boyd *et al*., 1997). Mothers must have been able to compensate for the cost of longer foraging trips and higher swimming costs, since pup growth in treatment and control groups was similar (Boyd *et al*., 1997). In this study, longer traveling/foraging bouts and shorter feeding bouts for killer whales when boats were present than when they were absent could mean that whales near boats had to search for food longer, but not find it. Alternatively, it could mean that boats improved the whales' foraging efficiency. Perhaps the location of fishing boats and their nets helped whales to find fish quickly, enabling whales to return to other activities.

However, the masking effects of boat noise on killer whale echolocation ability (Bain and Dahlheim, 1995) are well established. The energetic cost of avoiding boats is

likely to be small. The energetic consequence of masking effects of boat noise, and missed foraging opportunities due to avoidance responses, on energy acquisition are unknown, but could be much larger than the cost of avoidance behaviour. Future research should continue to investigate the feeding ecology of resident killer whales.

5.4.6 Value of the Reserve

These findings have implications for the utility of protecting seemingly trivial fractions of a marine mammal's range. There is no evidence to suggest that whales use the Reserve to seek refuge from boats. This study does provide evidence, however, that the Reserve may confer benefit to animals in the form of aiding foraging efficiency, by reducing vessel-based interruptions to feeding activity in a small but important part of the animals' range. The importance to whales of removing human disturbance for only fractions of a day or year remains to be modelled. Ultimately, though, it would seem better to protect small areas than none at all, unless this digresses into exercises in tokenism, where 'paper reserves' create the appearance of protecting endangered species. "The world is littered with paper parks (Kelleher and Kenchington, 1993, cited in Reeves, 2000)."

Duffus and Dearden (1992) established criteria against which one could judge whether Robson Bight could be called a reserve in any other than a semantic sense. For Duffus and Dearden, one can justify calling Robson Bight a reserve only if one could (a) demonstrate the importance of the area to the whales, and (b) establish that the Reserve offers the whales some degree of protection. This study has shown that the activity of killer whales in Robson Bight – Michael Bigg Ecological Reserve differed significantly from their activity in the waters immediately adjacent to it (Figure 5.4). Whether the functional role of beach rubbing has to do with parasite removal or plays

some social role is currently unclear (Ford *et al.*, 2000). It is similarly unknown what the consequences might be of disrupting this activity. What is clear is that the activity is important enough to whales for it to have taken up 23% of whales' time spent in the Reserve, while the activity was essentially non-existent on the similar beaches outside RBMBER. Indeed, the greatest value of the Reserve may be in conserving rare behaviour (Sutherland, 1998). However, the role of RBMBER in protecting whales from disruption of feeding activity (Figure 5.3) in prime foraging habitat (Figure 5.4) must not be dismissed. There are obvious benefits to a food-limited killer whale population of setting aside good foraging habitat from which human disturbance is removed.

It is more difficult to say whether Robson Bight currently avoids the charge of being a paper park by conferring protection to whales. Hooker *et al.* (1999) note that unlegislated reserves are best thought of as "gestures," which easily can be revoked. Clearly, RBMBER offers some protection to whales in the sense that its existence is legislated by one level of government. That creates a provision for prohibiting some human activities, such as walking on the rubbing beaches, and could allow for greater control by preventing fishermen from anchoring or tying seine nets to shore. Currently, RBMBER prevents boaters from disrupting at least some of the whales' feeding activity by fostering exceptionally good boundary compliance by recreational and whalewatch boaters (Wong and Williams, 1998). Robson Bight, then, meets the two-fold challenge of Duffus and Dearden (1992) to qualify as a reserve: the whales used this area differently from the adjacent habitat; whale feeding and beach rubbing activity were reduced in the presence of boats; and the Reserve boundaries created a zone where most whale-oriented traffic is eliminated from an area that whales use

heavily for feeding and beach rubbing. It would be difficult to argue with claims that the Reserve could confer greater benefit if boundary compliance by all vessel types were improved.

5.4.7 Wider Implications

Studies of animal behaviour have an important role to play in conservation biology, but linking the two fields has been slow (Sutherland, 1998). Partly, conservation biologists may be sceptical of equating animal disturbance (a function of human activity that is confounded by the animal's tolerance, habituation and tradeoffs) with conservation risk (Gill *et al*., 2001). One way that behavioural studies can be integrated into biological conservation is to help quantify the extent to which human disturbance might reduce quality of habitat or resources. Taken to their extreme, increasing whales' energetic cost, or reducing their ability to acquire prey, will change the demographic parameters that influence effective population size (Anthony and Blumstein, 2000).

