Seasonal and pod-specific differences in core use areas by resident killer whales in the Northern Gulf of Alaska

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ABSTRACT

The resident killer whale is a genetically and behaviorally distinct ecotype of killer whale (*Orcinus orca*) found in the North Pacific that feeds primarily on Pacific salmon (*Oncorhynchus spp* .). Details regarding core use areas have been inferred by boat surveys, but are subject to effort bias and weather limitations. To investigate core use areas, 37 satellite tags were deployed from 2006 to 2014 on resident killer whales representing 12 pods in the Northern Gulf of Alaska, and transmissions were received during the months of June to January. Core use areas were identified through utilization distributions using a biased Brownian Bridge movement model. Distinct differences in these core use areas were revealed, and were highly specific to season and pod. In June, July, and August, the waters of Hinchinbrook Entrance and west of Kayak Island were primary areas used, mainly by 3 separate pods. These same pods shifted their focus to Montague Strait in August, September, and October. Port Gravina was a focal area for 2 other pods in June, July, and August, but this was not the case in later months. These pods were responsible for seven of eight documented trips into the deeper fjords of Prince William Sound, yet these fjords were not a focus for most groups of killer whales. The seasonal differences in core use may be a response to the seasonal returns of salmon, though details on specific migration routes and timing for the salmon are limited. We found strong seasonal and pod-specific shifts in patterns between core use areas. Future research should investigate pod differences in diet composition and relationships between core area use and bathymetry.

1. Introduction

Resident killer whales are a genetically distinct piscivorous ecotype of killer whale found only in the North Pacific Ocean (Hoelzel et al., 1998; Morin et al., 2010; Parsons et al., 2013). They have diverged behaviorally, genetically, and acoustically from other sympatric ecotypes of killer whales, including the 'transient' killer whale ecotype which eats mammals (Ford et al., 1998; Heimlich-Boran, 1988), and the 'offshore' killer whale ecotype which preys on sharks and other fishes (Ford et al., 2011). The 'resident' ecotype has been observed feeding exclusively on fish, primarily Pacific salmon (*Oncorhynchus sp.*), and has never been observed feeding on mammals or sharks (Ford et al., 1998, 2016; Saulitis et al., 2000). Scale and tissue samples collected during predation events imply Chinook (*Oncorhynchus tshawytscha*), coho (*Oncorhynchus kisutch*), and chum salmon (*Oncorhynchus keta*) as primary prey for resident killer whales in the Northern Gulf of Alaska (Matkin et al., 2013; Saulitis et al., 2000).

Resident killer whales typically spend their entire lives within their natal matrilines, which consist of a female, all of her adult offspring,

and any of the offspring of females born to her (Bigg et al., 1990; Matkin et al., 1999). Dispersal from the natal matriline is rare in Washington, British Columbia and Alaska (Barrett-Lennard, 2000; Parsons et al., 2009). Killer whale pods are defined as social units consisting of related matrilines that are together during more than 50% of sightings, and are believed to have common lineage (Bigg et al., 1990). The relatedness of calls within these pods and matrilines parallel genetic relatedness (Yurk et al., 2002).

Pod structure for resident killer whales has been very well documented in three different populations, including the southern residents in Puget Sound and the northern residents in British Columbia. The third, and the subject of this study, is a population known as the southern Alaska residents. This population spans from southeastern Alaska to Kodiak, and includes approximately 700 whales (Matkin et al., 2014).

Killer whale pods and matrilines transmit cultural traditions through generations, including acoustic repertoires and call types (Filatova et al., 2015; Ford, 1991; Yurk et al., 2002). Cultural transmission is also believed to contribute to similarities in space use

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between groups (Similä et al., 1996), hunting and feeding techniques (Guinet and Bouvier, 1995; Similä and Ugarte, 1993), and beach rubbing (Rendell and Whitehead, 2001). Pod-specific core use areas have been documented in the southern resident killer whale population (Hauser et al., 2007), but have yet to be reported in Alaskan waters. Core use areas are important to monitor, as they illustrate temporal trends and inform potential variation within a population.

Satellite telemetry is a useful tool in describing core use areas, and is a method that is less subject to bias than boat surveys, which are limited by weather, survey locations, and daylight hours. In the Puget Sound, satellite telemetry is currently being used to assess important winter habitat use of the declining southern resident killer whale population (Northwest Fisheries Science Center, NOAA, 2014). Satellite telemetry has given insight into winter areas for that stock, and has enabled researchers to re-sight tagged animals and gather winter predation data that were previously lacking (Northwest Fisheries Science Center & NOAA, 2014). Telemetry has also proven to be a useful tool in describing important areas for many other cetacean species, such as false killer whales (*Pseudorca crassidens*), narwhals (*Monodon monoceros*), humpback whales (*Megaptera novaeangeliae*), and Hectors dolphins (*Cephalorhynchus hectori*) (Baird et al., 2013; Heide-Jørgensen et al., 2002; Kennedy et al., 2014; Rayment et al., 2009).

