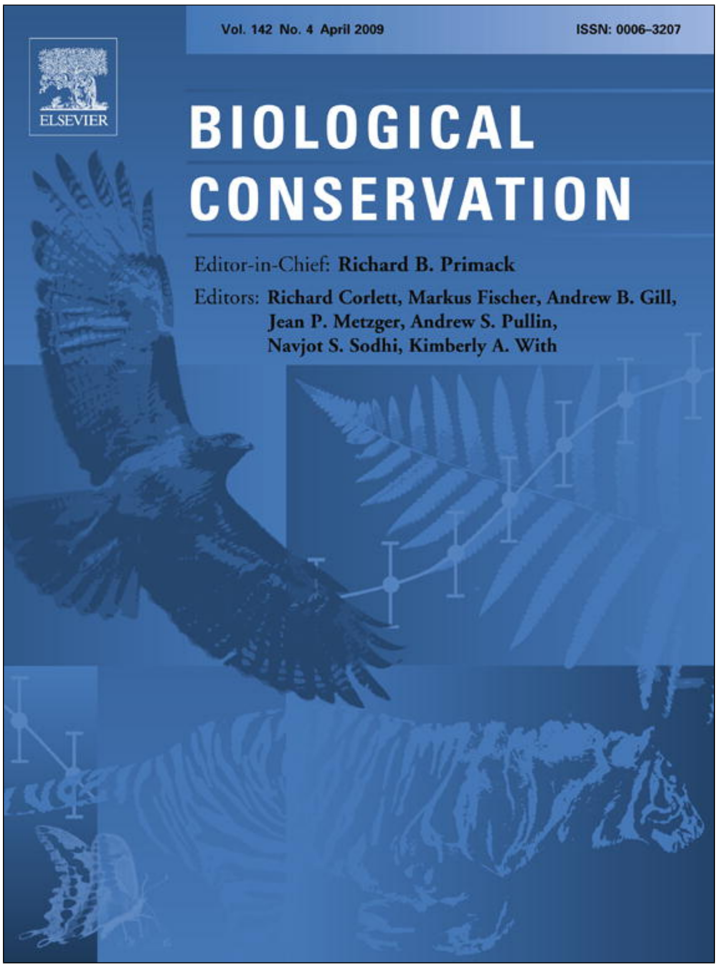

Vol. 142 No. 4 April 2009
ISSN: 0006-3207
ELSEVIER
BIOLOGICAL CONSERVATION
Editor-in-Chief: Richard B. Primack
Editors: Richard Corlett, Markus Fischer, Andrew B. Gill, Jean P. Metzger, Andrew S. Pullin, Navjot S. Sodhi, Kimberly A. With

BIOLOGICAL CONSERVATION 142 (2009) 709–719

available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/biocon

The role of social aggregations and protected areas in killer whale conservation: The mixed blessing of critical habitat

Rob Williams[a,b,*], David Lusseau[c], Philip S. Hammond[a]

[a]Sea Mammal Research Unit, Gatty Marine Laboratory, University of St. Andrews, St. Andrews, Fife KY16 8LB, Scotland, UK
[b]Marine Mammal Research Unit, Aquatic Ecosystems Research Laboratory, Room 247, 2202 Main Mall, University of British Columbia, Vancouver, BC, Canada V6T 1Z4
[c]University of Aberdeen, Institute of Biological and Environmental Sciences, Tillydrone Avenue, Aberdeen AB24 2TZ, UK

ARTICLE INFO

Article history:
Received 12 March 2008
Received in revised form
26 November 2008
Accepted 4 December 2008
Available online 23 January 2009

Keywords:
Cetacean
Extinction
Marine mammal
Marine protected area
Oil spill
Reserve
Sociality

ABSTRACT

Protected areas are often proposed as tools for conserving endangered populations of marine megafauna. Our study area includes a voluntary no-entry reserve embedded within wider critical habitat for Threatened 'northern resident' killer whales under Canada's Species at Risk Act. Our study quantified the reserve's importance to whales by assessing habitat preference in a behavioural context, and population-level implications of that preference given threats from human activities, such as oil spills resulting from shipping traffic. We recorded summertime activities of whales from 1995 to 2002. Whales were observed on 397 of 530 (74.9%) days. Whales showed strong preference for the reserve over adjacent waters, and used it preferentially for feeding and beach-rubbing. While the area comprises ∼0.001% of the whales' range, an overall average of 6.5% of the population was present each day. Frequently, >50% of this small population was aggregated in the restricted and heavily trafficked waterway of Johnstone Strait. Using the Potential Biological Removal equation, we calculated potential annual mortality limits (ML) of 2.2 animals. Mean group size in the area exceeded ML on 55.8% of days overall, and 98.8% of days when conditioning on whale presence. The whales' high reliance on a trivial fraction of their range means that opportunities are routine for one stochastic, catastrophic event to cause population decline. On 20 August 2007, a barge loaded with ∼10,000 L of diesel sank in the area, exposing 25% of the population. This underscores the importance of identifying critical habitat for threatened populations, and ensuring meaningful protection.

> *"Hemmed-in ground – Ground which is reached through narrow gorges, and from which we can only retire by tortuous paths, so that a small number of the enemy would suffice to crush a large body of our men: this is hemmed-in ground."*
>
> Sun Tzu – *The Art of War*

1. Introduction

Anthropogenic activities are commonly identified as conservation threats to top predators, and a mitigation measure often proposed is the use of protected areas. In the terrestrial realm, protected areas have been used to mitigate effects of human activities on mammals such as grizzly bears (Noss et al., 1996), African dogs (Woodroffe and Ginsburg, 1999),

---

[*] *Corresponding author:* Address: Sea Mammal Research Unit, Gatty Marine Laboratory, University of St. Andrews, St. Andrews, Fife KY16 8LB, Scotland, UK.

E-mail addresses: r.williams@fisheries.ubc.ca (R. Williams), pearseisland@hotmail.com (R. Williams).

0006-3207/$ - see front matter
doi:10.1016/j.biocon.2008.12.004

and Eurasian badgers (Revilla et al., 2001). Protected areas have been found also to provide crucial nocturnal feeding habitat for dabbling ducks (Guillemain et al., 2002) and wintering grounds for many duck species in France (Duncan et al., 1999). However, protected areas take on a wide range of meanings in marine management (Reeves, 2000; Hoyt, 2005). Marine protected areas (MPAs) aim to protect habitat that encompasses the whole species (or other management unit) or important habitats that are frequented by the management unit in question. Sometimes, protecting small patches of habitat is the only feasible socioeconomic option open to managers working in either the terrestrial or marine realm (Fischer and Lindenmayer, 2002), but providing effective habitat protection for highly mobile marine predators is fraught with difficulty (Wilson et al., 2004).

