Aquatic Mammals 2016, *42*(2), 168-183, DOI 10.1578/AM.42.2.2016.168

Surface-Based Observations Can Be Used to Assess Behavior and Fine-Scale Habitat Use by an Endangered Killer Whale (*Orcinus orca*) Population

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Abstract

Behavioral observations can provide insight into the ecology and habitat use of marine species. Studies have shown that movement patterns are influenced by prey availability and that the presence of vessels can reduce foraging, resting, and/or social behaviors in delphinids, including killer whales (*Orcinus orca*). Southern resident killer whales are listed as "Endangered" in both the United States and Canada. Reduced prey availability and vessel disturbance are risk factors for this population. Surface observations were conducted to understand southern resident killer whale behavior and habitat use in their Endangered Species Act-designated core summer critical habitat. The activity budget comprised 70.4% travel, 21.0% forage, 6.8% rest, and 1.8% social behavior. Dive duration, surface duration, and swim speed varied significantly among activity states and validated the activity state classifications. For example, traveling killer whales swam the fastest and had the lowest surface to dive duration ratios, which presumably minimizes energetic costs while maximizing distance traveled. Movement patterns, spatial arrangements, and configurations of killer whales also varied significantly among activity states and, to some extent, varied by geographic location. We found that killer whale spatial arrangement and configuration patterns were strikingly different in two adjacent areas, indicating that these may change abruptly. This may be informative for vessel operators who are required to maintain a 182.9-m distance from killer whales. Killer whales engaged in most activity states throughout the area, but foraging and resting predominantly occurred in some localized regions. Activity budgets reported in the present and other contemporary studies differ from those reported 20 to 30 y ago. The proportion of forage in the activity budget has decreased in recent years, yet the main foraging area has persisted for several decades. These findings are important for understanding key risk factors for southern resident killer whales and may aid in formulating mitigation measures to protect them from vessel traffic and other human activities.

Key Words: activity state, behavior, forage, killer whale, *Orcinus orca*, MPA, rest, vessel impact

Introduction

Understanding behavior and habitat use of marine species provides insight into their trophic interactions, ecology, and risk factors. Models of marine mammal habitat use, based on probability of animal presence and environmental factors (for a review on techniques for cetacean-habitat modeling, see Redfern et al., 2006), have been used to identify priority conservation areas (e.g., Cañadas et al., 2005; Bailey & Thompson, 2009). It is important to not only determine where animals spend their time, but it is also vital to identify where activities such as foraging, reproduction, and resting occur. For example, establishing the timing and location of foraging is crucial to understanding trophic interactions (Austin et al., 2006). Studies on cetaceans have been conducted to identify important feeding areas (Heimlich-Boran, 1988; Hoelzel, 1993; Hastie et al., 2004; Ashe et al., 2010); assess niche segregation among sympatric species (Kiszka et al., 2011); understand impacts of acute catastrophic events on foraging activity and location (Smith et al., 2013); and identify "hot spots" of behavioral states, including foraging, that are impacted by anthropogenic activities (Lusseau & Higham, 2004; Ashe et al., 2010).

Southern resident killer whales (*Orcinus orca*) are listed as "Endangered" under the U.S. Endangered Species Act (ESA) and the Canadian Species at Risk Act (SARA). The major threats facing these killer whales are reduced prey availability and quality, vessel disturbance, and high levels of persistent contaminants (Krahn et al., 2002, 2004). Southern residents travel in long-term, cohesive groups called pods (Heimlich-Boran, 1988) and spend the majority of the summer months (May to September) in the U.S. San Juan Islands and neighboring Canadian Gulf Islands (Bigg, 1982; Krahn et al., 2002, 2004). This area includes the migration route of Fraser River chinook salmon (*Oncorhynchus tshawytscha*), which is the preferred prey of southern resident killer whales during the summer months (Hanson et al., 2010).

The southern resident killer whales' predictable presence in the inland waters of Washington state during the summer months (Heimlich-Boran, 1988; Hoelzel, 1993; Hauser et al., 2007) led the U.S. to designate Haro Strait and waters around the San Juan Islands as the core summer critical habitat for these killer whales (National Marine Fisheries Service [NMFS], 2006). Predictability of killer whale presence has also facilitated intensive commercial and private recreational whale-watching activity in this region. Resident killer whales respond to boat traffic and amplified noise levels by modifying swimming paths (Williams et al., 2002, 2009); increasing the amplitude of calls produced (Holt et al., 2009); increasing the performance of surface active behaviors (Noren et al., 2009; Williams et al., 2009); and reducing time spent engaged in behaviors necessary for survival, including feeding (Williams et al., 2006; Lusseau et al., 2009). Increased daily energetic costs (Williams et al., 2006; Noren et al., 2012, 2013; Holt et al., 2015) and physiological signs of stress (Romano et al., 2004; Ayres et al., 2012) in cetaceans have also been linked to vessel disturbance.

Because vessel traffic disrupts killer whale foraging behavior (Williams et al., 2006; Lusseau et al., 2009), an earlier study used models to predict feeding areas and identified a candidate Marine Protected Area (MPA) within the southern resident killer whale core summer critical habitat (Ashe et al., 2010). Proposed U.S. vessel regulations included a vessel "no-go zone" (NMFS, 2009) that comprised much of the candidate MPA (Ashe et al., 2010); however, the final regulations did not include the exclusion zone, pending the collection and analysis of additional data (NMFS, 2011).

Identifying areas where southern resident killer whales engage in specific activity states is important to inform the placement of no-go zones should they be deemed necessary. Feeding areas may be important to protect, not only because of the impact on this behavior by vessels, but also because these killer whales may be food limited (NMFS, 2009). However, because southern residents could be in an energy deficient state due to reduced prey availability or quality (Krahn et al., 2002, 2004; Noren, 2011; Williams et al., 2011), it also may be important to protect resting areas that are important for minimizing energy expenditure. Indeed, previous studies on other delphinid species have shown that both foraging/feeding and resting activities (Stockin et al., 2008; Arcangeli & Crosti, 2009; Christiansen et al., 2010; Montero-Cordero & Lobo, 2010) are reduced in the presence of vessels. The existing U.S. vessel regulations prohibit vessels from approaching killer whales closer than 182.9 m and from positioning in the whales' path within 365.8 m (NMFS, 2011). These regulations require vessel operators to be cognizant of killer whale movement and group cohesion patterns to avoid approaching them too closely. Therefore, elucidating southern resident killer whale group cohesion and movement patterns in their designated critical habitat is important for revealing areas that may be challenging for compliance with vessel regulations.