As an apex predator, resident killer whales are important to monitor for both conservation and management, particularly due to their strong preference for salmon. In the present study, we use the location data from 37 deployed satellite tags on killer whales in the northern Gulf of Alaska to assess core use areas. We document seasonal use differences from June through October for certain pods, and describe variation in use between pods. We hypothesize that distinct differences occur in core areas throughout the seasons, in response to prey availability and that pod-specific use of the region is non-random.

2. Materials and methods

2.1. Study area and animal selection

The study area spanned the northern Gulf of Alaska from Southeast Alaska to the Alaska Peninsula (Fig. 1). The bays and passes of Prince William Sound, the Kenai Coast, Kodiak Island, and Cook Inlet are glacially carved and therefore relatively deep (300–500 m), and experience strong tidal currents (Halverson et al., 2013). The coastwise portion of this study area includes the continental shelf, which extends from 30 to 170 km offshore. The shelf ranges in depth from 100 to 300 m in this region, and is subject to a general westward flow of the Alaska Coastal Current (Royer, 1981). Strong downwelling conditions in winter promote inflow into Prince William Sound through Hinchinbrook Entrance and outflow through Montague Strait, but this pattern is less distinct in the summer months as offshore downwelling conditions relax (Halverson et al., 2013).

Thirty-seven satellite tags were deployed on killer whales amongst 14 pods between 2006 and 2014 in Prince William Sound and Kenai Fjords (Table 1). Given the extremely rare dispersal from matrilines (Barrett-Lennard, 2000), the movement of one individual was taken to be representative of the movements of its entire matriline, and representative of its pod. Tagging locations were opportunistic, performed during photo identification surveys in Prince William Sound and Kenai Fjords (Fig. 1).

2.2. Tagging method

Whales were tagged with low impact minimally percutaneous external-electronics transmitter (LIMPET) satellite tags (Andrews et al., 2008). Tag designs were Wildlife Computers (Redmond, WA) SPOT 5 (AM-240, B, and C), and SPLASH10 (AM-266A and AM-292A). Tags were deployed by crossbow or air rifle at a distance of 6–20 m from a 12-m survey vessel. Two 6.5 cm long titanium darts equipped with

backward-facing barbs were used to anchor the tags in the connective tissue of the dorsal fin (Andrews et al., 2008). These transmitters sent ultra-high frequency (UHF) radio signals to Argos receivers onboard weather satellites.

To conserve power, transmissions were limited to whale surface time by a submersion sensor, but otherwise transmitted during all hours of the day. If tags lasted more than 50 days they were programmed to transmit every other day afterward (3 tags fit this category). If tags lasted more than 65 days, they were programmed to transmit every 5 days (2 tags fit this category).

2.3. Data analysis

Locations were calculated by the Argos system using the method of least squares, and each location was assigned a location class. Location classes (LC) 3, 2, and 1 are assigned an accuracy estimate by Argos, with the 68th percentile error ranging from 0.25 to 1.5 km, while the remaining LCs (0, A, B, and Z) are not assigned an error. All location data were subsequently processed with the Douglas Argos Filter, based on location class and realistic movement parameters, including turning angles and distance ratios between positions (Douglas et al., 2012). For core use analyses, the first 24 h of data were removed from each deployment to minimize potential tagging site bias. Twenty four hours were considered sufficient because killer whales can make mean daily movements of over 100 km (Matthews et al., 2011; Williams and Noren, 2009).

Locations of core use areas were estimated using kernel density estimation and measured with utilization distributions (UDs). UDs are defined as the minimum area encompassing a certain probability of relocation (Kie et al., 2010; Seaman and Powell, 1996). Core use areas are defined as the 50% UD probability contour (Fieberg and Kochanny, 2013; Kie et al., 2010; Schuler et al., 2014). One challenge with telemetry data and kernel density estimators is the potential for results to be biased by temporal and spatial autocorrelation. To minimize autocorrelation, we estimated UDs using a biased Brownian Bridge model. This model improves the traditional kernel density algorithms by placing calculated relocation probability between locations that satisfy limited time parameters, not only at received locations (Horne et al., 2007). This lessens the dependence on each location and provides a more accurate representation of the used space.

We calculated UDs for each pod, for each month, and each year, using the R package adehabitatHR (Calenge, 2011). A user-defined grid of 1 million pixels was established over the entire area of received locations, in order to assign the UD densities. However, cell size is reported to have little effect on the density distribution (Calenge, 2011). To adjust for variation in sample size due to tag transmission duration, UDs were first calculated for each animal, and the subsequent density values were weighted by the number of days of tag deployment. After summing the individual densities, values were standardized so that the probability across the grid still summed to a value of 1.

