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Identifying overlap between humpback whale foraging grounds and the Antarctic krill fishery

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ABSTRACT

The Antarctic krill fishery is the largest in the southern ocean, but currently operates without fine-scale information on whale movement and behavior. Using a multi-year dataset of satellite-tagged whales, as well as information on krill catch levels, we analyzed the spatial distribution of whales and fisheries effort within the small-scale management units defined by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). Using a Bayesian movement model to partition whale movement into traveling and area-restricted search states, we found that both whale behavior and krill catch effort were spatially clustered, with distinct hotspots of the whale activity in the Gerlache and southern Branfield Straits. These areas align with increases in krill fishing effort, and present potential areas of current and future conflict. We recommend that the Antarctic West and Bransfield Strait West management units merit particular attention when setting fine-scale catch limits and, more broadly, consideration as critical areas for krill predator foraging.

1. Introduction

Minimizing overlap between fishing effort and predators is a persistent challenge in managing marine fisheries. To create ecologically informed guidelines, managers need detailed information on occurrence, abundance and behavior of predator species. This is especially difficult in polar regions where information can be scarce and observation windows are curtailed due to extreme climate. High-resolution tracking data provides a bridge between species locations and geographically dependent behaviors (Hays et al., 2016). By incorporating behavior into conservation action, we gain greater insight into the threats animals face, and increase the likelihood that management plans achieve positive conservation goals (Ellison et al., 2012 Trathan et al., 2015).

The Antarctic krill (*Euphausia superba*) is the keystone species of the Antarctic ecosystem, providing the primary food source for a diverse group of predators including fish, penguins, seals, and whales (Hill et al., 2006). Antarctic krill form dense swarms, sometimes in excess of 10,000 individuals per cubic meter, extending 200–300 m in depth and several kilometers wide (Tarling et al., 2009, Nowacek et al., 2011; Espinasse et al., 2012). The Antarctic Krill fishery is the largest in the Southern Ocean with a reported total catch of 293,815 metric tonnes (mt) in 2015. This catch has fluctuated greatly, with a peak of nearly 500,000 mt in the 1980s, to a low of < 100,000 mt in the early 2000s, to a rapid increase to 300,000 mt since 2009 (Nicol et al., 2012). This rise is due to the expansion of the fishery by new nations, as well as an extension of fishing effort into austral autumn and winter months (CCAMLR, 2015).

The krill fishery is managed by the Commission for the Conservation of Marine Living Resources (CCAMLR). CCAMLR was formed in 1982 as part of the Antarctic treaty system with the goal of ‘providing maintenance of the ecological relationships between harvested, dependent and related populations of Antarctic marine resources’ (Constable et al., 2000). The CCAMLR management guidelines require that the krill fishery not interfere with the population growth of Antarctic krill predators (Kawaguchi et al., 2006). However, the management of the krill fishery has not assessed the needs and behavior of baleen whales, which are the largest krill predators in the Antarctic.

The krill fishery historically included large expanses of Antarctic waters, but is currently concentrated in the South Atlantic (FAO statistical Area 48). Records from 2015 report 146,191 mt taken from the Antarctic Peninsula and South Shetlands Islands (Subarea 48.1), 72,455 mt from the South Orkneys Islands (Subarea 48.2), and 75,169 mt from South Georgia Island (Subarea 48.3) (CCAMLR, 2015). Our study focuses solely on subarea 48.1 (Fig. 1), an area of increasing importance to the fishery. The current precautionary annual