Like southern resident killer whales, dolphins in Doubtful Sound, New Zealand, are more sensitive to vessels while engaged in distinct behaviors. To address this conservation issue, Lusseau & Higham (2004) identified potential reserve locations in Doubtful Sound to protect resting and socializing—two sensitive behavioral activities. Instead of constructing complicated models that have the potential to identify areas in which no behavioral observations are collected (i.e., Ashe et al., 2010), Lusseau & Higham (2004) selected potential reserve locations based on proportions of observations of resting and socializing dolphins within a grid system overlaid on the study area.

We took a similar approach to describe geographic variability of southern resident killer whale behavior in their core summer critical habitat. This study builds on previous work aimed at identifying localized regions where southern resident killer whales engage in specific activities (Heimlich-Boran, 1988; Hoelzel, 1993; Ashe et al., 2010). The present study also investigates whether spatial arrangements and configurations of killer whale groups vary geographically. The purpose of the study is twofold: (1) identify regions where activities related to maintaining energy balance (forage and rest) occur and (2) identify regions where specific killer whale spatial arrangement and configuration patterns occur and, in particular, identify areas where there might be abrupt changes in these patterns. To our knowledge, no studies have described geographic variability in spatial arrangement and configuration patterns of any cetacean species. Finally, we compare our results to those of similar studies conducted on the same population 20 to 30 y ago to assess whether daily activity budgets and/or localized regions where killer whales engage in distinct activity states have changed.

Methods

Study Area

Research was conducted from 18 May through 2 August 2006 in nearshore waters off the San Juan Islands in the U.S. and off the east coast of Vancouver Island and the southern Gulf Islands in Canada (approximate range of study area: 48° 15' N to 49° N, 122° 35' W to 123° 30' W). Data were collected only in Beaufort sea states ≤ 3 between 0700 and 1800 h, and during visibility conditions adequate for locating and following killer whales. Southern resident killer whales were located each day by searching areas they frequent and by monitoring the VHF radio channel and pager network used by commercial whale-watchers (network described in Hauser et al., 2006). The pager network provides accurate locations of southern resident killer whales throughout the summer period (Hauser et al., 2006), which enabled us to reliably locate killer whales if they were within the study area on any given day.

Behavioral Data Collection

Behavioral data from groups of individually identified southern resident killer whales were collected using instantaneous scan sample and focal follow approaches (Martin & Bateson, 1993), according to methods described in Noren et al. (2009). Data were collected from a research vessel (7.9-m aluminum boat with a 225-hp 4-stroke outboard motor) that was operated according to voluntary guidelines for watching southern resident killer whales (*Be Whale Wise*, 2006). Specifically, after southern resident killer whales were sighted, the research vessel slowly approached a focal group from behind and parallel to the killer whales' path. Data were collected while the vessel traveled at a slow speed (1.9 ± 1.2 m s^{-1}) in parallel with a focal whale at a distance of ≥ 100 m. These procedures were identical to those followed by commercial whale-watchers, though the research vessel usually paralleled the killer whales at distances that were well beyond 100 m (see Noren et al., 2009, for more detail).

Killer whale groups were selected in the field at random, with an overall goal to collect data from multiple members of each of the three pods (J, K, and L) each day. Geographic location (latitude and longitude) and behavioral data from each group of killer whales were recorded every 10 min via instantaneous scan sampling on a handheld PDA (Palm III*xe*, Palm, Inc., Sunnyvale, CA, USA) using *Event 3.0* software (program designed by J. Ha, Department of Psychology, University of Washington, Seattle, WA, USA) while in the presence of southern resident killer whales. Data included activity state (forage, rest, travel, and social), movement pattern (nondirectional or directional), spatial arrangement (contact, tight, loose, and spread), and configuration (flank, linear, and nonlinear) of the group (Table 1). Each scan was considered to be an independent observation. Activity state definitions are from Noren et al. (2009), based on Heimlich-Boran (1988) and Ford (1989), while definitions of other behavioral categories (e.g., movement pattern, spatial arrangement, and configuration) were modified from Osborne (1986).

Focal follows were simultaneously conducted by a second observer on individual adult killer whales (including a few adolescent males) within the group to determine respiration rate, dive characteristics, and swim speed (for methods, see Noren et al., 2009). Killer whale swim speed (horizontal speed through the water) was approximated by the speed of the paralleling research boat, measured by a hand-held global positioning system (Garmin GPS 72 personal navigator). A focal follow was terminated whenever a surfacing event of the focal killer whale was missed by the observer, other vessels obstructed observations, or after approximately 40 min of continuous data collection from the focal whale (Noren et al., 2009). Given that activity state data could be considered subjective, despite strict definitions for each state, we present some objective, quantifiable variables (e.g., swim speed, respiration rate, dive duration, surface duration) that were calculated from the focal follow data to assess whether killer whale swimming and diving characteristics differed across activity states. Another criticism of assigning activity states to killer whales based solely on observations from the water's surface is that the bulk of their activities are under water where they are not observed. To address this concern, we included variables that incorporated behavior below the water's surface (e.g., dive duration and surface duration to dive duration ratio). Differences in these objective surface and subsurface variables provided support that the distinct activity states likely serve diverse functions.

Spatial Analysis of Scan Sample Data

Spatial analyses of killer whale behavioral observations were conducted in *ArcGIS 9.2* (ESRI, St. Charles, MO, USA). Scan sample positions were converted to a grid system described by the number of observations (scans) per cell for each descriptor in the four categories: activity state, movement pattern, spatial arrangement, and configuration. A 1 km^2 grid size was used for consistency with

Table 1. Definitions of activity states (following Noren et al., 2009), movement patterns, spatial arrangements, and configurations for southern resident killer whales (*Orcinus orca*) used in the study

Behavioral categories and descriptors	Definition
Activity state	
Forage	Searching for and/or locating food indicated by a fish in a whale's mouth,[1] arch dives, nondirectional swimming, and lunges at the surface; often includes long duration dives.
Rest	Swimming at speeds of less than 2 kts or completely stationary with respiratory synchrony and tight spatial associations among whales
Travel	Directional movement at a steady pace, often with coordination of the entire group
Social	Interacting with other members of the pod, members of other pods, or with inanimate objects; can include sexual and surface active behaviors.
Movement pattern	
Directional	Heading in the same generalized direction between surfacings and making significant forward progress in one direction
Nondirectional	Not heading in the same direction between surfacing; often surfacing ≥ 90° from the previous direction of travel and not making significant forward progress in one direction.
Spatial arrangement	
Contact	Whales physically touching
Tight	Whales less than approximately 1 m apart
Loose	Whales approximately 1 to 10 m apart
Spread	Whales greater than 10 m apart
Configuration	
Flank	Whales arranged side-to-side
Linear	Whales arranged head-to-tail
Nonlinear	Whales arranged in no particular orientation within the group

[1]This was not observed in the present study and is rarely observed in this population of killer whales.

the spatial scale of vessel counts (number of vessels within 1 km of killer whale groups) that have been taken in the region (e.g., Lusseau et al., 2009; Williams et al., 2009; Noren, unpub. data). Because our observations are a true representation of killer whale locations within our study area, no standardization of effort was necessary. To consider the spatial distribution of each behavior category, we first identified the number of observations per grid for each descriptor. These observations were then divided by the total number of observations in each cell to calculate the proportion of observations per cell for all descriptors within the four categories, thus providing an indication of the percentage of observations in which killer whales were engaged in a given activity state, movement pattern, spatial arrangement, or configuration.