To assess variability in use, we examined the core use (50% UD) by pod, month, and year. Probability polygons were created which were imported into QGIS for analysis and comparison of UD sizes for each month, each pod, and each year. Each pod was identified by a 2-letter code and in some cases with an additional number. To examine temporal variation in the areas used, we examined seasonal and interannual variability within pods that had large sample sizes (AJ pod, 10 deployments, 4354 locations, 348 days), or by pooling pods, e.g. AD16 and AK pods, which are known to be closely related (4 deployments, 1155 locations, 166 days). The land portions of the UD's were eliminated for core use areas size calculations.

To limit erroneous calculations of short-term movements, we used speed and distance calculations only for positions that were separated by more than one hour and less than six hours. Speed calculations from Argos positions that are less than one hour apart can be greatly exaggerated by erroneous positions, and positions that are more than six
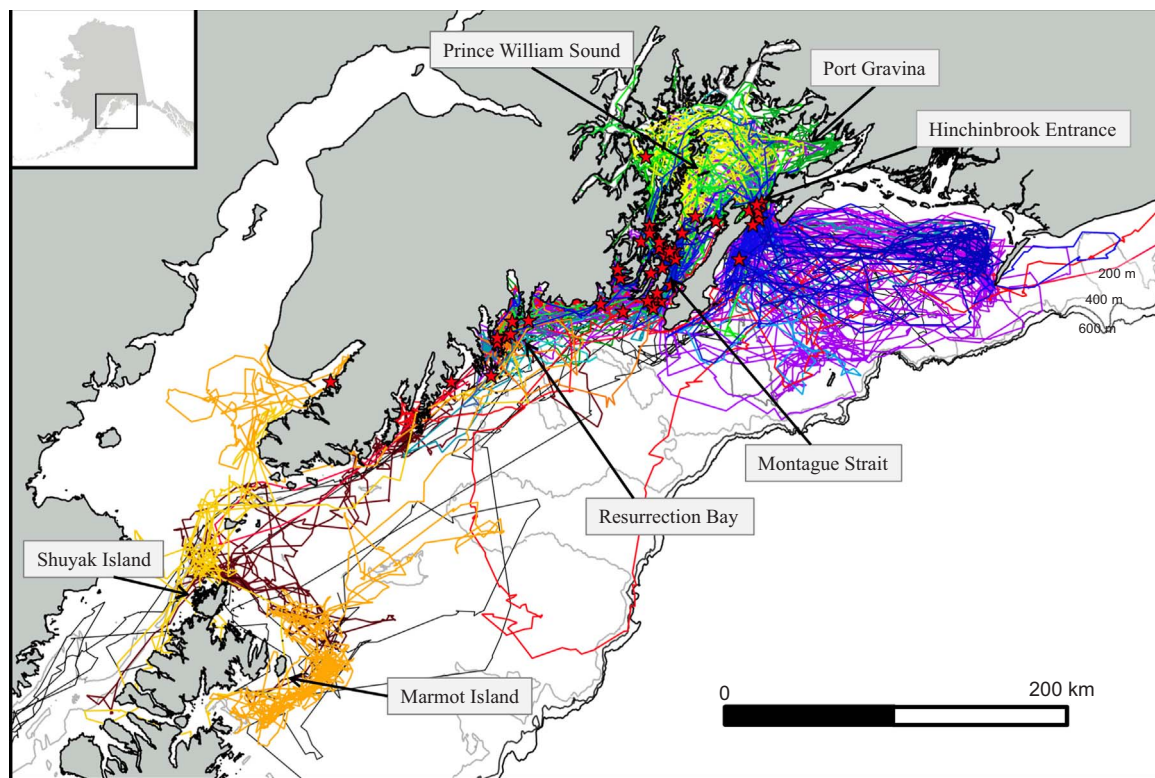
Fig. 1. Study area for resident killer whales (*Orcinus orca*) with tag deployment locations (red stars) and 200 m, 400 m, and 600 m bathymetry contours. Tracklines are colored by pod, AB (blue), AD5 (gold), AD16/AK (green), AE (yellow), AF/AG (black), AI (light blue), AJ (purple), AX48 and AY (dark red). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Number of tagged animals, locations, and transmission days from tagged resident killer whales (*Orcinus orca*), by pod, 2006–2014.

Pod	Tag Deployments	Filtered Locations	Total days	Months represented
AB	5	1287	113	6,7,8,9,10,11
AD5	3	746	127	6,7,10,11,12
AD16/AK	4	1155	166	6,7,8,9,10
AE	2	357	73	8,9,10
AF/AG	3	884	55	7,8,9
AI	3	831	47	8,9,10,11
AJ	10	4534	348	6,7,8,9,10,11,12
AX48	4	890	100	6,7,8
AY	2	847	77	6,7
AW	1	250	35	8,9
Total	37	11,781	1141	6,7,8,9,10,11,12

hours apart are likely to miss non-linear movements.