In addition, the outcome of repeated disturbance illustrated here could have implications also that simply were not measured. Repeated disturbance, and random (from the whale's perspective) interruptions also reduce the ability of animals to learn about their changing environment (Dall *et al*., 1999). It is difficult to model what the implications might be to killer whales of interrupting opportunities to learn.

It may be useful to examine these findings in the context of the endangered southern resident killer whale community, which is not only in a more vulnerable situation than northern residents, but also experiences far greater levels of boat traffic (Baird, 2001). One major implication for upcoming southern resident vessel impact studies is

apparent immediately from the results of this study. Vessel-impact studies ought to target the most vulnerable activities and individuals in order to be informative and precautionary. Therefore, southern resident vessel-impact studies should incorporate scan-sampling to record activity of all individuals in a study area to avoid unintentionally excluding the most challenging (but perhaps the most informative) scenarios from behavioural studies. Similarly, experiments that unintentionally exclude females and calves (*e.g.* Chapter 4), due to the difficulty in discriminating them reliably from conspecifics on each surfacing, may inaccurately reflect the average response of whales to disturbance.

Furthermore, future southern resident studies should include observations of whales across the entire range of activity states. If northern and southern killer whales are equally unlikely to alter their behaviour in response to approaching boats while engaged in socialising activity, for example, then it would be difficult to interpret a null finding from a vessel-impact study conducted in an area that whales use primarily for socialising. A suitable site for a land-based southern resident killer whale vessel impact study might be found on the southwest corner of San Juan Island, which has been shown to be heavily used by those whales for feeding (Hoelzel, 1993; Felleman *et al.*, 1991). If land-based studies on the endangered southern resident killer whale population show similar results to these, then it may be prudent to identify important feeding habitat, and to lobby for that area's protection, rather than protecting a travel corridor or an area that whales use primarily for socialising. The southern residents' Depleted status under the U.S. Marine Mammal Protection Act requires a management plan that reduces 'take,' which includes harassment, of whales. Marine protected areas could play a role in reducing this so-called 'take' of southern resident killer

whales, as long as no-entry zones are placed in areas where whales feed, rather than in areas used primarily by transiting or socialising whales.

In the context of the threatened northern resident killer whale population, Fisheries and Oceans Canada (DFO) should continue to be encouraged to recognise the marine boundaries of Robson Bight – Michael Bigg Ecological Reserve by declaring it to a no-take, no-entry marine protected area. The federal government should work with the wardens contracted by the provincial government to ensure compliance with the boundaries by all vessel types. Current impact of boat traffic on northern resident killer whales is likely to be relatively low in terms of increasing energetic demands. However, ongoing research to model energetic effects of boat traffic on killer whale population dynamics should attempt to incorporate the masking effects of boat noise on prey acquisition, which has unknown potential to cause population-level impacts. Marine protected areas could play an important role in protecting this, and other threatened cetacean populations, provided that areas are chosen to protect critical feeding habitat, and are truly protected.

5.5 ACKNOWLEDGEMENTS

Chapter 6

Discussion

"Mathematics may be compared to a mill of exquisite workmanship, which grinds your stuff to any degree of fineness; but, nevertheless, what you get out depends on what you put in; and as the grandest mill in the world will not extract wheat flour from peascods, so pages of formulae will not get a definite result out of loose data." (Huxley, 1894)

6.1 Overview

This thesis achieved its primary goal of using inexpensive methods to obtain useful quantitative information to aid decision-making about conservation and management of wild cetaceans that interact with, compete with, and are exploited by humans. The four case studies provided information that contributed to answering the kind of questions that applied wildlife biologists are routinely asked: How many animals? Where are they? Are we disturbing them? What resources do they need? Each case study achieved its goal through partnerships with resources that at first, might seem unrelated to the task at hand, but it is hoped that they serve as models where the platform was opportunistic, but the research was designed specifically to answer a question to assist management and conservation.