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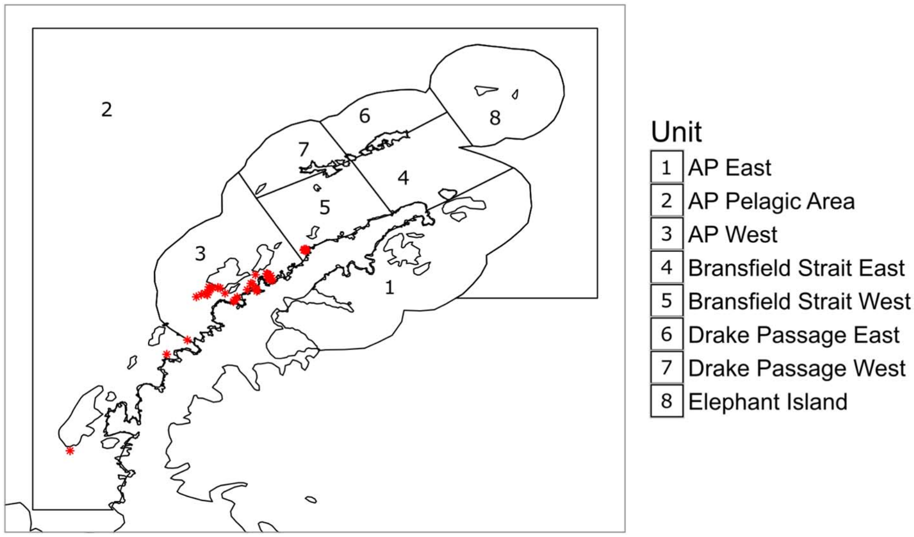

Fig. 1. CCAMLR small-scale management units for the West Antarctic Peninsula krill fishery (CCAMLR Sub-unit 48.1). For brevity "Antarctic Peninsula" is abbreviated AP.

catch limit of 5.61 million mt is shared among all subareas, and is substantially more than the total annual catch (Nicol et al., 2012). In 2009 CCAMLR adopted an interim measure (Conservation Measure 51-07) to distribute 620,000 mt of catch limit across subareas, with a limit of 155,000 mt for subarea 48.1. This level has been reached four times since 2010, with each event leading to the closure of the subarea for the remainder of the season (Nicol and Foster, 2016). CCAMLR has attempted to further manage the spatial distribution of fishing effort by agreeing upon small-scale management units (SSMUs; Fig. 1). However, to date, CCAMLR has failed to agree on a method to distribute the total precautionary catch limit between SSMUs (Hewitt et al., 2004). Our aim is to determine the overlap between the krill fishery and areas of whale foraging, in order to recommend whether specific small-scale management units should have restrictions in fishing effort or duration.

Since the cessation of commercial whaling in the Southern Hemisphere in the late 20th century, humpback whales (*Megaptera novaeangliae*) have recovered to become the most numerous whale species in the region (Clapham et al., 1999 Herr et al., 2016 Matsuoka et al., 2006). Previous work has shown that humpback distribution is related to the distribution and abundance of krill (Friedlaender et al., 2006 Nowacek et al., 2011). At the fine-scale, the foraging behavior of humpback whales is affected by the depth and density of krill patches, due to the energetic demands of whale foraging and life-history (Friedlaender et al., 2013 Tyson et al., 2016). Humpbacks whales may therefore be vulnerable to disturbance from the krill fishery due to their reliance on krill as a primary food source (Nicol et al., 2008). Current information on the foraging behavior of Antarctic humpback whales comes largely from short-term tagging efforts (e.g. Friedlaender et al., 2013 Johnston et al., 2012), and from ship-based surveys (Hedley et al. 2001 Herr et al., 2016 Santora et al., 2010). We used a large multi-year dataset (> 40,000 Argos locations) of tagged humpbacks to assess the space use and behavior within CCAMLR small-scale management units. Our goals are to 1) describe the areas of humpback presence in reference to the CCAMLR small-scale management units, 2) partition movement into traveling and area-restricted search states, and 3) compare the areas of whale behavior with the distribution of krill fishery activity along the Antarctic Peninsula.

2. Methods

2.1. Satellite tagging and tracking

We deployed Wildlife Computers (Redmond, WA, USA) SPOT5 Platform Transmitting Terminals (PTTs) in 2012, 2013, 2015, and 2016 (Table S1). Each tag is contained in a sterilized housing designed to penetrate the whale's skin and blubber up to 290 mm, and is anchored in the tissue beneath the blubber with stainless steel barbs, with the transmitting antenna remaining free outside of the animal. Tags were deployed by experienced researchers from a Zodiac Mark V or a Solas ridged-hulled inflatable boat with a 40 hp 4-stroke engine using an ARTS Whale Tagging PLT compressed air system. Whales were approached at idle speed from oblique angles so as not to cross over the flukes. No dependent calves were tagged, all whales were presumed to be adults based on their size. Tags were deployed from a range of 3–10 m and placed near the dorsal fin, which contains the thickest blubber layer, and also provides the greatest height to transmit positional information via the exposed antenna.