3. Results

Transmissions were received from 37 deployments on killer whales for a total of 1141 transmission days between 2006 and 2014. Transmissions were received between the months of June and December in all years and from one tag in January 2011 (Table 1). The majority (91.9%) of transmissions were received between June and October. The mean number of days that each tag transmitted was 26.1 days. Of the locations that passed the Douglas Argos Filter, none were received from beyond the continental shelf break (Fig. 1). Median short-term movements in this study were estimated at 4.43 km/h, which extrapolates to 106 km/day.

Strong seasonal differences in core use areas were evident, particularly between summer and fall months. Hinchinbrook Entrance was a strong focal area for the AJ pod during June, July, and August, but was used much less in September and October (Fig. 2). Montague Strait was heavily used in August, September, and October, but not in earlier months (Figs. 2,3). The waters west of Kayak Island saw consistent use in June, July, and August, but less use in September and October (Fig. 2). Port Gravina was a focal area for two pods during June, July, and August, but had no evident use during September or October (Fig. 3).

Differences in core use were also evident between individual pods. The AB, AI, and AJ pods accounted for most of the use in Hinchinbrook Entrance and most of the use in Montague Strait, and they were the only pods that demonstrated regular use of waters west of Kayak Island (Fig. 4). The waters west of Kayak Island are likely important, as 12 out of the 16 tagged animals from the AB, AI, and AJ pods made at least one visit to this area. The AB, AI, and AJ pods were also the primary pods to use offshore areas ranging near the shelf break. The AD16 and AK pods did not use offshore waters, and were the primary users of the northern edges of Prince William Sound, including the long glacially carved fjords (Fig. 1). These two pods were responsible for seven out of the eight trips recorded into these long fjords. The AE pod used the inside waters of Prince William Sound, but were not observed using the long fjords, nor offshore waters (Figs. 1,4). The AD5 and AY pods were the primary pods to use Resurrection Bay and the waters adjacent to Shuyak and Marmot Islands, near the northern end of Kodiak Island (Figs. 1 and 4).

A high percentage of positions in Montague Strait were located within a glacially carved trench that is 200–300 m deep (Fig. 5). Within Montague Strait, 1346 of 2035 locations (66%) were in waters between 200 and 300 m deep, even though this only represents 21% of the possible area. The 200-m isobath creates a clear boundary for the majority of these locations. Furthermore, the AB, AI, and AJ pods were the primary pods to concentrate over these deeper waters (Fig. 5). This dynamic was not observed in other areas of Prince William Sound or the northern Gulf of Alaska.
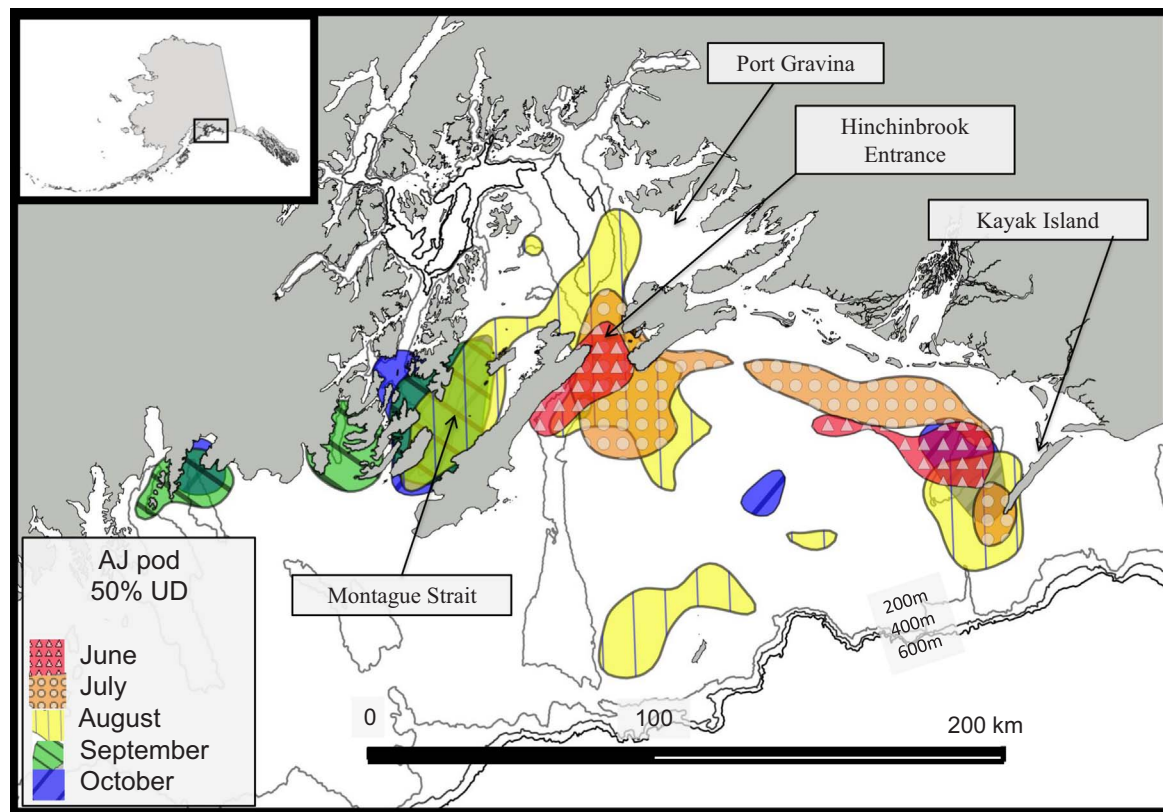
Fig. 2. Monthly variation in space use by AJ pod of resident killer whales (*Orcinus orca*). Core area use, or 50% UD, is displayed by month. Monthly 50% UD is displayed with color and symbols; June (red with triangles), July (orange with circles), August (yellow with vertical lines), September (green with back diagonal), October (blue with forward diagonal). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