6.2 Estimating abundance and variance with limited resources

Wildlife biologists worldwide struggle with ways to assess the size of cryptic populations while working within (often very) limited means. In the absence of information on animal density, researchers working on pheasants in southeast Asia assessed population status using changes over time in the number of localities from which species were reported as having been seen (McGowan *et al.*, 1998). Some have taken this approach further to estimate absolute abundance. A statistically significant correlation was found between sampled density of four endemic bird species in

Namibia and the rate at which they had been reported by bird-watchers (Robertson *et al*., 1995). This relationship was used to convert reporting rate in other areas to density, in order to estimate abundance of the four species throughout northwestern Namibia. The high cost of marine studies suggests that similarly creative ways are needed to obtain coarse information on abundance of cetaceans in understudied areas, providing that such techniques give the correct answer.

Ships of opportunity can be used for collecting data that inform us about the abundance estimation process itself. In Chapter 2, a variety of studies were conducted to reveal that error and bias in visual and reticule estimates of range to cetaceans is complex, and has the potential to introduce large bias in abundance estimates in either direction. In future, one use of non-randomised survey platforms in this context may be for training observers in survey protocols and for field-testing new methods to estimate g(0), measure range or to study how cetaceans respond to ships during sightings surveys (Leaper and Gordon, 2001; Palka and Hammond, 2002; Bravington, 2003). The ability to see a whale, measure distance to it and to record data are unaffected by placement of tracklines. And a dolphin's response to a ship will not depend on whether the ship was following a randomised survey design.

Chapter 3 provides another piece of evidence that given good coverage of a study area, ships of opportunity can be used for collecting line-transect data that can be modelled to estimate abundance (Hedley *et al.*, 1999, Bravington, 2000; Clarke *et al*., 2000; Marques, 2001; Hedley and Buckland, In prep.). The flexibility of GAM-based spatial modelling techniques gives them some advantages over conventional distance sampling analyses. However, the models' flexibility can also be problematic (Wood,

2001). Unrestricted flexibility in the model can result in biologically implausible abundance estimates in resampling methods to estimate variance (Hedley *et al.*, 1999; Clarke et al., 2000; Bravington, 2003).

New analytical methods are being developed to address these concerns, though (Bravington, 2003), so the framework outlined in Chapter 3 holds promise for places that receive tourist attention but little scientific attention. The precision of estimates from opportunistic survey platforms will never match those of dedicated sightings surveys. However, the potential conservation benefit justifies using these methods in areas where abundance is unknown, and where lack of funding makes dedicated surveys unlikely to occur (IWC, 2001). In such areas, perhaps conservation strategies could be implemented based on relative scarcity or highly localised distribution, even if accurate estimates of abundance cannot be derived.

To some extent, existing problems with variance estimation in a spatial modelling framework are unsurprising. Ecological systems are complex, and uncertainty and variability are inherent features of the systems we study (Roslin, 2002). Indeed, in a novel analysis of 43 earlier meta-analyses of ecological, environmental and evolutionary studies, on average, the single most important factor in a study was able to explain only 2.5-5.4% of the natural variation in the response data (Møller and Jennions, 2002). This is important to keep in mind when communicating the limits of ecology to resource managers. Our statistical power, even in well-designed studies, may be low, simply because the animals we study are highly variable (Taylor and Gerrodette, 1993).

As conservation and management initiatives attempt to incorporate uncertainty (*i.e.*, variance), it will become increasingly important for population monitoring to provide not only the best estimates of abundance, but also the best possible estimates of variance (Taylor and Gerrodette, 1993; Wade, 1998; Butterworth and Punt, 1999; Harwood, 2000;). In some cases, the variance of an abundance estimate is used to establish a minimum population size against which anthropogenic mortality is judged for sustainability (Wade, 1998). Variance estimators that perform reliably are key when assessing the sustainability of harvests (Johnston *et al.*, 2000). In other words, variance can be high, but the estimates of variance must be accurate.

In the absence of empirical estimates of uncertainty, researchers have turned to less desirable alternatives: estimating variance from expert opinion (Ayyub, 2000), and setting conservation priorities based on researchers' "degree of belief" in given propositions (Colyvan *et al.*, 1999). Even these approaches are better than ignoring uncertainty altogether. BC's trophy hunting quotas for grizzly bears use abundance estimates estimated simply by the amount of suitable habitat that is available to bears (Peek *et al.*, 2003). No attempts are made currently to assess uncertainty associated with that estimate, despite the fact that uncertainty in abundance accounted for 60.5% of the uncertainty in population viability analyses for the population (McLoughlin, 2003). Gauging the sustainability of this hunt is compromised by an unwillingness to quantify and incorporate uncertainty.