All tags transmitted positional information via the Argos satellite system and were activated via a salt-water switch. In 2012, tags transmitted only during the hours 00:00–04:00 and 12:00–16:00 GMT. All subsequent tags were set without duty cycling and attempted to transmit data on each surfacing. Our raw data included 46,421 observations for 42 humpback whales from 2012 to 2016. We filtered observations without location data (n = 103), duplicate timestamps (n = 186), locations on land (n = 1800), and implausible speed between consecutive locations (n = 2552) to create a filtered set of observations. The duty cycle from the 2012 tags made it difficult to use tracks with large gaps and they were removed (n = 6). From this initial dataset, we kept tracks that had points within 6 h intervals, and discarded tracks < 24 h (Fig. S1).

2.2. CCAMLR units krill fishery data

Commercial krill catch data were provided with permission by CCAMLR for Subareas 48.1–48.4, aggregated into 0.5° latitude and 1.0° longitude grid cells. CCAMLR's small-scale management units range in size from 16,000 km^2 to 440,000 km^2 covering the northern section of the Antarctic Peninsula to south of Anvers Island (Fig. 1). Krill catches in kg were used from 1980 to 2015 and summed across all CCAMLR member nations. Catch is reported on a haul-by-haul basis, on either monthly or 5-day intervals, depending on the amount reported. The haul-by-haul data requires locations for start and end fishing positions. For analysis, the total amount of krill collected in each georeferenced grid cell was aggregated across seasons to represent the catch intensity in the waters surrounding the western side of the Antarctic Peninsula (Fig. 2).

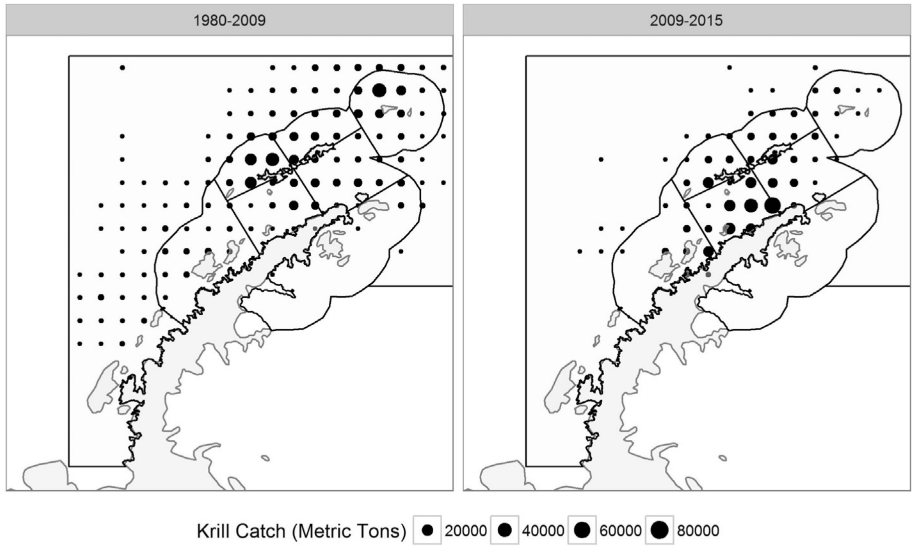

Fig. 2. Total krill catch between 1980 and 2009 and 2009–2015 in the West Antarctic Peninsula. The krill fishery has moved inshore during recent years. The eight CCAMLR small-scale management units for region 48.1 are shown in black lines.