Differences in core use areas occurred seasonally for the tagged resident killer whales in the northern Gulf of Alaska, and these differences were at times specific to individual pods. We presume that the observed seasonal shifts in core use areas (Montague Strait, Hinchinbrook Entrance, Port Gravina) may be related to the specific timing of returns of Chinook, chum and coho salmon to their natal spawning streams, and the congregation of Chinook salmon while foraging in nearshore waters. Salmon perform highly predictable seasonal returns to their natal streams, and Chinook, coho, and chum salmon have been shown to comprise a major portion of the summer diet for resident killer whales in south central Alaska (Matkin et al., 2013; Saulitis et al., 2000). The arrival of resident killer whales and salmon has been shown to occur concurrently in British Columbia (Hanson et al., 2010), and Chinook and coho salmon have been shown to dominate the summer diet of resident killer whales in that area as well (Ford and Ellis, 2006; Ford et al., 2016). Survival rates for resident killer whales in British Columbia have been linked with abundance of Chinook salmon (Ford et al., 2010). In Alaska, prey samples have been collected at two of the high-use areas (Hinchinbrook Entrance and Montague Strait) noted in this study, and were dominated by scales from Chinook, coho, and chum salmon (Matkin et al., 2013; Saulitis et al., 2000). Seasonal dietary shifts from Chinook to coho have been documented in both Alaska and the Pacific Northwest (Ford et al., 2016; Matkin et al., 2013).

The Alaska Department of Fish and Game reports peak chum return timing to occur in late June in Prince William Sound (ADFG, 2002), which could be partially responsible for the high use of Hinchinbrook Entrance in early summer. Chum salmon scales from predation by resident killer whales have been collected in Hinchinbrook entrance in June (Matkin et al., 2013). Hinchinbrook Entrance is one of the two main entrances to Prince William Sound, and is the main influx of water into the sound (Halverson et al., 2013). Scale collection during predation events has not occurred in Port Gravina, but the timing is consistent with Chum salmon runs in the area. Further collection of scat or scales and flesh from predation events is warranted.

The high use in Montague Strait in late summer and fall coincides with large congregations of adult Pacific herring (*Clupea pallasi*) and the Humpback whales (*Megaptera novaeangliae*) that prey on them (Moran et al., 2015). Although herring are important in the diet of killer whales in Norway and Iceland, the technique for hunting them is evident from the surface (Samarra and Foote, 2015; Similä et al., 1996). Herring predation is very rare for well studied killer whales in the North Pacific based on observations from surface kill remains and scat analysis (Ford and Ellis, 2006; Ford et al., 2016; Saulitis et al., 2000). It is possible that this aggregation of herring attracts feeding Chinook and coho salmon.

