

# Animal behaviour and marine protected areas: incorporating behavioural data into the selection of marine protected areas for an endangered killer whale population

E. Ashe<sup>\*1</sup>, D. P. Noren<sup>2</sup> & R. Williams<sup>3,4</sup>

<sup>1</sup> School of Biology, University of St Andrews, St Andrews, Scotland, UK

<sup>2</sup> Marine Mammal Program, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest Fisheries Science Center, Seattle, WA, USA

<sup>3</sup> Sea Mammal Research Unit, Gatty Marine Laboratory, University of St Andrews, St Andrews, Scotland, UK

<sup>4</sup> Marine Mammal Research Unit, University of British Columbia, Vancouver, BC, Canada

## Keywords

disturbance; marine protected area; habitat conservation; behaviour; spatial model; hotspot.

## Correspondence

Erin Ashe, School of Biology, University of St Andrews, St Andrews KY16 8LB, Scotland, UK.

Email: erineashe@gmail.com

\*Current address: Pearse Island, Box 193, Alert Bay, BC, Canada V0N 1A0.

Received 16 February 2009; accepted 28 September 2009

doi:10.1111/j.1469-1795.2009.00321.x

## Abstract

Like many endangered wildlife populations, the viability and conservation status of 'southern resident' killer whales *Orcinus orca* in the north-east Pacific may be affected by prey limitation and repeated disturbance by human activities. Marine protected areas (MPAs) present an attractive option to mitigate impacts of anthropogenic activities, but they run the risk of tokenism if placed arbitrarily. Notwithstanding recreational and industrial marine traffic, the number of commercial vessels in the local whalewatching fleet is approaching the number of killer whales to be watched. Resident killer whales have been shown to be more vulnerable to vessel disturbance while feeding than during resting, travelling or socializing activities, therefore protected-areas management strategies that target feeding 'hotspots' should confer greater conservation benefit than those that protect habitat generically. Classification trees and spatially explicit generalized additive models were used to model killer whale habitat use and whale behaviour in inshore waters of Washington State (USA) and British Columbia (BC, Canada). Here we propose a candidate MPA that is small (i.e. a few square miles), but seemingly important. Killer whales were predicted to be 2.7 times as likely to be engaged in feeding activity in this site than they were in adjacent waters. A recurring challenge for cetacean MPAs is the need to identify areas that are large enough to be biologically meaningful while being small enough to allow effective management of human activities within those boundaries. Our approach prioritizes habitat that animals use primarily for the activity in which they are most responsive to anthropogenic disturbance.

## Introduction

Marine protected areas (MPAs) can be an effective conservation tool for cetaceans (Hooker, Whitehead & Gowans, 1999; Hooker & Gerber, 2004) when boundaries reflect the biology of target species (Wilson *et al.*, 2004). Defining critical habitat for cetaceans is difficult, but there is recognition that habitat-use data can show hierarchies of importance – evidence for discernible habitat preference within an animal's broader range can reveal areas essential to a population's survival (Hyrenbach, Forney & Dayton, 2000; Ingram & Rogan, 2002; Cañadas *et al.*, 2005) – and these high-use marine areas can be targeted for protection. In the terrestrial realm, researchers have demonstrated that results from behavioural studies can be used to protect populations in need of conservation (Jeffries & Brunton, 2001). Such a framework is not widely used for choosing candidate MPAs

for cetaceans (Hoyt, 2005). However, this approach makes intuitive sense, particularly when anthropogenic impacts do not affect all behaviours evenly (Lusseau & Higham, 2004).

Three killer whale, *Orcinus orca*, ecotypes live in the north-east Pacific, including two populations of a fish-eating ecotype, termed 'northern residents' and 'southern residents' (Ford, Ellis & Balcomb, 2000). An MPA exists in Robson Bight, British Columbia (BC), Canada to protect important habitat for northern resident killer whales (NRKW), which number about 240 individuals (Fisheries and Oceans Canada, 2008). This reserve was designed initially to protect a rare behaviour, namely the tendency for NRKWs to rub on smooth pebble beaches. Robson Bight provides NRKWs with some measure of protection from repeated disturbance (Williams, Lusseau & Hammond, 2006a), although its ability to protect killer whales

from catastrophes such as oil spill is negligible (Williams, Lusseau & Hammond, 2009b).