Demographic information is necessary for conservation and management, but it is costly and difficult to obtain. Perhaps the solution to this dilemma is neither to rely solely on mining existing datasets and opportunistic platforms, nor to conduct costly,

large-scale and long-term ecological monitoring programs annually until a trend is detected. An optimal, cost-effective sampling design was developed for monitoring populations of boreal birds in Alberta, Canada (Carlson and Schmiegelow, 2002). Sensitivity analyses were conducted to assess whether the power to detect trends would be improved most by increasing the number of times per year a survey was conducted or by increasing the number of samples within each survey set. This case study serves as a model for conducting long-term monitoring on a minimal budget. Models that help us to predict how populations will respond to management or conservation actions are crucial (Bradbury *et al*., 2001). But monitoring how populations actually responded is of equal importance in sound marine resource management (Butterworth and Punt, 1999).

6.3 Modelling cetacean distribution

Line-transect surveys conducted from non-randomised designs were used to map density gradients for humpback, fin and minke whales. This may serve as a pilot study, where areas of predicted high density could be targeted to increase encounter rate to make future photo-identification and biopsy studies more efficient. Similarly, the high-density area could be used to define strata in future line-transect surveys, making surveys cheaper and more precise (by allocating more effort to the high-density stratum) than a single-stratum survey (Buckland *et al*., 2001).

Covariates could be included that are of direct interest, such as sea-surface temperature, in addition to the simple spatial covariates used here, as long as values are known along the trackline and for every square in the predictive grid. Spatial models of whale distribution will play an important role in predicting how cetaceans will respond to global climate change. Proximity to other species could be included as

a candidate covariate. Killer whale predation on large whales was recently considered as having played a role in the sequential collapse of marine mammal populations in the northeast Pacific (Springer *et al.*, 2003). Efforts have been made to forge a similar link between decline of Antarctic minke whales (Branch and Butterworth, 2001a) and increased killer whale predation (Branch and Williams, 2003). It would be interesting to see whether Antarctic killer whale distribution is influenced strongly by the distribution of minke or large whale prey (Pitman and Ensor, In Press).

Spatial modelling methods are easily expandable to spatio-temporal modelling. The Antarctic tourist season is longer (IAATO, 2000) than a typical IWC survey season (Burt and Stahl, 2000; Branch and Butterworth, 2001ab). The methods and ships described in Chapters 2 and 3 could be used to model timing of minke whale migration and for mapping migration corridors. That information would be very valuable in assessing whether observed declines in Antarctic minke whales (Branch and Butterworth, 2001a) might be related to changes in the timing of the surveys.

Animal distribution is of interest in its own right, rather than just for informing future research. These methods could be used to identify spatial and temporal overlap between whale distribution and human activity, to identify the best time and place to fish to minimise bycatch (van Waerebeek, 1994; Trippel *et al.*, 1996) or to reduce local competition between commercial fisheries and marine mammals (Trites *et al.*, 1997; Boyd, 2002). With the enormous attention paid to the decline in Steller sea lions (NAS, 2002), a similar spatial model of at-sea distribution could be made from line-transect data to identify where animals are feeding. Spatio-temporal models of whale distribution could be used to isolate the safest time to introduce potentially

harmful noise (Richardson *et al.*, 1995) into the marine environment (for seismic surveys, or naval use of mid-range sonar, for example).

6.4 Redefining platforms of opportunity
The term, "Platforms of Opportunity," covers a wide range of platforms, and research projects aimed at benefiting from those platforms. At the March, 2003, meeting of the European Cetacean Society, a workshop was held on using ships of opportunity for cetacean research. Prior to the meeting, attendees were asked to complete a questionnaire outlining the role of ships of opportunity in their research. A total of 24 questionnaires were returned, although some were incomplete (R. Williams, unpublished data).

Of those who answered the question, 9 of 20 studies offered observers no training, and 5 of 20 used no standardised searching protocol. Indeed, 5 of 24 respondents did not record search effort at all. When effort was recorded, often only trackline length was recorded: 8 of 21 respondents did not record radial angles or distances, so different relative abundance of species could not be distinguished from different detectability in those datasets. The results presented in Chapter 5 could not have been produced had efforts not been made to record effort and sightings data in a systematic way.