Pod specific core use preferences described in the present study may be the result of cultural transmission of learning through generations, as individuals swim with their mother or close relatives throughout their lives (Bigg et al., 1990). Cultural transmission has been documented amongst killer whale acoustic repertoires, foraging strategies, and habitat preferences (Guinet and Bouvier, 1995; Hauser et al., 2007; Similä and Ugarte, 1993; Yurk et al., 2002). Similar pod-specific core use patterns were noted in the San Juan Islands for southern resident killer whales (Hauser et al., 2007). Another possible cause of these patterns could be competition, but this has not been observed. To the contrary, killer whale pods are often attracted to one another for social and reproductive reasons. They have been shown to mate outside of their natal pod, particularly with pods that are least genetically similar (Barrett-Lennard, 2000). Furthermore, closely related pods in this study demonstrated similar patterns of space use. AB, AI, and AJ pods share the 'northern resident' haplotype (Parsons et al., 2013), and are the only pods shown to use offshore waters west of Kayak Island and
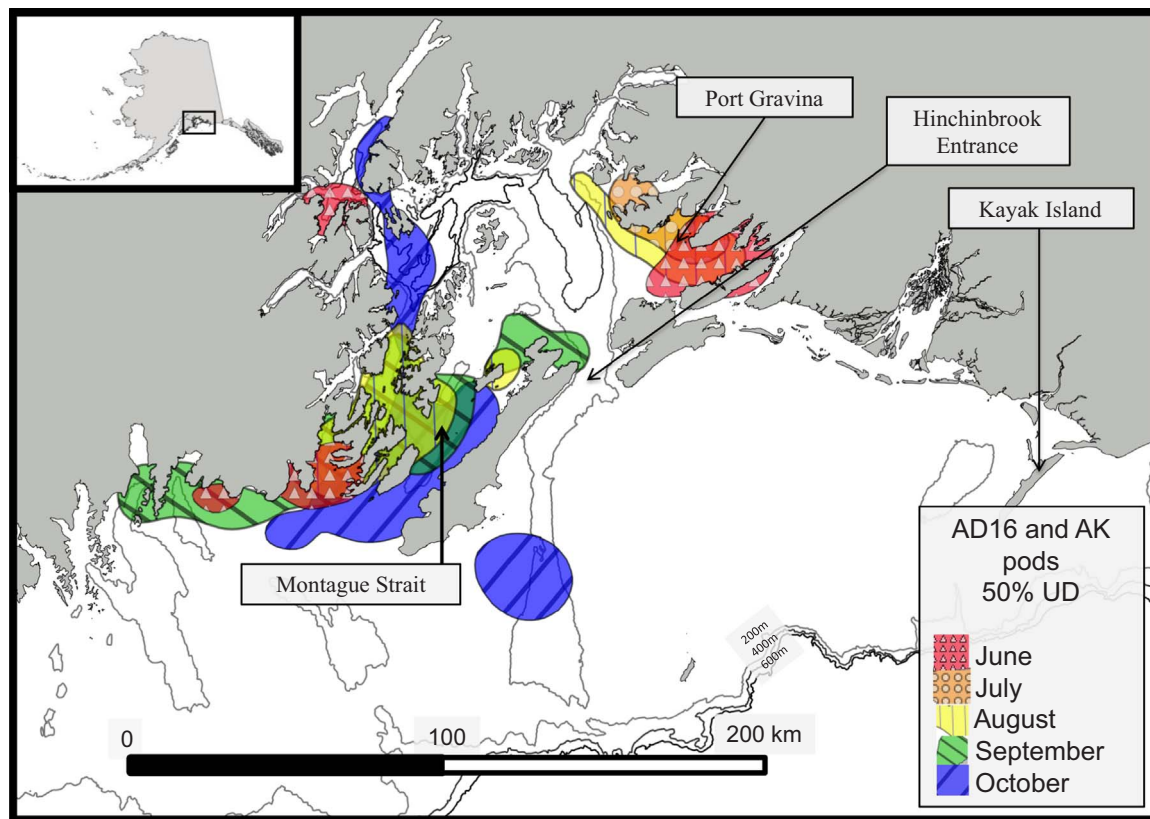
Fig. 3. Monthly variation in space use by combined AD16 and AK pods of resident killer whales (*Orcinus orca*). Core area use, or 50% UD, is displayed by month. Monthly 50% UD is displayed with color and symbols; June (red with triangles), July (orange with circles), August (yellow with vertical lines), September (green with back diagonal), October (blue with forward diagonal). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Hinchinbrook Entrance. AD16 and AK pods share the 'southern resident' haplotype, and are the only pods to use upper fjords and to focus on nearshore areas. The very large linear range difference between the unrelated AE pod (roughly 200 linear km) which has the 'southern resident' haplotype, and the AF and AG pods (1300 linear km) which have the 'northern resident' haplotype, is striking. While this difference could be attributed to diet differences, we suggest that these differences in linear range stem from social and reproductive behavior (Matkin et al., 1997).

Bathymetry appears to be important in some core use areas, and should be explored further. Our results show that the deeper waters (200–300 m) of Montague Strait and Port Bainbridge are important during summer and fall, particularly for the AB, AI, and AJ pods. Bathymetric features have been found to be preferential habitat for other delphinids (Dahood, 2009; Ingram and Rogan, 2002). Depth sensors were present on a limited number of tags in this study, and suggest that resident killer whales in this area regularly dive to or near the seafloor in 200–300 m (Matkin et al., 2013). Chum salmon in Japan have been observed to dive to the bottom in response to presence of Dall's porpoise (*Phocoenoides dalli*) (Yano et al., 1984), and Chinook salmon have been documented diving 300–400 m after release (Candy and Quinn, 1999). Furthermore, DTAGs deployed on northern resident killer whales in British Columbia documented the capture of Chinook, chum, and coho salmon as deep as 264, 164, and 165 m respectively (Wright, 2014). If salmon aggregate in these deep basins near the entrances to avoid predation, or to feed on congregating forage fish such as herring, the use of deeper waters within Montague Strait and near Kayak Island could be explained. Interestingly, many other deep glacial trenches in the continental shelf do not appear to be important for these Gulf of Alaska resident killer whales during the summer and fall.