To eliminate bias associated with small sample size, descriptors that were rarely observed (social activity state, $n = 10$ scans; contact spatial arrangement, $n = 1$ scan) and cells with less than three observations were removed from the analysis. The most commonly occurring activity state, movement pattern, spatial arrangement, and configuration were also identified for each cell by determining which descriptor(s) occurred at the greatest proportion (greater than or equal to 50% of all observations within the 1 km^2 cell). Finally, bathymetry data with 20 m^2 horizontal resolution (from which degree of slope change was calculated) were obtained from the University of Washington School of Oceanography. The position of each scan was then intersected with bottom topography, and average depth and slope were calculated for each activity state to coarsely assess whether these features differed across activity states.

Analysis of Focal Follow Data

Focal follows consisting of a minimum of 10 min of continuous data collection in which the killer whales consistently engaged in the same activity state were included in the analysis. Within each focal follow, durations of each dive and surface interval between dives were calculated from the "dive start" and "dive end" times. Mean dive duration (s), surface duration (s), surface duration to previous dive duration ratio, and swim speed (m s^{-1}) were calculated for each of the follows. It is important to reiterate that speeds reported herein are for horizontal distances traveled through the water rather than precise swim speeds. Thus, swim speeds are likely to be more accurate for killer whales that surface at regular, short intervals and travel in relatively straight paths compared to killer whales that dive for long durations and travel in more circuitous paths. Respiration rate (breaths/min^{-1}) for each focal follow was calculated

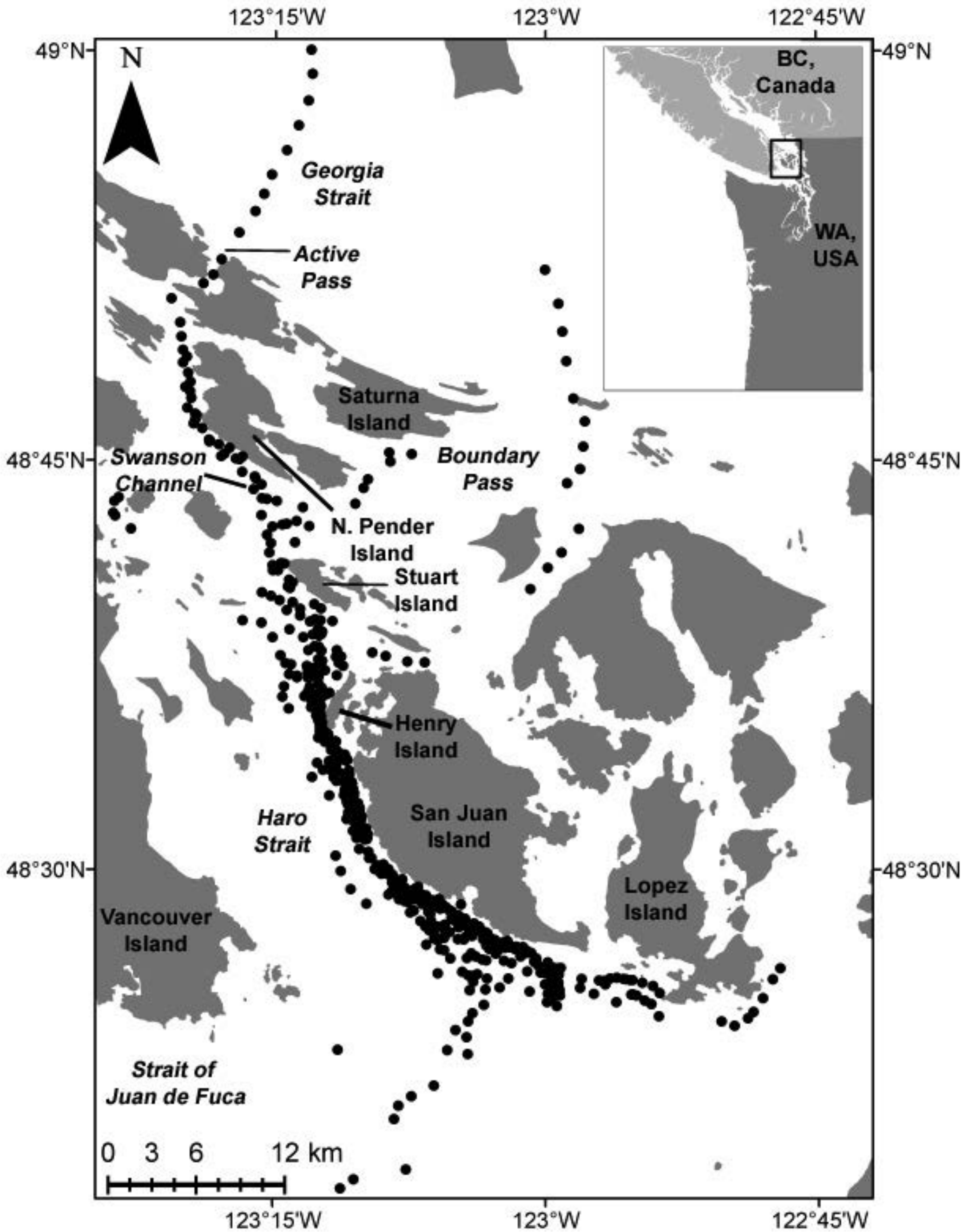

Figure 1. Study area and position of each scan (n = 571) conducted on southern resident killer whales (*Orcinus orca*) during summer 2006 in the inland waters of Washington state in the U.S. and British Columbia in Canada; place names referenced in the text are labeled.

by dividing the number of breaths recorded by the entire duration of the focal follow. Calculated variables from all focal follows were grouped according to relevant activity state (e.g., forage, rest, and travel) prior to analysis. Because no focal follows consisted of killer whales engaged solely in "social" behavior, this activity state was excluded from the analysis.