Researchers can generate informative results when data collection and study design are dedicated and rigorous, even when the ability to allocate sampling effort is lacking (Robertson *et al.*, 1995; McGowan *et al.*, 1998; Gregr *et al.*, 2000; Gregr and Trites, 2001; Pitman and Ensor, in press). It is important to weigh the time and money saved by using opportunistic resources against the research cost of reduced control and flexibility. In cases where resources for dedicated sightings surveys are non-existent,

rather than limited, the choice is clear: collecting precise line-transect survey data from a non-randomised survey platform is far better than no data at all. Existing methods enable these data to yield useful results, and emerging methods can only improve on current shortcomings.

6.5 Existing under-utilised prospects for using tourism ships

River dolphins globally are critically endangered (Vidal, 1993; Perrin, 1999; IWC, 2001). These animals represent an exceptional conservation challenge, because survey methodologies for freshwater cetaceans require attention, and even if appropriate methods were available, the developing countries in which river dolphins are found are unlikely to be able to fund basin-wide the surveys. The techniques described in Chapter 3 might be used to assist conservation efforts to protect freshwater cetaceans.

Many of the tour ships used in the Antarctic study spend the shoulder season in the Amazon River. Cruises from Belém, Brazil to Iquitos, Peru happen at least twice each year, with daily excursions by zodiac to explore tributaries, lakes and flooded forest. This represents a good, untapped chance to bring quantitative people in the field inexpensively to assess the problems inherent in freshwater surveys and to develop solutions to them.

The same tour companies spend the austral winter in the Arctic. While coverage is poorer typically than was seen in Chapter 3, annual tracklines run from Kamchatka (Russian Far East) to Scandinavia through the Canadian high Arctic. This platform would provide an opportunity to place pop-ups (self-contained hydrophones with long recording life and easily retrievable) one year, and to retrieve them the next (Christopher Clark, Cornell University, pers. comm.). Such a study would represent

an inexpensive way to monitor year-round cetacean usage of a relatively inaccessible, but biologically important, location.

6.6 Drawbacks in using platforms of opportunity

One of the most important findings is that while the ships used in this study were opportunistic, the assistants must be dedicated observers. With more than 90% of time spent as the only observer on deck, (early and late in the day, during mealtimes, and during lecture periods), it seems unlikely that g(0) estimation could be accomplished without dedicated assistants. Indeed, the nature of the platform may impose a limit on the feasibility of gaining assistance onboard. Guides and naturalists have extensive duties, and it is unrealistic to expect them to work as volunteer field assistants in addition to their full-time jobs.

The assistance of passengers is worth pursuing, but this would necessitate a cost-benefit analysis to achieve a time balance between collecting data and training observers. In a study using non-specialist volunteer divers to assist research on coral reef fishes, Darwall and Dulvy (1996) found that two weeks of training were sufficient to train observers until their ability to identify most species of reef fish and to measure their size reached that of an experienced researcher. It is likely that the 7-10 day trips to the Antarctic will not allow training and data collection to occur simultaneously. Researchers proposing to use these platforms in the Antarctic, the Amazon and the Arctic, for example, should focus on acquiring sufficient cabin space to house a team of experienced observers if their study requires more than one observer.

6.7 Effects of human disturbance on cetaceans

Chapters 4 and 5 illustrated cases where a resource dedicated primarily to mitigating negative impact of human activity on killer whales (a boat-based warden program) also provided logistical support to assessing the nature and magnitude of that impact. Chapter 4 considered a very specific activity about which community members were concerned. By agreeing to stay away from focal animals during the study, commercial whalewatchers made a controlled experiment possible.

One unanticipated side effect of working with an on-the-water environmental education project was that the wardens became spokespeople for the project, and for research in general. By sharing information about the research with the public, the scientists received logistical support, and much-needed cooperation from whalewatch operators. The wardens felt that they received better compliance with whalewatching guidelines from boaters because people knew the conservation rationale behind the guidelines. By working with environmental educators, the results of the study were disseminated quickly to the boaters most likely to encounter whales. The partnership worked. Shortly after the results were released, a local whalewatch operators association (http://www.nwwhalewatchers.org/) agreed not to operate their vessels at top speed within ¼ mile (c. 400m) of whales. This small but tangible link between research and conservation is rare and reassuring in a field in which the results of applied research are not always applied (Stinchcombe *et al*., 2002).