Alternatively, the deep waters of Montague Strait, Hinchinbrook Entrance, and Kayak Island could provide important foraging

opportunities on benthic species, including Pacific halibut (*Hippoglossus stenolepis*), lingcod (*Ophiodon elongatus*), and sablefish (*Anaplopoma fimbria*). It would be unlikely to be able to collect tissue samples from predation events on these species at the surface if they were consumed in deeper waters. However, despite the availability of these potential prey species in other deep waters at the edge of the continental shelf and in the deep glacial trenches that cut across the shelf, these locations were not used much by tagged individuals in this study. Additionally, recent studies of killer whale fecal samples from the southern resident killer whale population in the San Juan Islands demonstrate similar findings to the surface collections of fish scale and tissue after predation events, which is that salmonid prey dominate the diet in summer months (Ford et al., 2016). The seasonality of use by killer whales in Montague Strait, Hinchinbrook Entrance, and Kayak Island also supports surface observations of salmon predation (Matkin et al., 2013; Saulitis et al., 2000).

One of the important revelations of this project, and one of the main advantages of satellite telemetry over other methods of space use assessment, was the discovery of previously unknown core use areas. The region just west of Kayak Island appears to be an important area, particularly in June, July, and August (Fig. 2). Additionally, the areas southeast of Marmot Island and northeast of Shuyak Island appear to be important for at least the AD5 and AY pods (Fig. 1). Due to the remote location and difficult weather conditions, these areas would not likely be revealed by boat surveys, which can be biased by survey effort (Baird et al., 2010). Interestingly, most of the use near Kayak Island was from AB, AI, and AJ pods, and nearly every tagged member of AB, AI, and AJ pods visited this area. In the future, passive acoustics may help detail the importance of these areas.

The strong temporal patterns and pod-specific core use described in the present study should be considered in conservation management strategies. As an example, vessel traffic in the oil tanker lanes through
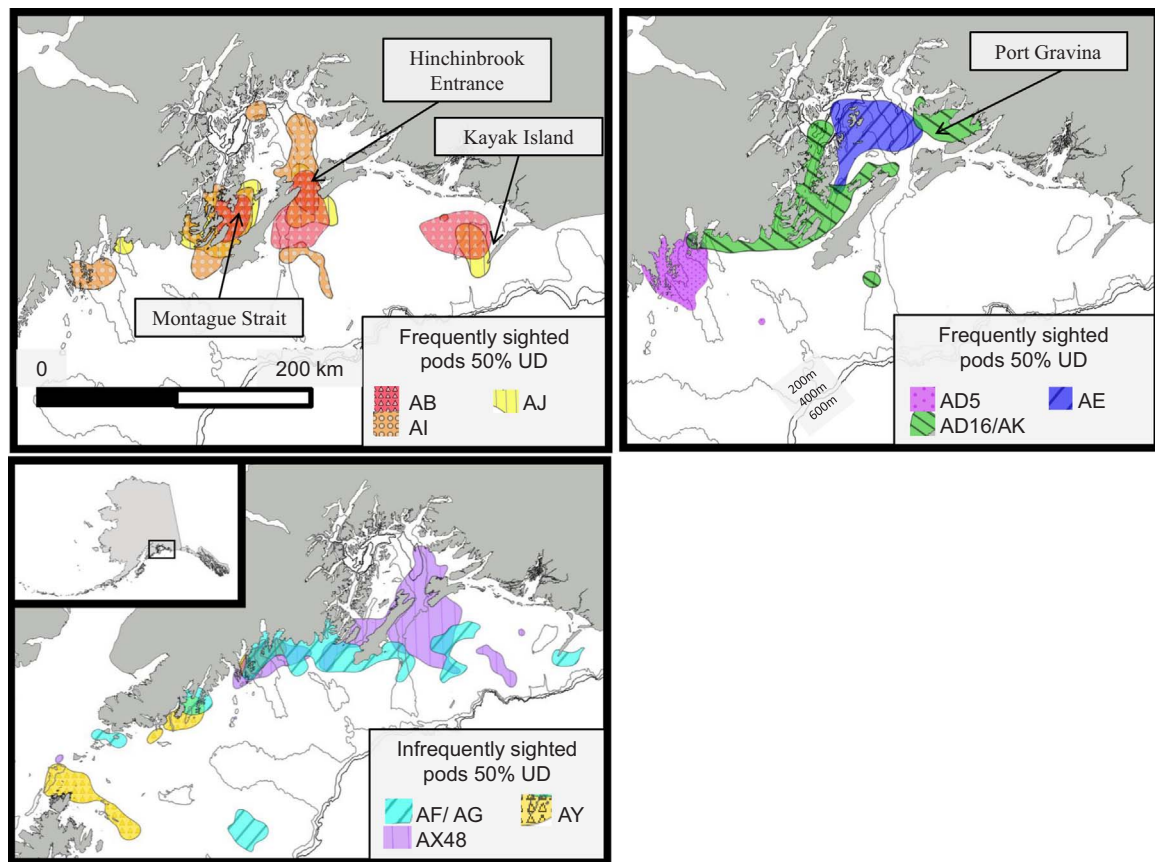
Fig. 4. Pod-specific variation in space use for resident killer whales (*Orcinus orca*). Pod 50% UD is displayed with color and symbols; AB (red with triangles), AI (orange with circles), AJ (yellow with vertical lines), AD5 (violet with circles), AD16/AK (green with back diagonal), AE (blue with forward diagonal), AF/AG (light blue with forward diagonal lines), AX48 (violet with vertical lines), AY (gold with triangles). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Hinchinbrook Entrance may have a much larger impact on resident killer whales in June and July than in September and October, and impact by winter vessel traffic is largely unknown. Additionally, the AB pod, which lost 25% of its members after swimming through the Exxon Valdez Oil Spill in 1989 (Matkin et al., 2008), appears to depend heavily on Hinchinbrook Entrance, Montague Strait, and the waters