Statistical Analysis

Differences in the number of observations of each movement pattern, spatial arrangement, and configuration across activity states were tested with Pearson's chi-square tests (Zar, 1999). Swim speed, dive duration, surface duration, surface duration to dive duration ratio, respiration rate, water depth, and bottom slope were each compared across the three predominant activity states—forage, rest, and travel—using one-way ANOVA or an equivalent ANOVA on ranks when tests for normality and/or equal variance failed. When results were significant, pairwise multiple comparison procedures were run (Holm–Sidak method following ANOVA; Dunn's method following ANOVA on ranks) to isolate the activity state(s) that differed. Results were deemed significant at $p < 0.05$. All means are presented ±1 SD.

Results

Killer Whale Behavior

Data were collected from southern resident killer whales on 38 d in the inland waters of Washington state and British Columbia. This effort resulted in 571 scans of killer whale groups representing all three pods (58%, 41%, and 25% of scan samples were comprised of members from J, K, and L pods, respectively) and 93 focal follows of individual killer whales within these groups. Focal follows ranged in duration from 10 to 35 min (mean duration = 25.6 ± 6.8 min). The highest density of observations occurred on the west side of San Juan Island in Haro Strait (Figure 1). Travel was observed during 70.4% (n = 402), forage during 21% (n = 120), rest during 6.8% (n = 39), and social behavior during 1.8% (n = 10) of the scans.

Group movement patterns, spatial arrangements, and configurations varied by the activity in which killer whales were engaged. Movement patterns ($p < 0.001$, $\chi^2 = 253.7$, df = 3), spatial arrangements ($p < 0.001$, $\chi^2 = 102.7$, df = 6, excluding "contact" arrangement to avoid small sample size test violation), and configurations (p < 0.001, $\chi^2 = 79.3$, df = 6) of killer whale groups differed significantly across the four activity states (Table 2). For example, animals engaged in travel were most commonly directional in movement (98.3%), spatially spread (50.0%), and nonlinear in configuration (59.2%), although tight spatial arrangement (35.6%) and flank configuration (36.3%) were also regularly observed during travel. Foraging animals were either nondirectional (57.5%) or directional (42.5%) in movement, spatially spread (65.8%), and nonlinear in configuration (94.2%). Resting was associated with directional movement (94.9%), tight spatial arrangement (89.7%), and flank configuration (69.2%). Nondirectional movement (70.0%), tight spatial arrangement (60.0%), and nonlinear configuration (80.0%) were most common for social behavior.

Table 2. The percent occurrence of each descriptor of movement pattern, spatial arrangement, and configuration within each activity state for southern resident killer whales is presented. The number of observations of each activity state is indicated in parentheses.

	Forage (n = 120)	Rest (n = 39)	Travel (n = 402)	Social (n = 10)
Movement pattern				
Directional	42.5	94.9	98.3	30.0
Nondirectional	57.5	5.1	1.7	70.0
Spatial arrangement				
Contact	0.0	0.0	0.2	0.0
Tight	8.3	89.7	35.6	60.0
Loose	25.8	7.7	14.2	40.0
Spread	65.8	2.6	50.0	0.0
Configuration				
Flank	3.3	69.2	36.3	20.0
Linear	2.5	2.6	4.5	0.0
Nonlinear	94.2	28.2	59.2	80.0

Individual swim speeds, dive parameters, and respiration rates also varied by the activity in which the killer whales were engaged. Dive durations, surface durations, surface duration to previous dive duration ratios, swim speeds, and respiration rates differed significantly (all $p < 0.05$) across the three activity states—forage, rest, and travel—included in the analysis (Table 3). Specifically, travel was characterized by the fastest swim speed (2.4 ± 0.8 m s^{-1}), shortest surface duration (2.1 ± 1.2 s), shortest surface duration to previous dive duration ratio (0.07 ± 0.03), and intermediate respiration rate (1.4 ± 0.3 breaths/min^{-1}). In comparison, rest was characterized by the longest dive duration (61.9 ± 19.6 s) and lowest respiration rate (1.0 ± 0.3 breaths/min^{-1}). Forage was characterized by the highest respiration rate (1.6 ± 0.3 breaths/min^{-1}), a dive duration that was similar to that of travel, and surface behavior variables (surface duration, surface duration to previous dive duration ratio, and swim speed) that were similar to those of rest.

Spatial Analysis of Behavioral Data

The data were reduced to a total of 377 scan samples for spatial analysis. Each of the 59 resulting cells contained a range of 3 to 20 observations (6.4 ± 3.5 scans/cell). The proportions of occurrence for descriptors of the four behavioral categories—activity state, movement pattern, spatial arrangement, and configuration—within the 59 cells are presented in Figure 2.

Certain behaviors tended to vary geographically. The highest proportion of travel occurred along the west side and northwest of San Juan Island in Haro Strait; resting animals were most commonly observed southwest of Lopez Island and northwest of San Juan Island off the southern tip of Henry Island; and small, localized regions of foraging occurred in greatest proportions along the southwest side of San Juan Island in southern Haro Strait (Figure 2a-2c). The spread spatial arrangements occurred most often in southern Haro Strait, southwest of San Juan Island; loose spatial arrangements were observed at low levels throughout Haro Strait; and tight spatial arrangements occurred in the greatest proportions southwest of Lopez Island and northwest of San Juan Island between Henry and Stuart Islands (Figure 2d-2f). Nonlinear configurations were common throughout Haro Strait, particularly the southern portion (Figure 2g). The linear configuration was rarely observed, and flank configurations were observed most frequently southwest of Lopez Island, although they occurred throughout Haro Strait (Figure 2h & 2i). Lastly, directional swimming was observed throughout Haro Strait, while the greatest proportion of nondirectional movement occurred just south of San Juan Island (Figure 2j & 2k).

The predominant activity state, movement pattern, spatial arrangement, and configuration were identified for each of the 59 cells. The predominant activity state was travel, which occurred throughout Haro Strait; foraging behavior dominated the southern region of Haro Strait southwest of San Juan Island; and rest occurred northwest of San Juan Island on the southern tip of Henry Island and south of Lopez Island (Figure 3a). The predominant configuration was nonlinear, occurring throughout Haro Strait (Figure 3b). However, flank was the dominant configuration in cells located south of Lopez Island and just north of San Juan Island, among others. No cells were dominated by the linear configuration, and a few cells had equally high proportions of flank and nonlinear configuration. Directional movement dominated cells throughout Haro Strait, while nondirectional movement dominated a few cells in Haro Strait southwest of San Juan Island (Figure 3c). The spread spatial arrangement was predominant along the west side of San Juan Island in Haro Strait, tight spatial arrangements dominated cells in northern Haro Strait, and no cells were dominated by loose spatial arrangements (Figure 3d).