The southern resident killer whale (SRKW) population comprises three stable, social units, termed J, K and L pods (Ford *et al.*, 2000). The pods return each year to inshore waters of Washington State, USA and BC to forage on migratory salmon (*Oncorhynchus* spp.; Felleman, 1986; Heimlich-Boran, 1988; Ford *et al.*, 2000; Baird, 2001). Every individual in the population is identifiable from unique, natural markings. A census has been carried out annually since 1974 to monitor abundance and population dynamics (Center for Whale Research, Friday Harbor, WA, USA). In 2001, the population declined to just 78 animals from 96 in 1993, which prompted an Endangered status listing under the US and Washington State Endangered Species Acts and the Canadian Species At Risk Act (Krahn *et al.*, 2002; Fisheries and Oceans Canada, 2008). Notwithstanding low abundance, a population with only three social units renders it particularly vulnerable to stochastic events (Anthony & Blumstein, 2000). As Reynolds *et al.* (2009) note, the SRKW population is among the 'most critically endangered marine mammals occurring regularly or exclusively in US waters.' Candidate drivers for this population decline include declines in prey populations, a legacy of an extensive live-capture fishery in the 1970s, and recent increases in whale-watching traffic (Krahn *et al.*, 2002). Owing to the potential risks associated with vessel disturbance, the ESA Recovery Plan for SRKWs requires evaluation of existing and potential vessel regulations, including protected areas or time-area closures (NMFS, 2008).

The small SRKW population is exposed routinely to intense commercial and recreational whalewatching traffic in core summer habitat. On a typical summer day, 14–28 vessels follow a group of killer whales (Erbe, 2002), and SRKWs have been observed accompanied by as many as 126 vessels at once (Koski, 2006). SRKWs are followed for 12 h per day during the peak summer season (NMFS, 2008). Recent studies have shown that SRKWs respond to boats by adopting more erratic swimming paths (Williams *et al.*, 2009b) and reducing the time spent feeding (Lusseau *et al.*, 2009). In contrast, the resting, travelling and socializing (which includes mating) activities of both NRKWs and SRKWs were less affected by vessels (Williams *et al.*, 2006a; Lusseau *et al.*, 2009). This impact of boat traffic on feeding activity may be due to the susceptibility of killer whales to increased ambient ocean noise levels (Bain & Dahlheim, 1994; Erbe, 2002; Foote, Osborne & Hoebel, 2004). Increased noise levels may mask echolocation clicks used for feeding or calls that may be used for coordinating group hunting (Bain & Dahlheim, 1994), which would reduce the potential for foraging success. Reduction in foraging efficiency in a prey-limited population can carry costs to individual and potentially population-level fitness (Winship & Trites, 2003; Williams *et al.*, 2006a). While it is not feasible to exclude all anthropogenic activities from the entire range of highly mobile animals, whale watching is localized relative to the animals' range. Waterways in the core SRKW summer

habitat are also important for recreational boating, commercial whalewatching, shipping and ferry traffic, so the region lends itself to protected-areas management (Stewart & Possingham, 2005) for vessel traffic. Since resident killer whale feeding behaviour is most disrupted by vessel traffic, the protection of feeding habitat would likely confer the highest benefit to this population.

Implementation of effective conservation action by selecting priority habitat for conservation relies on good spatial information (Margules & Pressey, 2000; Knight, Cowling & Campbell, 2006a; Knight *et al.*, 2006b, 2007). Thus, we conducted a spatial assessment to identify where preferred feeding locations exist within the killer whales' core summer habitat, and propose these as priority habitat for conservation. Our study was designed to inform ongoing government and grassroots (NGO) conservation activities linked to SRKW habitat protection (NMFS, 2008).

To that end, our study used two approaches. First, we identified priority habitat by mapping how animals used the study area in order to detect areas that killer whales were especially likely to be engaged in feeding activities. Second, interviews were conducted with local on-the-water environmental education coordinators to estimate the size of an area that could effectively be closed to boats and achieve high boundary compliance. Our objective was to identify areas that satisfied an overlapping set of whale-related (areas used by killer whales for feeding) and human-related (an area that is small enough for boat traffic to be excluded practically) attributes to guide the location of a candidate MPA for SRKWs.

## Methods

### Field data collection of killer whale behavioural and positional data

Data were collected from a 7.9 m boat with a 225 hp four-stroke outboard motor from May to August 2006 in inshore waters around San Juan Island, Washington State (USA) and adjacent Canadian waters [British Columbia (BC), Fig. 1]. Killer whales were searched for by five observers on the research boat and reports of killer whale presence and location were monitored using a local real-time paging system that disseminates killer whale sightings.