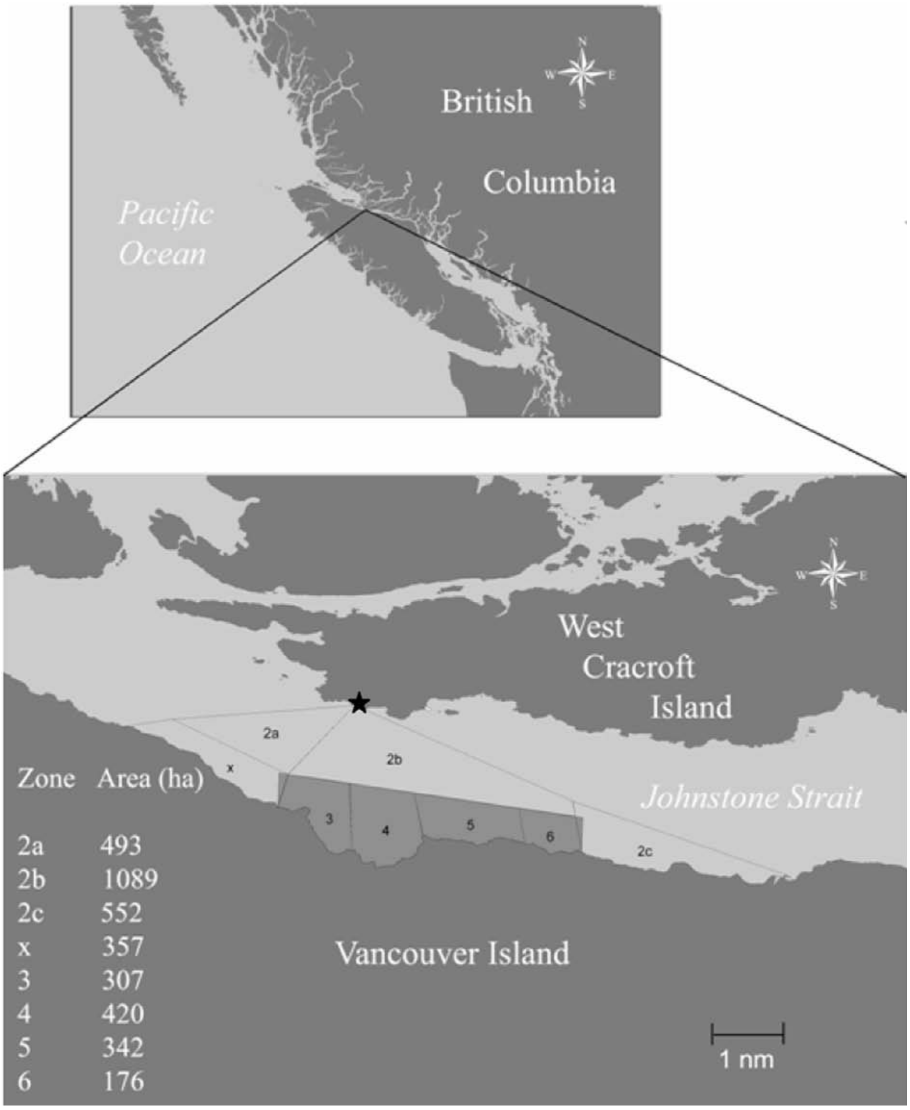
Much attention has been paid in recent years to desirable attributes of protected areas for marine megafaunal conservation (Hooker et al., 1999; Hooker and Gerber, 2004; Hoyt, 2005; Reeves, 2000; Wilson et al., 2004). It has been argued that protected areas should be designed also to protect ecosystem components that are “original” in the sense that they perform unique functions in their ecosystems (Mouillot et al., 2008). Top predators such as killer whales may satisfy such a criterion as biological originality. There are benefits to identifying and protecting habitat in which prey densities are high, so that marine reserves can satisfy nutritional needs of target species (Hooker et al., 1999). Alternatively, protected areas can be designed to protect large fractions of the population. The latter objective is frequently criticised as implausible, given the high rates of dispersal of highly mobile predators (Gerber et al., 2005). However, there are cases where large fractions of small populations may aggregate temporarily; we believe that protected-area management can play a useful role in protecting vulnerable populations from anthropogenic activities during these periods of assembly. Ehrenfeld (1970) compiled a now-classic list of attributes of a hypothetical composite, “most endangered animal.” Marine megafauna possess many of these traits, but one that has received little attention is a propensity to breed or feed in aggregations, which make populations vulnerable to catastrophic events.

Marine conservation biologists recognise the role of clustered distribution and clustered removals of wildlife in the context of fishing pressure on spawning aggregations of coral reef fishes. Some tropical reef fish stocks have been lost entirely because unsustainable fishing targets the spawning aggregations themselves (Sadovy and Domeier, 2005). On a much larger scale, international management and conservation efforts for southern bluefin tuna have been complicated by the fact that this widely dispersed predator appears to comprise a single spawning stock (Grewe et al., 1997). While the phenomenon is recognised for harvested species, we see similar potential for highly concentrated aggregations of non-harvested marine megafauna to be exposed to elevated levels of extinction risk due to anthropogenic catastrophes. Many marine megafauna associate in such a way that large fractions of populations are aggregated (at least temporarily) in relatively small places. Seasonal aggregations bring together hundreds of whale sharks each year at Ningaloo Reef, Western Australia (Colman, 1997). The Gulf of California provides breeding habitat for 70–98% of the global populations of six seabird species (Tershy et al., 1993). The upper Gulf of California is also home to one of the world’s most critically endangered odontocete species, the vaquita. This endemic species numbers only hundreds of individuals, and the majority of those tend to be found within a small core area of the species’ range (Jaramillo-Legorreta et al., 1999). The western gray whale is critically endangered, and its feeding grounds off Sakhalin Island overlap with an area of intense offshore oil and gas production (Weller et al., 2002).

In migratory baleen whales, life-history processes like feeding, mating and calving may take place in widely separated but well-defined areas that lend themselves amenable to protected-areas management strategies (Hooker and Gerber, 2004). For odontocetes, these life-history processes may occur in the same habitats, which may not always be easily defined. Odontocete social structure may involve a propensity for large fractions of populations to congregate occasionally in one area. The 1989 *Exxon Valdez* oil spill is estimated to have caused losses of 33% and 41%, respectively, to two groups of killer whales that have yet to recover to pre-spill numbers (Matkin et al., 2008).

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 *offshores*; and northern and southern communities of fish-eating *resident* killer whales. ‘Northern resident’ killer whales (NRKW) are individually recognisable, and their population size ranged between 201 and 220 animals during the course of our study (Fisheries and Oceans Canada, 2008). A core NRKW area is found in Johnstone and Queen Charlotte Straits and this area has been proposed as critical habitat for this population (Fig. 1; Fisheries and Oceans Canada, 2008). The NRKW recovery strategy does not define what is meant by the term “critical habitat” in this context. It draws from the generic definition of the term under Canada’s Species at Risk Act, which defines critical habitat, somewhat circularly, as “the habitat that is necessary for the survival or recovery of a listed wildlife species and that is identified as the species’ critical habitat in the recovery strategy or in an action plan for the species” (Species at Risk Act, 2003). The theme of critical habitat as it pertains to cetaceans has been explored at length in reviews (Reeves, 2000; Hoyt, 2005), and we do not aim to duplicate that review here. Our point is not to support the claim that Johnstone Strait should be designated as critical habitat for these whales, but simply to note that the region’s importance to whales has been recognised formally (Fisheries and Oceans Canada, 2008).