Travel tended to occur in the deepest water depths (mean: 181.6 ± 78.1 m), followed by forage

Table 3. Mean dive duration, surface duration, surface duration to dive duration ratio, swim speed, and respiration rate for each southern resident killer whale activity state are presented. Means for adolescent male, adult male, and adult female (≥ 13 to ~96 y of age) killer whales are presented with SD. Values for killer whales engaged in social behavior are not included because there were no focal follows in which killer whales were only engaged in social behavior for the entire duration of the follow. Asterisks (*) designate significantly different (all $p < 0.05$) values across activity states for each variable.

Variable	Forage (n = 9 follows)	Rest (n = 8 follows)	Travel (n = 76 follows)
Dive duration (s)	37.2 ± 10.8	61.9 ± 19.6*	44.2 ± 10.9
Surface duration (s)	2.9 ± 1.1	3.0 ± 0.9	2.1 ± 1.2*
Surface duration: dive duration	0.2 ± 0.2	0.2 ± 0.07	0.07 ± 0.03*
Swim speed (m s^{-1})	0.8 ± 0.6	0.6 ± 0.4	2.4 ± 0.8*
Respiration rate (breaths/min^{-1})	1.6 ± 0.3*	1.0 ± 0.3*	1.4 ± 0.3*

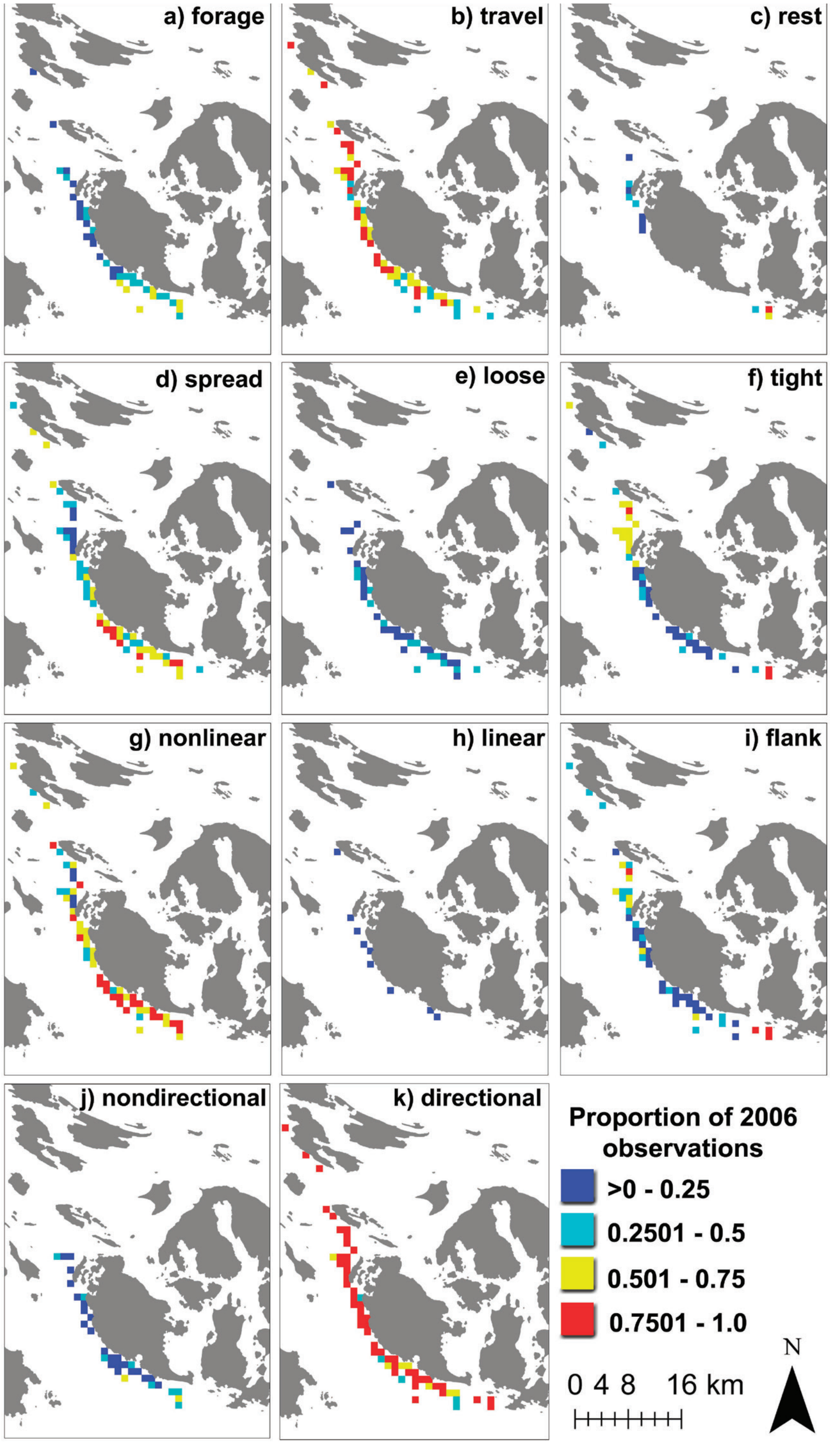

Figure 2. Proportion of observations for each activity state descriptor: (a) forage, (b) travel, and (c) rest; spatial arrangement descriptor: (d) spread, (e) loose, and (f) tight; configuration descriptor: (g) nonlinear, (h) linear, and (i) flank; and movement pattern descriptor: (j) nondirectional and (k) directional for southern resident killer whales in each 1 km^2 cell from 371 scans conducted in summer 2006