When killer whales were encountered, the boat operator maintained a distance of at least 100 m in accordance with the 'Be Whale Wise' local marine wildlife viewing guidelines (NMFS, 2008) in order to minimize the potential for vessel disturbance. In practice, the average operating distance from the focal killer whales was 225 m, measured every 5 min with a Bushnell Yardage Pro 1000 laser-range finder (Bushnell, Overland Park, KS, USA) (Noren *et al.*, 2009). We recorded activity state every 10 min for all focal subgroups in the observer's field of view, using a set of behavioural definitions provided below. Scan sample data and geographic position of killer whales were recorded via a Palm Handspring Visor PDA (Palm, Sunnyvale, CA, USA) with a Magellan GPS companion receiver (Magellan, Santa Clara, CA, USA). The



**Figure 1** Map of the study area, with place names referred to in the text.

**Table 1** Definitions and frequency of occurrence for field-classification of four coarse activity states of focal killer whale groups *Orcinus orca* (after Lusseau *et al.*, 2009 and Williams *et al.*, 2006a)

Definition	Probable function	Total observations	Percentage of total observed activities
Slow swimming with predictable sequences of several short (30 s) dives followed by 3–5-min dives and characterized by the absence of surface-active behaviour (e.g. breaching or tail-slapping)	Rest	63	8.2
Dive independently with entire group heading in the same general direction. Individual dive sequences characterized by pattern of several short dives followed by one long dive	Travel/Forage	485	63.5
Individuals spread out, diving independently in irregular sequences of long and short dives; display fast, non-directional surfacings	Feed	188	24.6
Tight groups with tactile contact among individuals; irregular surfacing, speeds and high rates of surface-active behaviour	Socialize	28	3.7

apparatus was programmed with customized CyberTracker software (<http://www.cybertracker.co.za>). Range and bearing were used to calculate the position of the killer whale as an offset from the boat's position using the GeoFunc add-in for Excel (Dr. Jeff Laake, National Marine Mammal Laboratory, Seattle, WA, USA), and then mapped in ArcView GIS 3.2 (ESRI, Redlands, CA, USA) (ArcView 3.2, ESRI, 1998).

During each 10-min scan sample, focal group behaviour was categorized into one of four broad activity states: travel/forage (TF), feed (FE), rest (RE) or socialize (SO). Activity states were defined (Table 1) to ensure that they were mutually exclusive, cumulatively definitive of the entire repertoire of the population, and were consistent with previous studies on impacts of vessel traffic on NRKW and SRKW behaviour (Williams *et al.*, 2006a; Lusseau *et al.*, 2009). To eliminate inter-observer variability, activity state was always scored by the same observer (E. A.).

### Defining manageable areas for exclusion zones

Interviews with on-the-water boater education coordinators were conducted to assess the spatial scale at which boat traffic can be managed in this location. This step was expert-driven, in that there are only two environmental education programmes currently trying to manage boat traffic around killer whales in the region; the process was meant to canvas the opinions of locals with relevant experience. Educators were asked to identify the size of an area that they felt could be kept reasonably clear of vessels, assuming typical levels of annual funding for zodiac crews and land-based spotters, good signage and reasonable boater compliance. The advice from local managers was used to choose the average cell size of a grid across which killer whale behaviour was predicted. The grid was overlaid on a digital map of the study area with the use of Manifold System and ArcView GIS 3.2 software (ArcView 3.2, ESRI, 1998). That resulting model prediction

was in turn used to guide placement of a potential vessel-exclusion zone (called ‘the candidate MPA’).

### Analysis of behavioural data to map killer whale habitat use

The goal of our spatial analysis was to identify areas within the study area that killer whales used more often for feeding than one would expect by chance alone. Two methods were used to model the probability of killer whales’ being observed feeding as functions of location (i.e. latitude and longitude) – a classification tree and a generalized additive model (GAM).

A classification tree was used to identify spatial covariates that correctly classified a response variable into increasingly homogeneous subgroups. A classification tree was fitted to the dataset in R using the ‘tree’ package (R Development Core Team, 2008). The method used recursive partitioning, a statistically robust and objective method to split the data into two subsets, each of which contained observations that tend to be composed of either feeding or non-feeding observations. Each subset was then considered for further splitting, such that data were split into progressively more homogeneous subsets (homogeneity was evaluated using a standardized statistical parameter) that ended in a ‘terminal node’ that displayed the prediction (Redfern *et al.*, 2006). Cross-validation was used to determine an appropriate end point by randomly sub-setting the data into training and testing sets, and by choosing a model that performed well at classifying both datasets. After model fitting in R, the values of the terminal nodes were exported to ArcView 3.2 GIS (ArcView 3.2, ESRI, 1998) to plot the ranges of locations in which killer whales tended to be observed feeding.