The NRKW community comprises ~35 matrilines (Ellis et al., 2007) or natal groups, many of which return to the area each summer to feed, mate, and rub their bodies on smooth pebble beaches. Narrow Johnstone Strait tends to concentrate migratory salmon, and inter-annual variability in chinook salmon abundance influences whale grouping behaviour (Lusseau et al., 2004). A number of vessel types also use the area heavily. Intensity of cargo and bulk carrier vessel movements in narrow Johnstone Strait is one to three orders of magnitude higher than that in less constricted waters of the BC coast (O’Hara and Morgan, 2006). Robson Bight (Michael Bigg) Ecological Reserve (RBMBER; Fig. 1) was recognised as a NRKW sanctuary by the provincial government of BC in 1982. Our study area includes both the reserve, and an area in John-



Zone	Area (ha)
2a	493
2b	1089
2c	552
x	357
3	307
4	420
5	342
6	176

Fig. 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 abbreviation "nm" in the scale bar relates to 1 nautical mile (1852 m).

stone Strait immediately adjacent to the reserve (Fig. 1). The reserve was intended to prevent boaters from approaching two gravel beaches on which the whales are known to rub. The functional role of this behaviour is unknown, but may have to do with parasite removal or play some social role (Ford et al., 2000); beach-rubbing is rarely seen in other cetaceans. The gravel beaches themselves have been the subject of some geological study, which revealed only subtle differences in sediment composition, slope and orientation between the main rubbing beach and adjacent beaches (Harper, 1995). While many gravel beaches in the study area share common characteristics, namely well-sorted pebble beaches with uniform slope, only the main rubbing beach is free of boulders below the low tide line (Harper, 1995).

In contrast, few studies have quantified for which activities in particular resident killer whales use available habitat. Clearly, western Johnstone Strait is known to be important to killer whales (Fisheries and Oceans Canada, 2008), but few metrics exist to quantify how integral it is, for what fraction of the population, and for what activities. Fisheries and Oceans Canada (DFO) has jurisdiction over marine affairs in Canada, and it permits commercial fishing activities within RBMBER. 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 (the rubbing beaches and seabed), but can only request that boaters voluntarily comply with their no-entry policy in the marine component. BC Parks makes requests for voluntary compliance strongly in the form of an on-the-water warden service, but the boundaries of the reserve remain "highly permeable" (Duffus and Dearden, 1992).

The need to quantify the importance of the habitat to whales has taken on urgency in recent years in light of a proposal to build an oil pipeline from the Alberta tarsands to BC's north coast. Depending on which refineries and markets become the ultimate destinations for the oil, some traffic scenarios would result in associated oil tanker traffic being transported through Johnstone Strait (Fisheries and Oceans Canada, 2007). One way to identify spatial variability in habitat use (a precursor to identifying habitat preference) is to assess spatial variability in animal density. A recent systematic line transect survey (Williams and Thomas, 2007) provided a point estimate for density of northern resident killer whales in Johnstone Strait (0.273 animals/km^2) that was 41 times that of BC coastal waters as a whole (0.00661 animals/km^2). Given the patchy nature of killer whale distribution and the snapshot nature of line transect surveys, such an effect could have been atypical, but it fits with expectations: after all, the whale-watching businesses that target northern resident killer whales are based near Johnstone Strait. Here we analyse data collected during eight summers to quantify the importance of the study area to the population. The primary goal of our study is to estimate the average number of killer whales that use Johnstone Strait to assess the vulnerability to oil spills of this small Threatened population. A secondary goal was to assess how animals used the area, by testing whether killer whales showed fine-scale preference for RBMBER over adjacent habitat, and to compare activity budgets inside and outside the reserve. We hypothesised that fine-scale differences may exist in habitat use, because the reserve was designed to protect only two of the many gravel rubbing beaches in the area (Harper, 1995). Finally, we used objectives outlined under the US Marine Mammal Protection Act to estimate potential limits to annual anthropogenic mortality in this population (Wade, 1998; Berggren et al., 2002). We then estimated the likelihood that number of whales would be found in the study area on any given day, thereby exposing the population to high levels of risk if an oil spill were to occur.

2. Methods

2.1. *Data collection on number and identity of whales using the study area*

Data were collected from a cliff (Fig. 1) that offered an expansive view of RBMBER and adjacent waters. The study area was divided into eight zones; four inside the reserve, and four immediately adjacent to it. Zones were readily identifiable from the cliff based on sightlines drawn to prominent landmarks. Field seasons varied in length among years, but sampling occurred at least 1 July–31 August in all 8 years (1995–2002). Three observers scanned the area every 15 min from 08 h00 to 20 h00 daily with 7 × 50 binoculars and/or a 25 × 50 spotting scope. Whalewatchers and other researchers cued observers as whales approached the study area, so whales spent relatively little time in the study area unobserved. Once whales entered the study area, observers used both visual and underwater acoustic cues (Ford, 1989) from a shore-based hydrophone system to identify individuals and matrilines. The term matriline is used when indicating relatedness (Ford et al., 1994, 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. The identity of individuals was determined by comparing natural markings to published photo-identification catalogues (Ford et al., 1994, 2000; Ellis et al., 2007). Whale identity could not always be determined, so unidentified whales were given a temporary designation and monitored such that the activities of that group could be followed.

2.2. *Data collection on whale activities inside and outside the reserve*

The predominant activity state of whale groups was recorded at each 15-min scan sample. The definitions of these states were adapted from those used in other behaviour and energetics studies for this species (Felleman et al., 1991; Ford et al., 2000; Williams et al., 2006). The five categories (resting, beach-rubbing, travelling/foraging, feeding, and socialising) used to record activity state were defined structurally so that states were mutually exclusive and cumulatively defined the entire activity budget. Each of the five activity states is defined as follows and correspond to those used in previous studies (Williams et al., 2006):

2.2.1. *Rest*

Whales were swimming at slow speed with predictable sequences of several short (30 s) dives followed by a long dive of 3–5 min. This activity state was characterised by the absence of surface-active behaviour (e.g., breaching or tail-slapping).

2.2.2. *Travel/Forage*

Whales surfaced and dove independently but all whales in the group were heading in the same general (e.g., 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.

2.2.3. *Feed*

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 surfacing in the form of frequent directional changes.

2.2.4. *Socialise*

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.

2.2.5. *Beach rub*

Whale presence within 50 m 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.