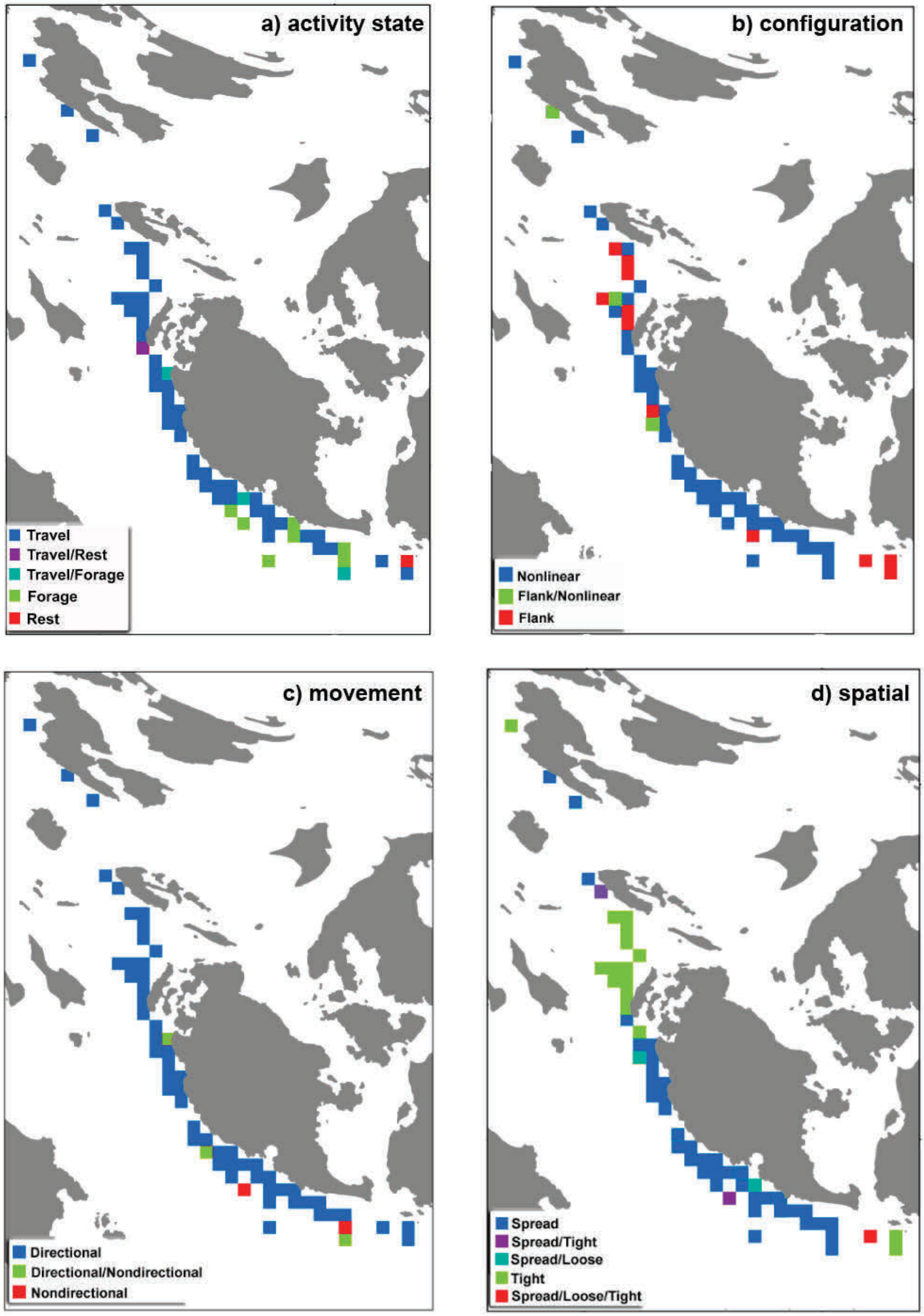

Figure 3. Predominant descriptor of (a) activity state, (b) configuration, (c) movement pattern, and (d) spatial arrangement for southern resident killer whales in each 1 km^2 cell from 371 scans conducted in summer 2006. The descriptors for each category that occurred at the greatest frequency are identified for each cell. Some cells identify multiple descriptors that occurred at the same frequency.

Table 4. Activity budgets reported for southern resident killer whales in the inland waters of Washington state and southern British Columbia from contemporary and historical studies. Data collection protocol, sample size, and percent occurrence of each activity state descriptor from the present study are compared to those of previous studies. NR = data were not reported. Descriptor terms are from the present study, but related terms used by previous studies are indicated in parentheses.

Reference/ (Years data were collected)	Collection protocol	*N*	Forage	Rest	Travel	Social
Present study and Noren, 2011/ (2006)	Scan samples collected every 10 min	571 scans	21.0%	6.8%	70.4%	1.8%
Holt et al., 2013/ (2007-2009)	Scan samples collected every 10 min	289 scans	39.1% (active foraging)	NR (included in "other" category)	53.6% (search phase of foraging, travel)	NR (included in "other" category)
Ashe et al., 2010/ (2006)	Scan samples collected every 10 min	764 scans	24.6% (feed)	8.2%	63.5% (travel/ forage)	3.7%
[1]Felleman et al., 1991/ (1976-1982)	15-min sampling period overlaid on continuous data	985 h	47% (foraging, percussive foraging, milling)	13%	25% (travel, percussive travel)	15% (play, intermingling)
[1]Heimlich-Boran, 1988/ (1976-1983)	15-min sampling period overlaid on continuous data	3,940 scans over 985 h	47.1% (foraging, percussive foraging, milling)	13.3%	24.4% (travel, percussive travel)	15.2% (play, intermingling)
[1,2]Heimlich-Boran, 1988/ (1976-1983)	15-min sampling period overlaid on continuous data	2,438 scans	47.3% (foraging, percussive foraging, milling)	15.6%	23.8% (travel, percussive travel)	13.3% (play, intermingling)
[1]Osborne, 1986/ (1976-1981)	Continuous data	967 h	46% (forage/ feed)	12% (sleep/rest)	27%	15% (play, intermingling)

[1]Studies that used the same dataset for their analysis

[2]Data collected in Haro Strait quadrats only (61.9% of data collected by Heimlich-Boran [1988]; overlaps the majority of the area where data were collected for the present study)

(mean: 170.3 ± 76.5 m), and then rest (mean: 164.9 ± 98.0 m). A similar pattern in degree of bottom slope was observed (travel: 6.2 ± 8.1°, forage: 5.4 ± 7.5°, and rest: 5.0 ± 5.3°). However, there were no significant differences in depth or bottom slope across the activity states.

Discussion

Killer Whale Behavior

This study demonstrated that observations conducted at the water's surface can provide valuable insight into the behavior and habitat use patterns of southern resident killer whales in their ESA-designated core summer critical habitat. Our results also validated that the four activity states—travel, forage, rest, and social—serve discrete functions due to variation in dive duration, surface duration, swim speed, movement pattern, spatial arrangement, and configuration across states. Previous researchers found that resident killer whale acoustic signals also varied across activity states and that the characteristics of their acoustic behavior supported the proposed function of each state (Hoelzel & Osborne, 1986; Osborne, 1986; Holt et al., 2013).