GAMs (Wood, 2006) were fitted in R using the ‘mgcv’ package to model killer whale behaviour as a binary response, namely feeding (scored as a 1) or not feeding (i.e. socializing, resting and travel/forage observations were all scored as 0). Package mgcv offered generalized additive modelling functions in a penalized regression spline framework, which used generalized cross-validation (GCV) to identify smoothed relationships between candidate explanatory and response variables (Wood, 2006). The approach used a manual, backwards stepwise method for allowing analysts to gauge whether terms should be retained or dropped from a model, relying on GCV score and goodness-of-fit statistics that carry a penalty for unnecessary terms. The appropriate degree of smoothing (i.e. basis dimension) was determined automatically by mgcv using penalized regression splines (Wood, 2006). The explanatory variable was location, namely a two-dimensional smooth of latitude and longitude with a maximum degree of smoothing of 20 degrees of freedom, which is the default for a two-dimensional smooth in mgcv (Wood, 2006). GAMs have been widely used in cetacean-habitat modelling (Hedley, Buckland & Borchers, 1999; Cañadas *et al.*, 2005; Redfern *et al.*, 2006) to estimate animal abundance (Hedley *et al.*, 1999; Williams, Hedley & Hammond, 2006b), and to model complex relationships between sets of explanatory variables

and killer whale behaviour (Williams & Ashe, 2007; Williams *et al.*, 2009a).

The model was of the form:

$$\text{Probability}_{(\text{Feeding vs. Not-feeding})} \sim s(\text{Longitude, Latitude})$$

in which  $s$  is a spline function with a binomial family and a logit link function (Wood, 2006). After fitting a GAM to the data, the selected model was used to predict the probability of killer whales feeding at every point in our prediction grid, predicted from the latitude and longitude at the midpoint of each grid cell. The probability of feeding was mapped in greyscale and classified using the natural breaks (Jenks) method in ArcView GIS 3.2 (ESRI, 1998).

## Results

### Sample size of behavioural data

A total of 764 observations were recorded between 15 May and 2 August 2006 (Fig. 2). The ‘travel/forage’ activity state was the predominant category while ‘socialise’ was least common overall. Frequencies of occurrence of activities observed are shown in Table 1. The activity of interest, feeding, comprised 24.6% of all observations in the raw data (Table 1). Feeding activities occurred for the most part along the south and west sides of San Juan Island (Fig. 2).

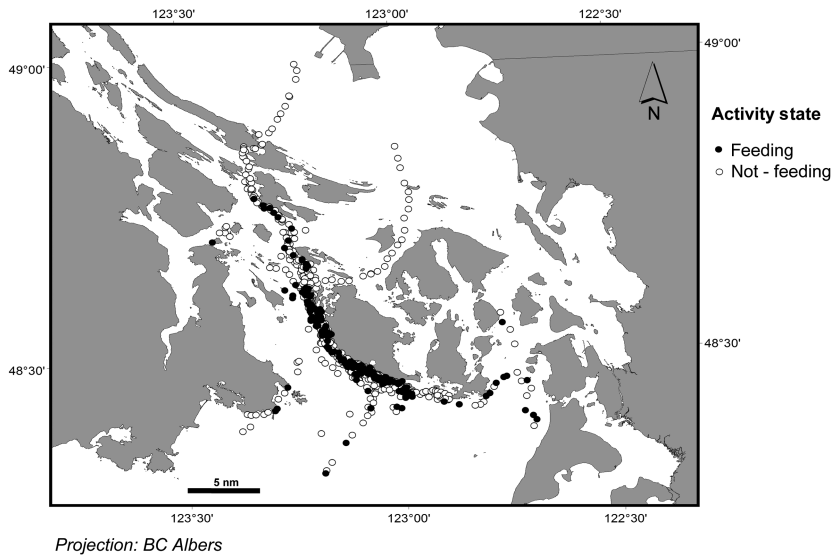
### Guidance from on-the-water educators

Two coordinators from both regional boater-education programs responded to our request for interviews, conducted independently. There was agreement among the four participants that their current model (i.e. zodiac-based crews intercepting all passing recreational traffic) is influencing boat traffic on the order of 1 square nautical mile in the core whalewatching area for resident killer whales. Consequently, our subsequent GAM-based spatial analyses were conducted based on this advice, namely by using a grid with an average cell size of 1 square nautical mile.

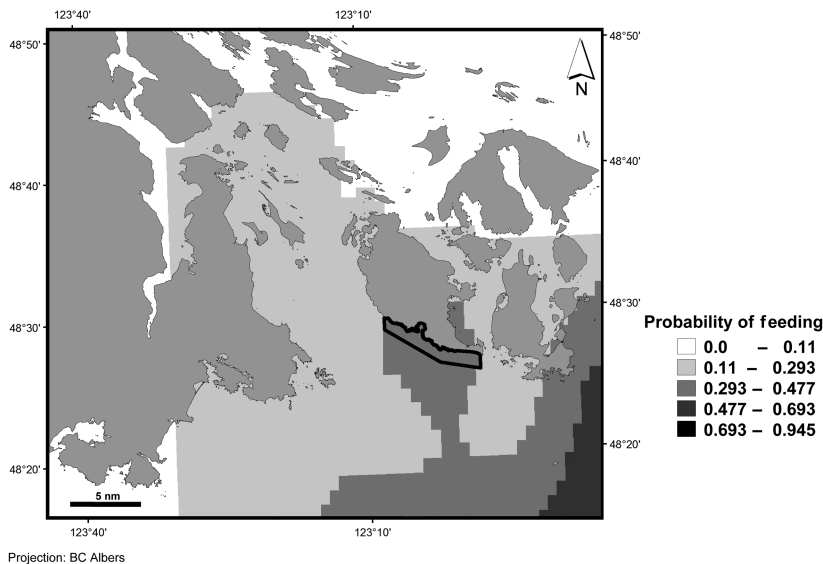
### Results from classification tree and GAM