2.3. *Constructing Markov chains and activity budgets from scan-sample data*

Group focal follows, reconstructed from scan samples, were used to estimate the transition probability matrix that whale groups observed in activity state *i* at one scan sample and were subsequently in state *j*. This defined a first-order time discrete Markov chain (Caswell, 2001; Lusseau, 2003). If group composition changed between scans, then that marked the beginning of a new chain. Markov-chain modelling has proven to be a useful way to detect effects of anthropogenic activity on cetacean behaviour in several studies (Lusseau, 2003; Williams et al., 2006). Here, we assessed the influence of location on these transition probabilities by comparing transition matrices constructed from samples in which whales were either inside or outside the reserve. Boats can affect these transition probabilities, but this effect has been described previously (Williams et al., 2006), and is mentioned just to note that we accounted for this confounding effect in the analyses and held it statistically constant. Subsequent discussions therefore refer to the partial contribution of the location effect on whale activities. Contingency tables were constructed with the following categories: preceding activity (five states, factor labelled **P** in Table 1), succeeding activity (five states, labelled **S**), 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 presence (independent covariates) was tested using general log-linear analysis. The response variable was the observed frequency of one state following another. We tested for the influence of location in two ways. First, we added the location effect to a null model that only assumed the dependence of succeeding behaviour on preceding behaviour (included terms **PS** and **PBL**, Table 1). The location effect was tested by adding the dependence of **S** on each of these factors (by adding the terms **LS** and **LPS**). Significance of the difference in explanatory power (G^2) was tested between the two models (Caswell, 2001; Table 1). The best fitting model was selected using Akaike's Information Criterion (AIC; Akaike, 1973), which carries a penalty for adding 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. We also tested whether the location effect still influenced transition probabilities after the boat effect was taken into consideration. We therefore carried out the same analysis as above but starting with a null model including a boat effect (**BPS, PBL**, Table 1).

The stationary distribution of each transition probability matrix (the activity budget given the independent variable considered) corresponded to the left eigenvector of the dominant eigenvalue of the matrix (Caswell, 2001; Lusseau, 2003). Activity budgets were calculated both for inside and outside the reserve.

2.4. *Estimating potential limits to anthropogenic mortality*

The fact that every individual in this population is known (Ellis et al., 2007) allows group size to be converted to proportions of the population. The data on absolute abundance also facilitates assessment of allowable limits to anthropogenic mortality using the Potential Biological Removal (PBR) equation defined under the US Marine Mammal Protection Act (Wade, 1998). This quantitative approach has modest data requirements to estimate annual mortality limits (ML), and has been widely used to evaluate whether anthropogenic impacts exceed levels that would negatively impact marine mammal stocks according to well-defined management objectives (Berggren et al., 2002). While Canada does not apply a generic formula to calculate mortality limits in every marine mammal stock, the PBR approach has been used to assess sustainability of takes in the Canadian harp seal hunt (Johnston et al., 2000) and bycatch of small cetaceans in BC gillnet fisheries (Williams et al., 2008).

We calculated what the potential limits to mortality would be for this population if we adopted default values for the PBR calculation (Wade, 1998; Wade and Angliss 1997). PBR is calculated from a minimum population estimate (the complete count in this case), one-half the maximum theoretical net productivity rate (R_{MAX}), and a recovery factor (FR):

$$\mathrm{PBR} = N_{\mathrm{MIN}} \times 0.5R_{\mathrm{MAX}} \times \mathrm{FR} \qquad (1)$$

The default value used for the recovery factor for cetacean stocks of unknown status is 0.5, which is conservative (Wade and Angliss, 1997). While R_{MAX} is rarely known for cetacean populations and is often assumed to be 4% (Wade, 1998), a rate of increase has been measured for resident killer whale populations at very low population size (Olesiuk et al., 1990).

Table 1 – Results of the log-linear analyses. P: preceding behaviour, S: succeeding behaviour, B: boat presence, L: location. The null model assumed that succeeding behaviour was independent of boat and location effects, given preceding behaviour, as defined by a first-order Markov chain. Regardless of whether we added the location effect to the null model or after controlling for the boat effect (model BPS, PBL), the location effect provided significant improvement to the explanatory power of the log-linear model.

Model	Component added	ΔG^2, df, *p*-value	AIC	ΔAIC
Null (PS, PBL)			348.3	388.3
	LS,LPS	428.3, 20, <0.0001		
Location effect (LPS, PBL)			−40	0
Boat effect (BPS, PBL)			224.3	257.1
	LS,LPS	297.1, 20, <0.0001		
Boat + location (BPS, LPS, PBL)			−32.8	7.2
	BLS,BLPS	7.2, 20, >0.9		
Boat × location (BLPS)			0	40

As the populations recovered, their maximum rate of population increase observed was 2.92% (Olesiuk et al., 1990), and we use this as an approximation of R_{MAX}. Given the maximum size (220 individuals; Ellis et al., 2007) of the NRKW population observed during our study, PBR for the northern resident killer whale stock is 1.6 animals ($=220 \times (0.5 \times 0.0292) \times 0.5$). PBR would be slightly higher if 2.92% were not used as the intrinsic rate of natural increase (because populations were not brought sufficiently below carrying capacity, for example). Recalculating PBR with default $R_{MAX} = 4\%$ increases PBR to 2.2 individuals.

3. Results

This study synthesises observations from eight seasons, during 530 days (Table 2) of search effort. Activity budgets were calculated from data collected during 496 days (5952 h) of field effort during which weather conditions were good, including 2000 h observing killer whales. After censoring (to remove cases where group identity was ambiguous, or where chain length was only one scan), 7517 transitions of focal groups or individuals from one activity state to another were observed.

3.1. *Killer whale habitat use, aggregations and PBR implications*

Whales were present between 50% (in 1999) and 88% (in 1998 and 2002) of days in the study (Table 2). When present, 10–20 animals tended to be in the study area (the smallest and largest mean values observed during each of the eight years of the study), which corresponds to 5–9% of the population in any given year (Table 2). Recall that each individual in the population is known from annual censuses and photo-identification catalogues (Ellis et al., 2007), so we are confident that we were counting unique individuals. Thus, the study area was routinely occupied by substantial fractions of the population, with the maximum proportion of the population ever observed in the area on a given day ranging from 17% in 1997 to 67% in 2000.

Regardless of which value (2.92% or 4%) is used for R_{MAX}, and consequently which PBR value was the more reasonable (1.6 or 2.2 animals per year), mortality limits calculated under any scenario will be low for such a small population. Mean group size exceeded ML (that is, three or more animals were present) on 55.8% of days overall, and 98.8% of days when conditioning on presence. Mean number of animals using the study area on any given day during the 8-year study was 17 individuals, including days when whales were absent and 22.4 individuals when restricting analyses to days on which whales used the study area.

The number of matrilines using the study area on any given day (Table 3) ranged from 1 (the minimum in all years) to 20 (the maximum ever observed, in 2002) of the 35 matrilines in the population. The mean number of matrilines using the area on a given day ranged from 2.6 (in 1997) to 5.8 (in 2001) of the 35 NRKW matrilines (Table 3).

While members of all three acoustic clans (Ford, 1989) used the area in most years, the study area was used overwhelmingly more often by members of the A clan (Ford, 1989) than by whales belonging to G or R clans (Table 4). In each year, the matriline using the area most often was an A-clan matriline (Table 4), alternating between the A12 matriline (in most years: 1995, 1996, 1997, 1998 and 2002) and the A8 matriline (in 1999, 2000, and 2001). No R-clan whales were observed in the study area in 1997 or 1999.

3.2. *Effect of location on activity budgets*

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. Whales spent significantly more time in the reserve than one would expect by chance, after accounting for the different sizes of the areas inside and outside the reserve (Fig. 1: outside the reserve 2491 ha, reserve 1245 ha; 48% versus 33% by chance (1245/(1245 + 2491)). Put another way, whales spent 45% more time in the reserve than one would expect by whales using the two areas (inside versus outside the reserve) in proportion to their sizes (proportion test: $Z = 18.25$, $p < 0.0001$).