6.8 Resource requirements of killer whales

Chapter 5 made use of a government agency's desire to monitor which of the resident killer whales were using a protected area annually, and how boaters respected the Reserve boundaries. By converting the 'cost' of vessel traffic to whales to units of

fish, people can intuitively see what is meant, in a way that proxies such as directness index and swim speed (Chapter 4) do not permit. By demonstrating numerically that Robson Bight matters to whales, the results provide an objective rationale for protecting small fractions of the area that the whales use. The results provide objective evidence that the Reserve is a better candidate for protection than adjacent waters (Duffus and Dearden, 1993), because the whales used Robson Bight disproportionately often and for activities that were rarely seen elsewhere. The results provide a framework that would allow decision-makers to model the effects on whales of different management strategies (Butterworth and Punt, 1999): time-area closures of the area to fishing or whalewatching.

Expansion of this work could provide point estimates of the salmon 'quota' that resident killer whales require (Ford *et al*., 1998). Salmon play a keystone role in the coastal regions of the northeast Pacific (Willson and Halupka, 1995). In addition to feeding cetaceans and pinnipeds, among other consumers in the marine environment, salmon transfer nutrients throughout the ecosystem in their estuary and freshwater life-history stages. Their lipid content, up to twice that of other fish prey species, makes them a valuable resource to predators and scavengers (Willson and Halupka, 1995). All told, salmon have been documented as prey items for 137 species of vertebrates alone (Cederholm *et al*., 2000). While in the rivers, salmon are preyed upon by wolf, mink, eagle, grizzly and black bears among other species (Willson and Halupka, 1995; Ben-David *et al*., 1998; Reimchen, 2000; Cederholm *et al*., 2000). Carnivores transfer marine-derived nutrients to nearby vegetation by dragging salmon carcasses into the forest, and by defecating there. This closes a feedback loop in which healthy

vegetation shades salmon spawning habitat, and in turn increases fish survival (Ben-David *et al.*, 1998; Reimchen, 2000).

Fisheries pressure on Pacific salmon has been estimated at more than 10 times the exploitation rates of all non-human predators put together (Fowler *et al.*, 1999). At present, this ecosystem demand for salmon is subsumed in fisheries management by a point estimate of natural mortality. Some would like to see the nutritional demands of marine predators incorporated explicitly into fisheries management (Read and Brownstein, 2003). Such ecosystem approaches to fisheries management (Larkin, 1996) will benefit from the kind of information collected in this thesis. Information on abundance, distribution and nutritional demand of marine mammals will play an important role if resource managers want to allocate fisheries quotas spatially and temporally in such a way that they do not affect the fitness of marine mammal populations (Boyd, 2002). The results of allocating different proportions of salmon to commercial fishermen, sport fishing and wildlife could be predicted (Bradbury *et al.*, 2001), and the outcomes monitored to test performance of the predictive models (Butterworth and Punt, 1999).

6.9 Future work
It is hoped that this thesis demonstrates that for some studies, a data collection platform can be opportunistic while the data collection is not. It is important conceptually to separate working with opportunistic sightings data of unknown quality, from seeing how dedicated research projects could be merged with unrelated ventures that happen to require spending time in cetacean habitat. In the coming years, the platforms must take on a variety of forms. Some will continue look like ferries, other people's oceanographic research cruises, or other people's holidays, but

others will take on a form that no one has yet considered. If ways exist to get necessary information by studying animals using unlikely platforms, then it is important to pursue those options creatively and rigorously. Some of the most endangered animals live in countries with the least funding for conservation work. And even in developed countries, wildlife tends to be found in wilderness. The more that scientists can access remote and pristine areas inexpensively, the more likely we are to acquire the information we need to prioritise conservation strategies.

The link between conservation biology, as an academic discipline, and conservation, as action, can be tenuous (Stinchcombe *et al*., 2002). Prioritising conservation issues must involve input from scientists. One recommendation from scientists could be that if demographic data used to set conservation priorities are too costly to obtain, then ecological criteria should be established to assist the process (Harcourt, 1996). In some cases, priorities for protecting species is linked directly to the species' status as determined by the International Union for the Conservation of Nature (IUCN), for example, even though IUCN lists were never designed for that purpose (Possingham *et al*., 2002). Worse, this approach could be counterproductive, because protecting some species will require a great deal of money for a small chance at success while others can be protected for relatively little cost. Harcourt's (1996) suggestion that ecological information be used to inform the conservation priority setting process is wise. It would allow incorporation of what we know to be life-history attributes that make some animals more vulnerable to extinction than others (Ehrenfeld, 1970). Ultimately, it would allow conservation biologists to make reasonable inferences in the absence of information on trends and abundance. In the meantime, we should continue to make

progress on the ability to provide information on trends and abundance as inexpensively as possible.

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