The selected model had four terminal nodes, and successfully predicted the activity state (feeding vs. not-feeding) of 83% of the observations. Killer whales tended to be feeding in a latitudinal band between 48.4476°N and 48.4894°N (upper and lower dark lines in Fig. 3) and a longitudinal sector east of 123.05°W.

The two-dimensional smooth function of latitude and longitude showed a complex relationship with killer whale behaviour, as indicated by an estimated 14 degrees of freedom afforded to the relationship by mgcv. Figure 3 shows the predicted probability of feeding activity occurring throughout the study area in greyscale. The predicted probability of feeding ranged from 0 (i.e. highly unlikely to be feeding, and shown in light greyscale in Fig. 3) to 0.95 (i.e. highly likely to be feeding, and shown in dark greyscale in Fig. 3). A high-probability feeding area was predicted along



**Figure 2** Map of locations for all feeding (closed circles) and non-feeding (open circles) activity observations ( $n=764$ ) in the study area.



**Figure 3** The predicted values of feeding throughout the study area (the greyscale values in each grid cell). The results from the classification tree identified the area between  $48.4476^{\circ}\text{N}$  and  $48.4894^{\circ}\text{N}$  as a high-probability area for feeding, so these limits are drawn as the northern and southern boundaries of our proposed marine protected area (MPA). Interviews with on-the-water environmental educators suggested that a 1 nautical mile area was considered manageable, so this defined the offshore boundary of our proposed MPA. Integrating all three sources of information, we identified a region up to 1 mile off south-western San Juan Island as a priority feeding area to propose for interim protection (dark outline).

the south-west side of San Juan Island (Fig. 3). In contrast, feeding behaviour was predicted to occur rarely in waters directly north of San Juan Island (Fig. 3).

### Priority habitat for protection: integrating results

The information was integrated from all three sources: discussions with on-the-water educators; the classification tree and the GAM. While the GAM predicted a large region of high-probability feeding area off the south-west side of San Juan Island, the classification tree put northern and southern bounds of *c.* 8 nautical miles on this region. We illustrate our results by outlining an area (the ‘candidate MPA’) extending *c.* 1 nautical mile off the south-western shore of San Juan Island from which one could reasonably

expect to exclude boats (the dark outline in Fig. 3). Owing to the complex coastline, the candidate MPA we have drawn here, covers 7.4 square nautical miles. Our models indicate that a killer whale observed inside the candidate MPA would be 2.7 times as likely to be engaged in feeding activity than it would if the whale was observed outside the candidate MPA [i.e. 37.6% (95% CI: 35.7–39.5%) vs. 14.0% (CI: 13.4–14.5%)].

### Discussion

We present a flexible modelling method for use by researchers and managers to identify and protect important habitat within a wildlife population’s range. Our methods prioritize habitat for conservation quantitatively by: (1) assessing the activity state(s) during which wildlife are particularly

vulnerable to human activities (Williams *et al.*, 2006a,b; Lusseau *et al.*, 2009; this study); (2) collecting behavioural data and using spatial statistics (in this case, a GAM and classification tree) to evaluate how available habitat is used for these behaviours; (3) proposing a priority habitat for additional conservation measures (in this case, an MPA). There is a strong need to better integrate behavioural information into wildlife conservation strategies (Anthony & Blumstein, 2000). In the terrestrial realm, it is broadly accepted that results from behavioural studies can be used to protect populations in need of conservation. It is rare to incorporate behavioural data into habitat conservation plans for marine species, but integrating behavioural and habitat-use data with input from conservation practitioners into a spatial model to identify priority habitat for conservation strikes us as broadly applicable for both marine and terrestrial studies.