There was no support for the inclusion of an interaction term between location and boat effects in the log-linear model (Table 1). Hence, boat interactions had the same effect on whale behaviour inside and outside the reserve. Activity budgets were significantly different inside versus outside the reserve, regardless of whether we accounted for the boat effect (Table 1, Fig. 2). Beach-rubbing 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. Beach-rubbing observed only twice (0.04% of 3770 tran-

Table 2 – Summary of observer effort and daily usage of the study area by individual whales.

Year	Days surveyed	Days whales present	% Days whales present	Pop. size	Mean % whales present	Max % whales present
1995	61	50	82.0%	205	5.2%	22.0%
1996	62	43	69.4%	212	5.1%	28.3%
1997	62	44	71.0%	220	4.1%	16.8%
1998	60	53	88.3%	216	6.9%	43.1%
1999	60	30	50.0%	216	4.6%	19.4%
2000	73	55	75.3%	209	8.6%	67.0%
2001	77	56	72.7%	201	9.4%	45.8%
2002	75	66	88.0%	202	8.3%	55.0%

Table 3 – Summary of daily matriline usage of the study area. Note that the population included a total of 35 matrilines throughout the study.

Year	Min # matrilines present	Mean # matrilines present	Max % of matrilines present
1995	1	3.5	34.3%
1996	1	4.0	25.7%
1997	1	2.6	22.9%
1998	1	4.1	25.7%
1999	1	3.0	20.0%
2000	1	4.7	34.3%
2001	1	5.8	40.0%
2002	1	5.2	57.1%

sitions) when whales were near the similar beaches outside the reserve. Put another way, beach-rubbing was 585 times as common on the two beaches designated for protection than the nearly identical (Harper, 1995) gravel beaches just outside the reserve.

Feeding activity was observed inside the reserve (13.1%) 1.5 times as often as outside (8.7%). Conversely, whales were observed engaging in rest, travel/forage or social activity less frequently inside the reserve than outside (Fig. 2).

Whales were significantly less likely to enter the reserve and more likely to leave the reserve if boats were in the same quadrat as the focal animals (Fig. 3).

4. Discussion

The efficacy of protected-area management in marine megafaunal conservation will depend on drawing spatially and temporally appropriate boundaries around mobile predators, and monitoring whether management actions achieved the desired effects (Hooker and Gerber, 2004; Wilson et al., 2004). To the extent to which the goals of RBMBER are modest, namely to protect two gravel beaches and to set aside an area for killer whale research, the management action has achieved its desired effect (Duffus and Dearden, 1992). The gravel beaches outside the reserve's boundaries were used negligibly by whales. Whitehead et al. (2004) note that rare behaviours such as beach-rubbing can constitute cultural traits of evolutionarily significant units that should be taken into account in conservation planning for non-human ani-

Table 4 – Summary of matriline-specific use of the study area. Matrilines in bold were present during the 20 August 2007 diesel spill.

Clan	Matriline	1995	1996	1997	1998	1999	2000	2001	2002	Total days
A	A12	26	24	24	40	14	30	35	39	232
A	**A8**	11	15	12	29	15	33	37	17	169
A	**A30**	22	25	21	8	2	30	15	32	155
A	**A25**	8	20	2	25	7	25	34	20	141
A	**A11**	17	10	2	17	14	32	24	22	138
A	**A24**	15	9	2	16	15	25	28	24	134
A	A36	17	22	15	7	4	16	19	14	114
A	**A23**	9	17	16	3	0	12	25	16	98
G	**I15**	15	19	7	13	0	13	11	12	90
A	C10	12	0	2	17	12	14	13	16	86
G	**I31**	2	0	3	0	0	3	19	21	48
A	C6	1	0	3	7	1	0	13	6	31
A	B7	4	2	1	5	1	8	3	4	28
R	R2	6	1	0	3	0	7	4	2	23
G	G3	3	0	1	0	0	3	0	12	19
G	I11	1	0	2	1	0	0	8	7	19
R	R7	4	3	0	2	0	4	2	4	19
G	G29	0	0	0	4	0	0	2	8	14
R	W3	2	1	0	0	0	2	3	6	14
G	G17	1	0	0	0	0	0	3	8	12
A	D11	1	0	0	2	0	0	0	7	10
R	R5	0	0	0	0	0	1	4	5	10
A	I22	0	0	0	0	0	0	4	5	9
A	D7	1	0	1	0	0	0	0	6	8
G	G2	1	0	0	1	0	0	1	5	8
G	G31	0	0	1	0	0	0	0	6	7
A	I17	0	0	0	0	0	0	3	1	4
A	I18	0	0	0	0	0	0	3	1	4
G	G27	0	0	0	0	0	0	1	3	4
G	G4	0	0	0	0	0	0	1	3	4
A	H5	0	0	0	0	0	0	2	1	3
A	H3	0	0	0	0	0	0	2	0	2
A	I1	0	0	0	0	0	0	2	0	2
G	G16	0	0	1	0	0	0	1	0	2
G	G8	0	0	0	1	0	0	0	0	1
R	R17	0	0	0	0	0	1	0	0	1

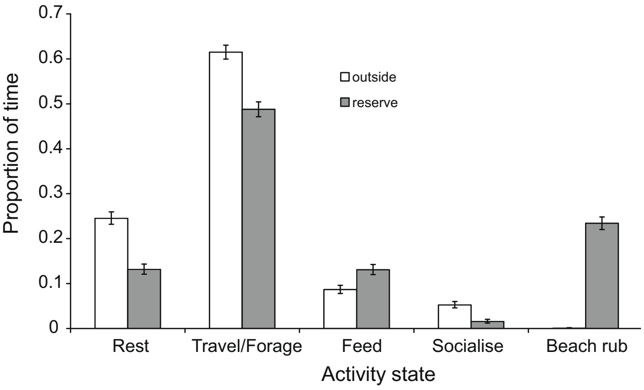


Fig. 2 – Activity budget of killer whales inside and outside the reserve. Bars represent 95% confidence intervals. All differences are significant at the conventional level ($p < 0.05$).

mals. Notwithstanding this behaviourally interesting result, the most important finding of this exercise is that the objectives of the reserve are simply too modest. The effectiveness of the reserve for protecting a rare behavioural or cultural trait (beach-rubbing) seems trivial compared to the demonstrated importance of this habitat to the population, both in terms of the proportion of the population found there, and the tendency for animals to spend more time feeding in the reserve than outside. The mandate of the reserve must be expanded in light of this new information on how extensively it is used by this population, which may be food-limited (Fisheries and Oceans Canada, 2008).