west of Kayak Island. Restoration plans for the AB pod should consider the protection of these areas. Future research should investigate the relationship between seasonal differences in core use and salmon migration routes, and also examine wintertime use.

From this study we have two main conclusions. First, is that core use areas in this population have extremely high variability between pods,
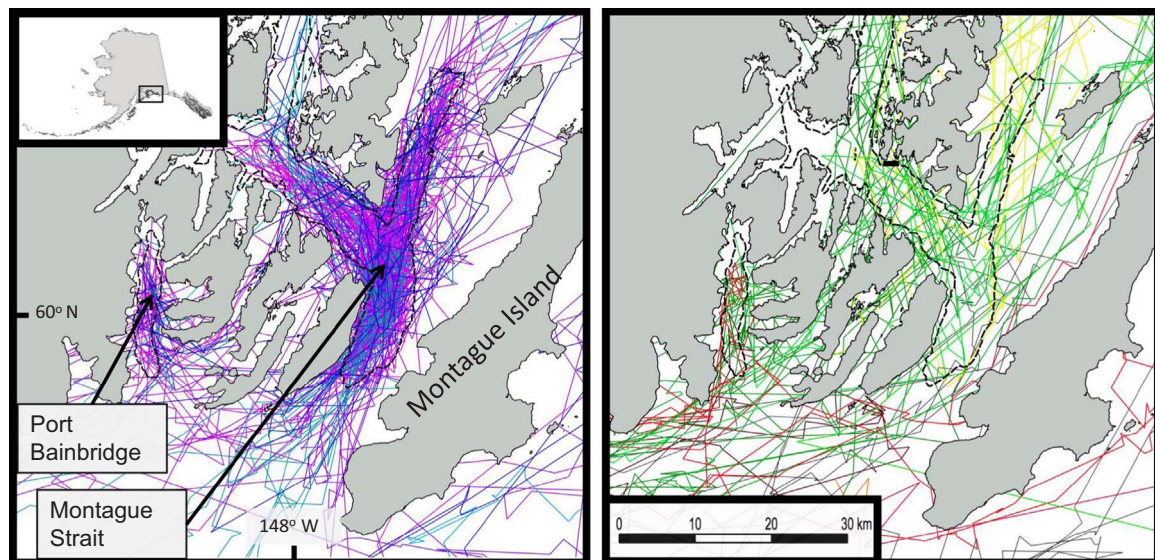

Fig. 5. Disproportionate use in lower Montague Strait and Port Bainbridge, with 200 m bathymetric contour (black dashed line). AB (blue), AI (light blue), and AJ pods (violet) are displayed together on the left panel. AD5 (gold), AD16/AK (green), AE (yellow), AF/AG (black), AX48 and AY pods (dark red), are displayed on the right panel. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

which may be due to cultural transmission within matrilineal groups. The second is that there are distinct seasonal differences in use patterns. These differences may be in response to the migratory return and feeding congregations of various species of salmon. Continued diet studies are warranted to investigate relationships between these seasonal differences in space use and the seasonal abundance of available prey.

Acknowledgements

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