Our analyses do not obviate the need for stakeholder consultation; rather they anticipate the need for consultation by incorporating recommendations from environmental educators about the spatial scale at which this high level of boat traffic could effectively be managed. This study is currently not a component of a broader systematic conservation-planning process to protect regional biodiversity (Margules & Pressey, 2000; Knight *et al.*, 2006a). However, our study does have important implications for US legal obligations under the Endangered Species Act to promote single-species recovery of SRKWs. Best practices for comprehensive MPA design and implementation encourage studies such as ours to contribute to conservation assessments as a first step in a systematic conservation-planning process (Knight *et al.*, 2006b). In US waters, federal MPA designation falls under the jurisdiction of the National Marine Fisheries Service (NMFS), which is the federal agency responsible for stewardship of living marine resources in US waters. If a systematic conservation-planning process were initiated to design a comprehensive MPA for SRKWs, our study of habitat use and high-probability feeding areas could provide information necessary to guide conservation activities. The candidate MPA site we identified off south-west San Juan Island is proposed to inform ongoing recovery action plans and rule-making by NMFS. In a systematic conservation-planning framework, the next conservation activities would include assessment of how conservation initiatives should be undertaken through planning and management actions. MPA design criteria such as size, socio-economic considerations and explicit conservation targets specific to the region could serve as additional inputs, along with the habitat-use information, in a quantitative decision-making framework to design the boundaries of a comprehensive MPA (Agardy *et al.*, 2003; Lombard *et al.*, 2007).

Our primary focus was not to preserve biodiversity, but rather, a single-species approach to identify priority feeding habitat for protection to support recovery of a critically endangered cetacean population. Identification and protection of critical habitat are notoriously difficult tasks in the marine environment. In Fig. 2, important feeding habitats do not emerge obviously by simply mapping observations.

Protection of breeding and foraging habitats is essential to conservation, but defining them varies in degree of difficulty across species and populations. On the one hand, one does not require sophisticated statistical methods to identify breeding lagoons of grey whales in Baja, California, or the smooth gravel beaches on which NRKWs rub (Fisheries and Oceans Canada, 2008). Similarly, the beaches on which Patagonian killer whales intentionally strand to hunt seals and sea lions are conspicuous, and immediately recognizable as discrete foraging habitat (Lopez & Lopez, 1985). However, for animals in which all critical life functions occur within the same habitats (National Research Council, 2005), a probabilistic approach is necessary to identify subareas within a range that constitute biologically important habitats for a given life function. A number of spatial statistical modelling tools are available to identify important habitats for highly mobile marine predators (Redfern *et al.*, 2006), and it is useful to build on these methods to incorporate behavioural data to identify areas used for the activity state(s) in which species are most sensitive to an anthropogenic stressor. The designation of a no-entry area alone is not a panacea, but rather should be viewed as one part of a broader recovery plan that aims to increase the species' resilience to environmental variability, including human activities (Fisheries and Oceans Canada, 2008). For NRKWs, excluding boats from Robson Bight was meant to protect a rare behaviour, namely beach-rubbing, by keeping boats away from special rubbing beaches (Fisheries and Oceans Canada, 2008). Incidentally, it ended up protecting a valuable feeding site (Williams *et al.*, 2009b) that was formally included in critical habitat (Fisheries and Oceans Canada, 2008). For small populations like SRKWs, the conservation stakes are particularly high (Reynolds *et al.*, 2009). The current challenge presents an opportunity to accomplish intentionally for SRKWs what the Robson Bight MPA achieved serendipitously for NRKWs.

The candidate MPA we propose covers 7.4 square nautical miles. To place this in context, the no-entry MPA at Robson Bight is 3.6 square miles in size, and has been patrolled every summer since 1982 with only modest funding from BC Parks and a high reliance on volunteer efforts (Williams *et al.*, 2006a, 2009b). While the boundaries of the candidate MPA will no doubt change, the statistical bounds placed on high-probability feeding areas (Fig. 3) encompass an area quite modest in size. We have reason to suspect that the preferred feeding area identified in this study will persist over time scales suitable for management action (Wilson *et al.*, 2004). Killer whales have been observed in the region for at least half a century (Ford *et al.*, 2000) and several studies have reported feeding activities in the preferred feeding habitat we identified (Felleman, 1986; Heimlich-Boran, 1988; Hoelzel, 1993). As such, our study addresses simultaneously two of the three main threats in the SRKW population decline (NMFS, 2008) – prey availability and anthropogenic disturbance. In terms of mitigating impacts of anthropogenic activities on marine wildlife, a multi-pronged approach is needed to define protective measures and priority habitats to protect. In cases where decline of a

critically endangered population is thought to have been caused by multiple factors, mitigation measures that address multiple stressors simultaneously should be favoured over approaches that address stressors singly.

## Acknowledgements

We thank Robin Baird, Sandy Chancey, Shannon Davis, Fred Felleman, John Ford, Brad Hanson, Jeff Hogan, Erich Hoyt, Kari Koski, Nancy McKay, Ivan Reiff, Doug Sandilands, Meike Scheidat, Jodi Smith and Ben Wilson for assistance and advice. We thank Ari Friedlaender, David Lusseau, Monique Mackenzie and Rene Swift for statistical advice. For field assistance, we thank Jacqueline Daly. Financial support for the project was provided by The Russell Family Foundation. Thank you to Doug Sandilands for assistance with the figures. We thank the software developers from Cybertracker and the R core development team. This work was permitted in the USA by ESA permit #781-1824-00 and in Canada by Marine Mammal 2006-07 and SARA-33 permits. This paper was improved by comments provided by Mike Ford and Sascha Hooker, Associate Editor Belinda Reyers and the anonymous reviewers.