Here we show that a substantial fraction of the Threatened NRKW population was present routinely in summer months in a spatially trivial fraction of its range across 8 years. We can quantify this importance in two ways. A recent survey, during which a much greater portion of the NRKW range was assessed, generated a density estimate for killer whales in Johnstone Strait that was 41 times that of BC coastal waters as a whole (Williams and Thomas, 2007). In the present study, an average of 6.5% of the population was found to use the study area on a typical summer day (Table 2), even though the study area comprises only ~0.001% of the NRKW range (Fisheries and Oceans Canada, 2008). At the time of greatest concentration during our study, 67% of the population was found to have visited the area on one day, which makes this population highly vulnerable to extinction due to stochastic, catastrophic events.

This extent to which the population clusters in a confined area needs to be incorporated into oil spill preparedness and response plans. As a rough rule of thumb, biologists are urged to pay close attention to situations in which cetacean bycatch approaches or exceeds 1% of population size (International Whaling Commission, 1996) equivalent to approximately two individuals in this population. Coincidentally, the default values to reach management objectives defined by the US Marine Mammal Protection Act would also set similar, very low potential annual limits to anthropogenic mortality (2.2 individuals). While neither of these values reflects a management objective of the Government of Canada, any quantitative procedure for setting potential limits to anthropogenic mortality for such a small, slowly reproducing and Threatened population will yield very low numbers. Our key finding is that the distribution of group sizes we observed suggests that opportunities are commonplace to exceed potential mortality limits with one stochastic, catastrophic event. The loss of any one cluster of whales would exceed thresholds that the population could sustain.

In addition to being important to whales, the study area is also heavily used by humans. The fact that intensity of movements of large ships in Johnstone Strait is among the highest observed anywhere in the whales' range (O'Hara and Morgan, 2006) suggests that this area warrants closer inspection to assess and mitigate other conservation threats associated with shipping, such as ship strikes, chronic exposure to oil, and acoustic habitat degradation from shipping noise. Thus, this habitat, which constitutes an essential area for the daily routine of a large portion of the population, offers the whales a mixed blessing of sorts. By virtue of being the narrowest point on the Inside Passage, salmon are bottlenecked in Johnstone Strait and killer whales aggregate to exploit that feature, but the process of aggregation lends large proportions of the population vulnerable to catastrophe or disease transfer. In an analogous trade-off, Barrett-Lennard et al. (1996) note that echolocation also serves as a mixed blessing for the 'tran-

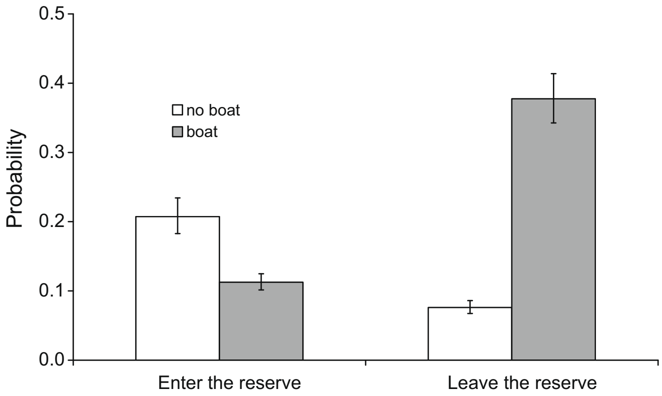


Fig. 3 – Probability that whales will enter or leave the reserve depending on whether boats are present in their vicinity. Error bars are 95% confidence intervals.

sient' killer whales, whereby the whales' use of sonar during foraging activities can alert mammalian prey to the predators' presence. For the resident, fish-eating whales observed in this study, Robson Bight appears to be an exceptionally good fishing spot within the broader region of Johnstone Strait. 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.). Ecological determinants of critical group size in killer whales add a compounding effect to this trend – as relative abundance of chinook salmon increases, so too does the critical group size of killer whales in Johnstone Strait increase (Lusseau et al., 2004). Paradoxically, the better the habitat quality is in terms of prey density, the greater the whales' vulnerability to stochastic, catastrophic events.

Conservation challenges arise routinely when significant habitat for threatened wildlife intersect with high-use and high-risk human activities. For example, ship collisions and fishing gear entanglement have long been known to be important contributors to mortality in western North Atlantic right whales (Kraus, 1990). It has also been predicted that decreasing mortality of adult females by only 2–3 females per year could reverse the negative trends observed in that small and highly endangered population (Fujiwara and Caswell, 2001). For other species, population-level data are lacking to quantify risk in this way, but the spatial component to extinction risk in other gregarious species is likely common. Spring aggregations of Pacific walrus are found around St. Lawrence Island and account for thousands of animals in dense concentrations (Udevitz et al., 2008). Substantial fractions of Melanesia's globally significant dugong population are distributed in a very restricted part of New Caledonia, South Pacific (Garrigue et al., 2008). In a survey for vaquita, 37% of the total number of groups was detected in a period of only a few hours (Jaramillo-Legorreta et al., 1999), and the patchy nature of vaquita distribution is mirrored by a similarly aggregated artisanal shrimp gillnet fleet. The role of bycatch in the dynamics and viability of this small population make this population vulnerable to one large mortality event. To complicate matters, factors that drive distribution of cetaceans, such as patchy distribution of prey, may also drive distribution of anthropogenic activities, such as fishing vessels, which adds a spatial component to the risk of bycatch, ship strike (collision with vessels) and oil spills. The approach we use to identify areas in which marine megafauna predictably assemble is broadly useful for protecting high-risk marine habitat. The approach we outline can be used to prioritise emergency-response preparedness activities for regions found to be most vulnerable to low-probability, high-impact events.

One criticism of the utility of RBMBER as a conservation measure was levelled by Duffus and Dearden (1992), who questioned whether this reserve might actually be counterproductive.

"It is known that, for whatever reason, the whales do congregate there during an important feeding period. That may make it a high priority for protection. On the other hand, the fallacy of tokenism – that is, giving the public the appearance of protecting an important whale habitat when neither the importance of the site to whales nor the veracity of the protection is established – creates a political 'success' that may mask an ecological failure. Clearly, calling this a 'killer whale reserve' is only justified in a semantic sense." (Duffus and Dearden, 1992)

We do not contend that Robson Bight is a paper park, but suggest that additional measures are needed for this small MPA to confer maximal conservation benefit to whales. In recent years, many studies have explored the 'veracity of protection' that the reserve confers, by assessing the influence of boat traffic on killer whale behaviour, activities and energetics (Williams et al., 2002a, b; Williams et al., 2006). The present study demonstrates that this portion of proposed critical habitat is important to substantial fractions of the NRKW population. This has taken on a sense of urgency in recent years, both because of the vulnerable status of the population, the identification of Robson Bight and Johnstone Strait in critical habitat for the population (Fisheries and Oceans Canada, 2008), and most importantly, industrial development applications proposed for the area. A proposal has been made to build a 400,000 barrel-per-day pipeline (Gateway) from the Alberta oilsands project to Kitimat on BC's central coast, to be taken from there by tankers to refineries (Fisheries and Oceans Canada, 2007). Oil spills have been identified as posing a threat to the recovery of transient and resident killer whales, and this proposed pipeline and associated tanker traffic are expected to increase oil spill risk substantially (Fisheries and Oceans Canada, 2007). Oil tanker traffic has been managed for decades to avoid transiting BC's inshore coastal waters, thus approval of this proposed industrial development would involve oil tankers either transiting narrow Johnstone Strait en route to California, or taking a longer route around western Vancouver Island in open waters. The west coast route would appear to be a lower-risk option, but similar risk assessments should be conducted to assess cetacean use of north coast waters while the de facto moratorium on tanker traffic remains in place. In any event, increased tanker traffic in our study area would result in dramatically increased oil spill risk to killer whales, and the highly permeable boundaries of the reserve currently offer no protection to whales from such a threat. We encourage oceanographic modelling studies to model the fate of oil spilled in the region.