Similarly, we found that the behavioral and physiological characteristics of killer whales engaged in each activity state corroborate the inferred purpose. For example, traveling killer whales had the shortest surface duration, the shortest surface duration to dive duration ratio, and the fastest swim speed (2.4 m s^{-1}), which approximates the minimum of resident killer whale optimal swimming speeds (approximately 2.6 to 3.0 m s^{-1}; Williams & Noren, 2009). These attributes decrease drag, maximize distance moved over a period of time, and reduce the cost of transport. Resting killer whales had the longest dive duration, lowest respiration rate, and slowest swim speed, which all result in, or are indicative of, a reduced metabolic rate in marine mammals (Williams et al., 1991, 1993; Williams & Noren, 2009; Noren, 2011; Gerlinsky et al., 2014). Finally, foraging killer whales had the highest respiration rate and a relatively slow surface swim speed (i.e., reduced horizontal transport), which suggests that these animals were engaged in pursuit of prey beneath the water's surface.

The southern resident killer whale activity budget in the core summer critical habitat has been mainly comprised of travel and forage for at least three decades. This is not surprising given that the killer whales' core summer critical habitat overlaps with the migration route of Fraser River chinook salmon runs, and the summer diet of these killer whales is dominated by this salmon (Hanson et al., 2010). In recent years (2006 to 2009), travel dominated the activity budget within the core summer critical habitat (present study: 70.4%; Ashe et al. (2010): 63.5%; Holt et al. (2013): 53.6%; see Table 4), while the activity budget 20 to 30 y ago was comprised mainly of feeding behavior (1976 to 1983; Heimlich-Boran (1988): 47.3%; see Table 4). Furthermore, the proportion of observations of rest was about 50% lower in recent years compared to several decades ago (Table 4).

Southern resident killer whale activity budgets may be related to salmon abundance and intrinsic population parameters. Several studies have shown that characteristics of foraging behavior and daily activity budgets of endothermic marine predators change with the availability of their prey (e.g., Irvine et al., 1981; Cairns, 1988; Mayo & Marx, 1990; Boyd et al., 1994; Boyd, 1999; Friedlaender et al., 2009) and can be further influenced by the population density of the predator (Cairns, 1988). For example, during periods of low salmon abundance, southern resident killer whale total space use was greater and movement patterns were more convoluted compared to when salmon abundance was greater (McCluskey, 2006). In addition, total space use and complexity of movement patterns were both greater while social cohesion was reduced (e.g., killer whales spent less time in large social groups) during periods when the killer whale population was decreasing compared to when the population was increasing (McCluskey, 2006; Parsons et al., 2009). Insufficient data precluded estimating salmon abundance in the southern resident killer whale core summer critical habitat during time frames in which activity budgets were determined. However, changes in activity budgets with respect to southern resident killer whale population dynamics follow what would be expected given the finding that space use is inversely related to southern resident killer whale population growth (McCluskey, 2006).

Specifically, between 2006 and 2009, when travel was the dominant activity and rest was reduced, the southern resident killer whale population was decreasing slightly (data from Center for Whale Research, www.whaleresearch.com). In contrast, during the earlier time period (1976 to 1983) when feeding dominated and rest was more prevalent, the killer whale population was generally increasing (data from Center for Whale Research, www.whaleresearch.com). The finding that the proportion of rest was greater during the same period in which feeding was the predominant activity state is not surprising. This is because forage/feed is most often followed by rest (Osborne, 1986); thus, when there are a greater number of observations of forage/feed, there are likely to be more observations of rest. From a practical standpoint, if prey are scarce and difficult to find, more effort must be spent searching for suitable feeding areas; less time is then spent engaged in feeding activity; and, consequently, less time can be devoted to rest.

Because forage is reduced and travel is increased when vessels are in the vicinity of southern resident killer whales (Lusseau et al., 2009), an alternative hypothesis for the reduction in forage with a concomitant increase in travel over the past three decades is that the killer whales are changing their behavior due to the increased presence of vessels. Indeed, prior to 1976, whale watching in the region was virtually non-existent. The number of active commercial whale-watching boats increased by a factor of approximately 10 from the early 1980s to 2006 such that the number of active commercial vessels reached 76 in 2006 (Koski, 2007). There are no data on the number of private vessels engaged in whale watching prior to 1998, but given the trends for private vessels from 1998 to 2006, it is likely that the number of private vessels has also increased in the region over the last 30 y and that these vessels outnumber the commercial whale-watching vessels (trends from 1998 to 2006; Koski, 2007).

Finally, although the southern resident killer whale activity budget appears to have changed over time, these results could be due to differences in sample size and/or the months in which data were collected across studies. Because seasonality and geographic location can influence delphinid activity budgets (Stockin et al., 2009), we attempted to minimize variability related to these factors by only comparing data collected in the core summer critical habitat during the summer months. Data collection for the earlier studies was also conducted during daylight hours (Osborne, 1986; Heimlich-Boran, 1988; Felleman et al., 1991), but there is insufficient information to determine whether the span of hours precisely overlap with that of the present study. Regardless of differences in sample size and study design across older and contemporary studies, the potential change in the southern resident killer whale activity budget over time should be explored further, particularly since these changes may be related to prey availability.

Spatial Distribution of Behaviors

Southern resident killer whales most heavily utilized the west side of San Juan Island in their core summer critical habitat. This is not surprising given that the west side of San Juan Island has been identified as an important area for this population during the summer for several decades (Heimlich-Boran, 1988; Hoelzel, 1993; Hauser et al., 2007). Although data were collected over just one summer season in the present study, which could lead to biased results, the highest density of observations in 2006 align perfectly with the high use area of Haro Strait determined from six consecutive years of data (1996 to 2001; Hauser et al., 2007). The present study enhances findings of previous studies by determining the spatial distribution of killer whale activity states and group spatial arrangement and configuration patterns throughout the core summer region.

Forage and travel occurred throughout the study area. Although neither forage nor rest was the dominant activity state within the southern resident killer whale activity budget (70.4% travel, 21.0% forage, 6.8% rest, and 1.8% social behavior), it appeared that the killer whales regularly performed these two activities in localized regions. In general, travel was the main activity state along the west side of San Juan Island while forage dominated the southwest coast of San Juan Island. Lusseau et al. (2009) reported similar locations for observed travel and forage behaviors. This foraging area also overlaps with the zone that Ashe et al. (2010) proposed as an ideal MPA because it was identified as an important feeding area for southern resident killer whales. One potential criticism is that surface-based observations cannot accurately assess whether foraging/feeding is occurring because, for the most part, foraging occurs beneath the water's surface. However, a study that collected prey remains following southern resident killer whale foraging events substantiates that this region is an important foraging ground for this population (Hanson et al., 2010).