## References

- Agardy, T., Bridgewater, P., Crosby, M.P., Day, J., Dayton, P.K., Kenchington, R., Laffoley, D., McConney, P., Murray, P.A., Parks, J.E. & Peau, L. (2003). Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. *Aquat. Conserv.* **13**, 353–367.
- Anthony, L.L. & Blumstein, D.T. (2000). Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce  $N_e$ . *Biol. Conserv.* **95**, 303–315.
- Bain, D.E. & Dahlheim, M.E. (1994). Effects of masking noise on detection thresholds of killer whales. In *Marine mammals and the Exxon Valdez*: 243–256. Loughlin, R.R. (Ed.). San Diego: Academic Press.
- Baird, R.W. (2001). Status of killer whales, *Orcinus orca*, in Canada. *Can. Field-Nat.* **115**, 676–701.
- Cañadas, A., Sagarminaga, R., De Stephanis, R., Urquiola, E. & Hammond, P.S. (2005). Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. *Aquat. Conserv.* **15**, 495–521.
- Erbe, C. (2002). Underwater noise of whale-watching boats and potential effects on killer whales (*Orcinus orca*), based on an acoustic impact model. *Mar. Mamm. Sci.* **18**, 394–418.
- ESRI. (1998). *Arc and grid command references*. Redlands: Environmental Systems Research Institute.
- Felleman, F.L. (1986). *Feeding ecology of the killer whale, Orcinus orca*. MS thesis. University of Washington, Seattle, WA.
- Fisheries and Oceans Canada. (2008). *Recovery strategy for the northern and southern resident killer whales (Orcinus orca) in Canada. Species at risk act recovery strategy series*. Ottawa: Fisheries and Oceans Canada, ix + 81pp.
- Footo, A.D., Osborne, R.W. & Hoebel, A.R. (2004). Whale-call response to masking boat noise. *Nature* **428**, 910.
- 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*. 2nd edn. Vancouver: University of British Columbia Press.
- Hedley, S.L., Buckland, S.T. & Borchers, D.L. (1999). Spatial modelling from line transect data. *J. Cetacean Res. Mgmt.* **1**, 255–264.
- Heimlich-Boran, J.R. (1988). Behavioral ecology of killer whales (*Orcinus orca*) in the Pacific Northwest. *Can. J. Zool.* **66**, 565–578.
- Hoelzel, A.R. (1993). Foraging behaviour and social group dynamics in Puget sound killer whales. *Anim. Behav.* **45**, 581–591.
- 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.
- Hooker, S.K., Whitehead, H. & Gowans, S. (1999). Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. *Conserv. Biol.* **13**, 592–602.
- Hoyt, E. (2005). *Marine protected areas for whales, dolphins and porpoises*. London: Earthscan.
- Hyrenbach, K.D., Forney, K.A. & Dayton, P.K. (2000). Marine protected areas and ocean basin management. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* **10**, 437–458.
- Ingram, S.N. & Rogan, E. (2002). Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus*. *Mar. Ecol. Prog. Ser.* **244**, 247–255.
- Jeffries, D.S. & Brunton, D.H. (2001). Attracting endangered species 'safe' habitats: responses of fairy terns to decoys. *Anim. Conserv.* **4**, 301–305.
- Knight, A.T., Cowling, R.M. & Campbell, B.M. (2006a). An operational model for implementing conservation action. *Conserv. Biol.* **20**, 408–419.
- Knight, A.T., Cowling, R.M., Roughet, M., Balmford, A., Lombard, A.T. & Campbell, B. (2007). Knowing but not doing: selecting priority conservation areas and the research-implementation gap. *Conserv. Biol.* **22**, 610–617.
- Knight, A.T., Driver, A., Cowling, R.M., Maze, K., Desmet, P.G., Lombard, A.T., Rouget, M., Botha, M.A., Boshoff, A.F., Castley, J.G., Goodman, P.S., Mackinnon, K., Pierce, S.M., Sims-Castley, R., Stewart, W.I. & Von Hase, A. (2006b). Designing systematic conservation assessments that promote effective implementation: best practice from South Africa. *Conserv. Biol.* **20**, 739–750.
- Koski, K. (2006). *2004–2005 final program report: soundwatch public outreach/boater education project*. Friday Harbor: The Whale Museum.
- Krahn, M.M., Wade, P.R., Kalinowski, S.T., Dahlheim, M.E., Taylor, B.L., Hanson, M.B., Ylitalo, G.M., Angliss, R.P., Stein, J.E. & Waples, R.S. (2002). *Status review of southern resident killer whales (Orcinus orca) under the*