Hooker et al. (1999) note that unlegislated marine reserves are best thought of as "gestures", which easily can be revoked. Conservation benefit to killer whales would presumably be improved by formal recognition of the marine boundaries of Robson Bight (Michael Bigg) Ecological Reserve by declaring it to be a no-take, no-entry marine protected area, and by keeping the region free from oil tankers. For example, on 20 August 2007, a small barge loaded with a fuel truck and other heavy equipment tipped over in the study area, spilling ~10,000 L of diesel fuel and a similar volume of other hydrocarbons. Approximately 25% of the NRKW population was seen in the vicinity of the spill (Table 3, with the names of affected matrilines in bold). One lesson learned from this experience is that additional resources (in the form of training and equipment) should be allocated to high-risk areas to build capacity for responding quickly to spills (Matkin et al., 2008). Given the number of commercial whalewatchers working around whales in remote and sparsely populated areas worldwide, this sector of skilled marine operators should be included in any list of potential first responders to oil spills in critical whale habitat.

In hindsight, it should come as no surprise that a relatively small diesel spill in Johnstone Strait exposed 25% of the NRKW population to fuel. Here we show that on a typical summer day, 17 individuals visited this negligibly sized area. We should plan as though accidents in this important habitat would impact far more animals than could be removed sustainably from the population, even if removals represented a random subset of the population (Wade, 1998). In fact, catastrophic events would likely impact a number of closely-associating matrilines at once. Previous work has shown that the social network of individuals in this population is more vulnerable to targeted, clustered removal of small numbers of animals than the same level of random removals (Williams and Lusseau, 2006). Catastrophes could jeopardise population viability, not only by removing a large proportion of individuals, but also by removing matrilines best adapted for utilising this critical habitat. One research priority should be to integrate information on sociality directly into the PBR equation and population viability analyses, both of which would require substantial methodological development (Gerber, 2006). Another lesson learned is that quantitative risk assessments should be conducted routinely using worst-case scenarios to identify areas of overlap between intense or high-risk human activities and relatively large aggregations of small populations. As important habitats become exposed to increasing human activities as a function of increased urbanisation, we should anticipate that risks posed to wildlife due to anthropogenic activities will also increase (McDonald et al., 2008). Such risk assessments can inform protected-areas management that integrates sociality of target species directly, and lead to efficient resource allocation for emergency preparedness and response measures. For critically endangered populations, such as the western gray whale off Sakhalin Island (Weller et al., 2002) or the southern resident killer whale, one cannot learn how to deal with an oil spill through a process of trial and error.

Acknowledgements

We thank the many staff and volunteers of Bion Research, Beaveridge Consultants and Cetus Conservation Society who collected these data while under contract to BC Parks, and Rik Simmons, Ian MacLellan and Linda Philipp (BC Parks) for permission to use the data. We thank Erin Ashe for volunteering hundreds of hours to put the 8 years' worth of data into a common format for analysis. We thank Erin Ashe, Per Berggren, Ian Boyd and three anonymous reviewers for comments on the manuscript. Paul Spong and Helena Symonds (OrcaLab) provided unpublished data from the 20 August 2007 diesel spill in Johnstone Strait. RW was supported by Canadian Whale Institute, the Jane Marcher Foundation and The Russell Family Foundation. We thank David Bain, Lance Barrett-Lennard, Graeme Ellis, John Ford, and other members of the Resident Killer Whale Recovery Team for interesting discussions about critical habitat, but the opinions presented here represent those of the authors.

REFERENCES

Barrett-Lennard, L.G., Heise, K.A., Ford, J.K.B., 1996. The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. Animal Behaviour 51, 553–565.

Berggren, P., Wade, P.R., Carlstrom, J., Read, A.J., 2002. Potential limits to anthropogenic mortality for harbour porpoises in the Baltic region. Biological Conservation 103, 313–322.

Caswell, H., 2001. Matrix Population Models: Construction: Analysis, and Interpretation, 2nd edn. Sinauer Associates Inc, Sunderland.

Colman, J.G., 1997. A review of the biology and ecology of the whale shark. Journal of Fish Biology 51, 1219–1234.

Duffus, D.A., Dearden, P., 1992. Whales, science and protected area management in British Columbia, Canada. The George Wright Forum 9, 79–87.

Duncan, P., Hewison, A.J.M., Houte, S., Rosoux, R., Tournebize, T., Dubs, F., Burel, F., Bretagnolle, V., 1999. Long-term changes in agricultural practices and wildfowling in an internationally important wetland, and their effects on the guild of wintering ducks. Journal of Applied Ecology 36, 11–23.

Ehrenfeld, D.W., 1970. Biological Conservation. Holt, Rinehart and Winston, New York, NY.

Ellis, G.M., Ford, J.K.B., Towers, J.R., 2007. Northern Resident Killer Whales in British Columbia: Photo-Identification Catalogue 2007. Fisheries and Oceans Canada, Nanaimo (ii + 38pp, available from Pacific Biological Station, Nanaimo, BC V9T 6N7).

Felleman, F.L., Heimlich-Boran, J.R., Osborne, R.W., 1991. The feeding ecology of killer whales (*Orcinus orca*) in the Pacific Northwest. In: Pryor, K., Norris, K.S. (Eds.), Dolphin Societies: Discoveries and Puzzles. University of California Press, Berkeley, pp. 113–147.

Fischer, J., Lindenmayer, D.B., 2002. Small patches can be valuable for biodiversity conservation – two case studies on birds from southeastern Australia. Biological Conservation 106, 129–136.

Fisheries, Oceans Canada, 2007. Recovery Strategy for the Transient Killer Whale (*Orcinus orca*) in Canada [Consultation Draft]. Species at Risk Act Recovery Strategy Series. Fisheries and Oceans Canada, Vancouver. 42pp.

Fisheries, Oceans Canada, 2008. Recovery Strategy for the Northern and Southern Resident Killer Whales (*Orcinus orca*) in Canada. Species at Risk Act Recovery Strategy Series. Fisheries and Oceans Canada, Ottawa. ix + 81pp.

Ford, J.K.B., 1989. Acoustic behavior of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. Canadian Journal of Zoology 67, 727–745.

Ford, J.K.B., Ellis, G.M., Balcomb, K.C., 1994. Killer whales: the natural history and genealogy of Orcinus orca in British Columbia and Washington State. UBC Press, Vancouver.

Ford, J.K.B., Ellis, G.M., Balcomb, K.C., 2000. Killer whales: the natural history and genealogy of Orcinus orca in British Columbia and Washington State, second ed. University of British Columbia Press, Vancouver.

Fujiwara, M., Caswell, H., 2001. Demography of the endangered North Atlantic right whale. Nature 414, 537–541.