2.3. Hierarchical state-space models

To associate spatial patterns of animal movement with predicted behavior states, we used a hierarchical state-space model. State-space movement models combine a process model that estimates movement parameters and an observation model that accounts for the spatial uncertainty using Markov Chain Monte Carlo (MCMC). We used a dynamic correlated random walk model following Jonsen et al. (2005) and Bestley et al. (2013), in which each movement stems from either a 'traveling' or 'area-restricted search' state (Bestley et al., 2013; Beyer et al., 2013 Jonsen et al., 2005). The traveling state is defined as long straight tracks with small turning angles. Area-restricted search is defined as short step lengths with large turning angles. We prefer area-restricted search over 'foraging', since we recognize that whales will not be exclusively feeding during the defined state. Humpbacks display a threshold response to prey availability, likely due to the physiological effort required for foraging (Goldbogen et al., 2008). This creates a characteristic spatial signature of whale foraging movements that may last up to several days (Dalla Rosa et al., 2008).

Our discrete time observation model assigns each Argos location to a behavioral state based on the movement characteristics among consecutive Argos locations. We chose to model movement on a six hour time step, with individuals assumed to move in a straight line within in each time step. This assumption allows us to balance between the tractability of model-fitting and the temporal autocorrelation of whale behavior. The six hour time step is a short enough that we believe it is unlikely that we would miss transitions between foraging and traveling state, but coarse enough that we can fit the model using the data available. Given the strongly stereotyped nature of whale movements and the coarse categorization of the CCAMLR management units, we do not believe addition fine-scale variation in Argos error will influence our analysis. Our movement process model states that the geographic location of individual (i) at time (t) along a track (g) is multivariate normally distributed with a mean (d) and a variance (σ). The mean position (d) is a first order markov process, meaning that it depends on the previous step ($Y_{i,g,t} - Y_{i,g,t-1}$), plus the movement step at time t. This movement is a function of the degree of autocorrelation in step length (γ) and the turning angle (T). Step lengths and turning angles are considered to come from two behavioral states, 'traveling' and 'area-restricted search'. The predicted behavioral state (S) is a multinomial draw with a probability of being in the traveling state ($\phi_{i,g,t}$) or in the feeding state ($1 - \phi_{i,g,t}$).The probability for each behavioral state at time t is a function of the parameter $\alpha_{s_{i,g,t-1}}$, which is the estimated temporal autocorrelation in behavioral states. The variance in the argos observation estimate (τ_{argos}) was fixed for Argos error following the results reported in Jonsen et al. (2005), Bestley et al. (2013), (2015) and Jonsen (2016).

Process model

$$Y_{i,g,t+1} \sim \text{Multivariate Nomal}(d_{i,g,t}, \sigma)$$

$$d_{i,g,t} = Y_{i,g,t} + \gamma_{s_{i,g,t}} {}^{*}T_{i,g,t}{}^{*}(Y_{i,g,t} - Y_{i,g,t-1})$$

$$T_{i,g,t} = \begin{matrix} \cos(\theta_{s_{i,g,t}}) & -\sin(\theta_{s_{i,g,t}}) \\ \sin(\theta_{s_{i,g,t}}) & \cos(\theta_{s_{i,g,t}}) \end{matrix}$$

$$S_{i,g,t} \sim Multinomial(\phi_{i,g,t} \quad 1 - \phi_{i,g,t})$$

$$\text{logit}(\phi_{i,g,t}) = \alpha_{s_{i,g,t-1}}$$

Observation model

$$w_{i,g,t,u} \sim \text{Multivariate Normal}(\hat{z}_{i,g,t,u}, \tau_{argos})$$

$$\hat{z}_{i,g,t,u} = (1 - j_{i,g,t,u})^{*}\, Y_{i,g,t-1} + j_{i,g,t,u}{}^{*}\, Y_{i,g,t}$$

We ran our Bayesian model in Jags (Plummer, 2003) for 2 chains, each with 40,000 runs, with a burn-in of 38,000 draws. To reduce correlation among chains, we thinned the posterior by saving every 4th draw, yielding 500 values for the posterior distribution of each parameter.

To associate specific geographic areas with whale activity, we overlaid our study area with a 100 by 100 grid of equal area cell ($\sim 23\ km^2$ in polar stereographic projection). We then calculated the total time each animal spent in each cell by taking the difference between the first and last timestamp of consecutive observations. The cell size was intentionally coarse, such that whales could only rarely pass through a cell in a single observation point. These single observations were ignored, since they did not represent stationery occupancy of a cell. By adding the individual time rasters together, we created a map of the total time in each cell based on traveling behavior, area-restricted search, and both behaviors combined. To assess whether our results had been influenced by the location of tag placement, we performed the same analysis after trimming the first 7 days of data off each tag deployment. Whales can travel > 100 km in this time frame, and we use these data to compare to the map of whale behavior from the full dataset.