- Endangered Species Act. NOAA Technical Memorandum NMFS-NWFSC-54*. Seattle: US Department of Commerce.
- Lombard, A.T., Reyers, B., Schonegevel, L.Y., Cooper, J., Smith-Adao, L.B., Nel, D.C., Froneman, P.W., Anson, I.J., Bester, M.N., Tosh, C.A., Strauss, T., Akkers, T., Gon, O., Leslie, R.W. & Chown, S.L. (2007). Conserving pattern and process in the Southern Ocean: designing a Marine protected area for the Prince Edward Islands. *Antarct. Sci.* **19**, 39–54.
- Lopez, J.C. & Lopez, D. (1985). Killer whales (*Orcinus orca*) of Patagonia, and their behaviour of intentional stranding while hunting nearshore. *J. Mammal.* **66**, 181–183.
- Lusseau, D., Bain, D.E., Williams, R. & Smith, J.C. (2009). Vessel traffic disrupts the foraging behaviour of southern resident killer whales (*Orcinus orca*). *Endang. Species Res.* **6**, 211–221.
- Lusseau, D. & Higham, J.E.S. (2004). Managing the impacts of dolphin-based tourism through the definition of critical habitats: the case of bottlenose dolphins (*Tursiops* spp.) in doubtful sound, New Zealand. *Tourism Mgmt.* **25**, 657–667.
- Margules, C.R. & Pressey, R.L. (2000). Systematic conservation planning. *Nature* **405**, 243–253.
- National Marine Fisheries Service. (2008). *Recovery plan for southern resident killer whales (Orcinus orca)*. Seattle: National Marine Fisheries Service.
- National Research Council. (2005). *Marine mammal populations and ocean noise: determining when noise causes biologically significant effects*. Washington: National Academies Press.
- Noren, D.P., Johnson, A.H., Rehder, D. & Larson, A. (2009). Close approaches by vessels elicit surface active behaviors by southern resident killer whales. *Endang. Species Res.* **8**, 179–192.
- R Development Core Team. (2008). *R: a language and environment for statistical computing* ISBN 3-900051-07-0. Vienna: R Foundation for Statistical Computing, Available at <http://www.R-project.org>.
- Redfern, J.V., Ferguson, M.C., Becker, E.A., Hyrenbach, K.D., Good, C., Barlow, J., Kaschner, K., Baumgartner, M.F., Forney, K.A., Balance, L.T., Fauchald, P., Halpin, P., Hamazaki, T., Pershing, A.J., Qian, S.S., Read, A., Reilly, S.B., Torres L. & Werner, F. (2006). Techniques for cetacean-habitat modeling. *Mar. Ecol. Prog. Ser.* **310**, 271–295.
- Reynolds, J.E., Marsh, H. & Ragen, T.J. (2009). Marine mammal conservation. *Endang. Species Res.* **7**, 23–28.
- Stewart, R.R. & Possingham, H.P. (2005). Efficiency, costs and trade-offs in marine reserve system design. *Environ. Model. Assess.* **10**, 201–213.
- Williams, R. & Ashe, E. (2007). Killer whale evasive tactics vary with boat number. *J. Zool. (Lond.)* **272**, 390–397.
- Williams, R., Bain, D.E., Lusseau, D. & Smith, J.C. (2009a). Effects of vessel traffic on behaviour patterns of individual southern resident killer whales (*Orcinus orca*). *Endang. Species Res.* **6**, 199–209.
- Williams, R., Hedley, S. & Hammond, P.S. (2006b). Modelling distribution and abundance of Antarctic baleen whales using ships of opportunity. *Ecol. Soc.* **11**. Available at <http://ecologyandsociety.org/vol11/iss1/art1/>
- Williams, R., Lusseau, D. & Hammond, P.S. (2006a). Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biol. Conserv.* **133**, 301–311.
- Williams, R., Lusseau, D. & Hammond, P.S. (2009b). The role of social aggregations and protected areas in killer whale conservation: the mixed blessing of critical habitat. *Biol. Conserv.* **142**, 709–719.
- Wilson, B., Reid, R.J., Grellier, K. & Thompson, P. (2004). Considering the temporal when managing the spatial: a population range expansion impacts protected areas-based management for bottlenose dolphins. *Anim. Conserv.* **7**, 331–338.
- Winship, A.J. & Trites, A.W. (2003). Prey consumption of Steller sea lions (*Eumetopias jubatus*) off Alaska: how much prey do they require? *Fish. Bull.* **101**, 147–167.
- Wood, S.N. (2006). *Generalized additive models: an introduction with R*. Taylor and Francis. London: Chapman & Hall/CRC.