Garrigue, C., Patenaude, N., Marsh, H., 2008. Distribution and abundance of the dugong in New Caledonia, Southwest Pacific. Marine Mammal Science 24, 81–90.

Gerber, L.R., 2006. Including behavioral data in demographic models improves estimates of population viability. Frontiers in Ecology and Environment 4, 419–427.

Gerber, L.R., Hyrenbach, K.D., Zacharias, M.A., 2005. Do the world's largest protected areas conserve whales or whalers? Science 307, 525–526.

Grewe, P., Elliott, N., Innes, B., Ward, R., 1997. Genetic population structure of southern bluefin tuna (*Thunnus maccoyii*). Marine Biology 127, 555–561.

Guillemain, M., Fritz, H., Duncan, P., 2002. The importance of protected areas as nocturnal feeding grounds for dabbling ducks wintering in western France. Biological Conservation 103, 183–198.

Harper, J.R., 1995. Robson Bight Coastal and Nearshore Sediment Transport Survey. Unpublished Contract Report Available from Ministry of Forests, 2100 Labieux Road, Nanaimo, BC, V9T 6E9, Canada (20pp + 2 appendices).

Hooker, S.K., Whitehead, H., Gowans, S., 1999. Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. Conservation Biology 13, 592–602.

Hooker, S.K., Gerber, L.R., 2004. Marine reserves as a tool for ecosystem-based management: the potential importance of megafauna. BioScience 54, 27–39.

Hoyt, E., 2005. Marine Protected Areas for Whales, Dolphins and Porpoises: A World Handbook for Cetacean Habitat Conservation. Earthscan, London.

International Whaling Commission, 1996. Report of the Scientific Committee. Annex H. Report of the Sub-Committee on Small Cetaceans. Reports of the International Whaling Commission, vol. 46, pp. 160–179.

Jaramillo-Legorreta, A., Rojas-Bracho, L., Gerrodette, T., 1999. A new abundance estimate for vaquitas: first step for recovery. Marine Mammal Science 15, 957–973.

Johnston, D.W., Meisenheimmer, P., Lavigne, D.M., 2000. An evaluation of management objectives for Canada's commercial harp seal hunt, 1996–1998. Conservation Biology 14, 729–737.

Kraus, S.D., 1990. Rates and potential cause of mortality in North Atlantic right whales (*Eubalaena glacialis*). Marine Mammal Science 6, 278–291.

Lusseau, D., 2003. Effects of tour boats on the behavior of bottlenose dolphins: using Markov chains to model anthropogenic impacts. Conservation Biology 17, 1785–1793.

Lusseau, D., Williams, R., Wilson, B., Grellier, K., Barton, T.R., Hammond, P.S., Thompson, P.M., 2004. Parallel influence of climate on the behaviour of Pacific killer whales and Atlantic bottlenose dolphins. Ecology Letters 7, 1068–1076.

Matkin, C.O., Saulitis, E.L., Ellis, G.M., Olesiuk, P., Rice, S.D., 2008. Ongoing population-level impacts on killer whales *Orcinus orca* following the *Exxon Valdez* oil spill in Prince William Sound, Alaska. Marine Ecology Progress Series 356, 269–281.

Mcdonald, R.I., Kareiva, P., Forman, R.T., 2008. The implications of current and future urbanization for global protected areas and biodiversity conservation. Biological Conservation 141, 1547–1559.

Mouillot, D., Culioli, J.M., Pelletier, D., Tomasini, J.A., 2008. Do we protect biological originality in protected areas? A new index and an application to the Bonifacio Strait Natural Reserve. Biological Conservation 141, 221–232.

Noss, R.F., Quigley, H.B., Hornocker, M.G., Merrill, T., Paquet, P.C., 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology 10, 949–963.

O'Hara, P.D., Morgan, K.H., 2006. Do low rated of oiled carcass recovery in beached bird surveys indicate low rates of ship-source oil spills? Marine Ornithology 34, 133–140.

Olesiuk, P., Bigg, M.A., Ellis, G., 1990. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Reports of the International Whaling Commission Special Issue 12, 209–244.

Reeves, R., 2000. The Value of Sanctuaries, Parks, and Reserves (Protected Areas) as Tools for Conserving Marine Mammals. Okapi Wildlife Associates, Hudson, PQ, 50pp.

Revilla, E., Palomares, F., Delibes, M., 2001. Edge-core effects and the effectiveness of traditional reserves in conservation: Eurasian badgers in Doñana National Park. Conservation Biology 15, 148–158.

Sadovy, Y., Domeier, M., 2005. Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. Coral Reefs 24, 254–262.

Species at Risk Act, 2003. Canada Gazette. Her Majesty the Queen in the Right of Canada, Ottawa.

Tershy, B.R., Van Gelder, E., Breese, D., 1993. Relative abundance and seasonal distribution of seabirds in the Canal De Ballenas, Gulf of California. The Condor 95, 458–464.

Udevitz, M.S., Burn, D.M., Webber, M.A., 2008. Estimation of walrus populations on sea ice with infrared imagery and aerial photography. Marine Mammal Science 24, 57–70.

Wade, P.R., 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. Marine Mammal Science 14, 1–37.

Wade, P.R., Angliss, R., 1997. Guidelines for Assessing Marine Mammal Stocks: Report of the GAMMS Workshop April 3–5, 1996, Seattle, WA. US Dep. Commer., NOAA Tech. Memo. NMFS-OPR-12. 93 pp.

Weller, D.W., Burdin, A.M., Würsig, B., Taylor, B.L., Brownell Jr., R.L., 2002. The western gray whale: a review of past exploitation, current status and potential threats. Journal of Cetacean Research and Management 4, 7–12.

Whitehead, H., Rendell, L., Osborne, R.W., Würsig, B., 2004. Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. Biological Conservation 118, 205–218.

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

Williams, R., Bain, D.E., Ford, J.K.B., Trites, A.W., 2002b. Behavioural responses of male killer whales (*Orcinus orca*) to a 'leapfrogging' vessel. Journal of Cetacean Research and Management 4 (3), 305–310.

Williams, R., Lusseau, D., 2006. A killer whale social network is vulnerable to targeted removals. Biology Letters 2 (4), 497–500.

Williams, R., Lusseau, D., Hammond, P.S., 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). Biological Conservation 133 (3), 301–311.

Williams, R., Thomas, L., 2007. Distribution and abundance of marine mammals in the coastal waters of BC, Canada. Journal of Cetacean Research and Management 9 (1), 15–28.

Williams, R., Hall, A., Winship, A., 2008. Potential limits to anthropogenic mortality of small cetaceans in coastal waters of British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 65, 1867–1878.

Wilson, B., Reid, R.J., Grellier, K., Thompson, P.M., Hammond, P.S., 2004. Considering the temporal when managing the spatial: a population range expansion impacts protected areas-based management for bottlenose dolphins. Animal Conservation 7, 331–338.

Woodroffe, R., Ginsburg, J.R., 1999. Conserving the African Wild Dog, *Lycao pictus*. I. Diagnosing and treating causes of decline. Oryx 33, 132–142.