The main southern resident killer whale travel and forage locations have persisted for several decades. Studies conducted 20 to 30 y ago found that feeding was concentrated on the southwest shore of San Juan Island (Heimlich-Boran, 1988; Hoelzel, 1993) and that travel predominantly occurred on the northwest coast of San Juan Island (Heimlich-Boran, 1988). Historically, the location of southern resident killer whale feeding areas in Haro Strait corresponded with regions utilized by the commercial salmon fisheries (Felleman et al., 1991). The long-term persistence of presumably high concentrations of salmon may be related to the bathymetric features of the environment. Accordingly, the spatial distribution of killer whale activity states might also be linked to physical features of the environment. Indeed, Heimlich-Boran (1988) determined that southern resident killer whales fed in areas characterized by high relief bathymetry and the presence of shallow reefs and that they traveled in deep water with low relief bathymetry (Heimlich-Boran, 1988). Our basic assessment of the association between bathymetric features and activity states also suggests that southern residents travel in deeper depths compared to the depths in which they forage, but the difference in water depth was not significant. Future studies with more complex analyses designed to elucidate how bathymetric features influence salmon and killer whale behavior are warranted.

We identified two areas in which southern resident killer whales often rested, though, admittedly, observations of this activity state were relatively rare (6.8%). Killer whales rested in areas southwest of Lopez Island and northwest of San Juan Island. The latter region was also identified as an important resting area in the 1970s-1980s (Heimlich-Boran, 1988). The behavior in this area is complex, however, since travel, not rest, was the predominant activity state in most cells, and forage was also observed. Because several activity states were observed in this particular area, and because rest was observed in a range of habitats, Heimlich-Boran (1988) concluded that there were no clear habitat requirements for rest. Nevertheless, the area northwest of San Juan Island has persisted as a key resting area for at least 30 y. We also found a resting area off the southwest shore of Lopez Island, but Heimlich-Boran (1988) did not present detailed results from this region, so there is no way to know whether it is also a traditional resting area.

Diverse killer whale spatial arrangement and configuration patterns occurred throughout the core summer critical habitat, though certain forms were dominant in some areas and were often related to the predominant activity state in the region. For example, killer whales were most often spread and moving in a nondirectional pattern on the southwest coast of San Juan

Island where the forage activity state dominated. Similarly, the resting area to the northwest of San Juan Island overlaps a portion of the region where killer whales were predominantly in a tight spatial arrangement and flank configuration, which is often indicative of resting killer whales. However, spatial arrangement and configuration patterns could not always be attributed to the killer whales' rest activity state within this region. Although rest was regularly observed in this location, the dominant activity state throughout much of the area was travel. Interestingly, the tight spatial arrangement and flank configuration of killer whales in this region are strikingly different from the spread spatial arrangement and nonlinear configuration of killer whales in the adjacent region to the southeast (west side of San Juan Island). This implies that killer whales often transition abruptly between the two most extreme spatial arrangements and modify their configuration as they move through this very small area. Indeed, we regularly observed this phenomenon during field observations in this location.

Implications for Management

These findings can inform management actions that address key risk factors for southern resident killer whales, including reduced prey availability and vessel disturbance. For instance, we found that foraging and resting areas have persisted in the core summer critical habitat for several decades and, thus, may be ideal locations to consider for future reserve areas. The finding of a persistent foraging area is different from what is expected for cetaceans in the open sea, where foraging areas might be ephemeral and depend on highly variable oceanographic conditions, making the process of identifying potential MPAs complex (Bearzi, 2012). Increased buffering from boats beyond the 182.9-m regulation may be necessary when killer whales are resting and, more importantly, foraging because vessels/vessel noise at distances greater than 182.9 m affect southern resident killer whale foraging behavior (Lusseau et al., 2009), hearing (Erbe, 2002), and call production (necessary for social cohesion and foraging behavior) (Holt, 2008; Holt et al., 2009). No study has examined the efficacy of an MPA in reducing vessel impacts to marine mammals; thus, the total benefit of such areas are unknown. However, a previous study has demonstrated that MPAs effectively reduced the risk of another anthropogenic impact (gillnet mortalities) to Hector's dolphins (*Cephalorhynchus hectori*) (Gormley et al., 2012). In general, MPAs are recognized as an effective management strategy for a wide variety of marine taxa (Halpern, 2003).

Another important finding is the identification of an area in which the spatial arrangement and configuration of killer whales changed drastically, presumably over a short timescale. Although earlier studies have identified important geographic regions for "resident" delphinid activity states (Heimlich-Boran, 1988; Hoelzel, 1993; Lusseau & Higham, 2004; Ashe et al., 2010), this is the first study that describes geographic variability in cetacean spatial arrangement and configuration patterns. Informing vessel operators of an area in which killer whale spatial arrangement and configuration could change abruptly may assist them in complying with the current 182.9-m approach regulation (NMFS, 2011).

Conclusions

Surface-based observations can provide valuable insight into the behavior and ecology of southern resident killer whales. Similar to earlier studies, we found that southern residents spent the bulk of their time traveling and foraging in the core summer critical habitat. However, activity budgets in this region have changed considerably in the past two to three decades. Mainly, the proportions of observations of forage and rest have decreased, while the proportion of observations of travel has increased over time. These changes may be related to reduced prey abundance, fluctuations in killer whale population dynamics, and/or increased vessel presence. We also found that the geographic distribution of killer whale activity states, spatial arrangements, and configuration patterns varied. This is the first study to identify a region where southern resident killer whale spatial arrangement and configuration patterns change abruptly. Our study also found localized regions in which killer whales engage in specific activity states such as foraging and resting. These regions are similar to those identified by earlier studies, suggesting that some resting and foraging areas in the southern resident killer whale core summer critical habitat have persisted for several decades. These findings can inform the management actions needed to address key risk factors, including reduced prey availability and vessel disturbance.

Acknowledgments

We thank Snug Harbor Resort; University of Washington (UW) Friday Harbor Laboratories; Orca Network; Soundwatch; the commercial whale-watching fleet; and Dr. J. Ha from the Department of Psychology, UW, for field support. We are grateful to J. Daly for safely operating the research vessel in the vicinity of killer whales, and we thank D. Rehder, E. Ashe, and D. Giles for data collection and assistance in the field. L. Barre, B. Hanson, P. Levin, and two anonymous reviewers provided constructive comments on previous drafts of this manuscript. This work was funded by the NOAA Northwest Fisheries Science Center. This research was conducted by the authority of the ESA Permit Number 781-1824-00, Canadian MML Number 2006-07, and SARA Permit Number 33.

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