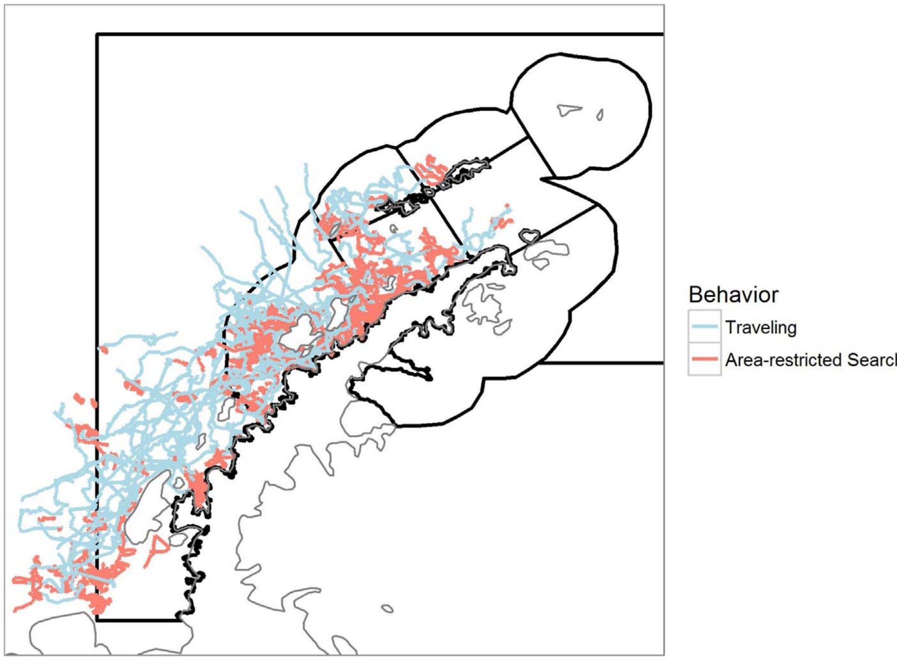

Fig. 3. Predicted behaviors for each filtered whale track based on the state-space model. If the mean probability of switching to the area-restricted state (ϕ_{ARS}) was > 0.5, the observation was labeled as area-restricted search. The eight CCAMLR small-scale management units for region 48.1 are shown in black lines.

2.4. Do whales occupy SSMUs non-randomly?

Given that the SSMUs cover almost the entire study area, we must determine whether the pattern of spatial use by whales differs from random. Given the number of observation hours, and the differences in size of each of the SSMU, which units are occupied more or less than expected? We used parametric randomizations to create a null distribution of whale occupancy days based on an equal probability of presence in any cell. Using a 100 × 100 grid to cover the study area, for each of the 4818 cells ($cell_{x,y}$) within the SSMUs, the null expectation for the number of whale days is:

$$\text{Whale days}_{x,y} \sim \text{Multinomial}(k, \rho)$$

where k is the total number of whale days (3129 days) and $\rho = (1/4818)$ (i.e. equal likelihood among all cells). We then summed the total number of whale days for each SSMU. We repeated this randomization 5000 times to generate a null distribution. We then compared our true number of whale days per SSMU to the null distribution of whale days per SSMU to determine if it was more, less or not-differing form random space use. If the observed value was outside the lower 5th or upper 95th of the null distribution, we considered it different from random.

2.5. Do whales behave non-randomly inside SSMUs?

To determine whether whale behavior differed from random within each SSMU, we used a null model to generate the expected proportion of area-restricted search given the total number of observations. Given that the model has to be in either traveling in area-restricted search state, the null expectation is a 50/50 split among behaviors. As the observation time decreases, there may be insufficient power to differentiate our results from random behavior. We evaluated this using the following null model:

$$\text{Proportion Area restricted search}_{x,y} \sim \text{Binomial}(n, k)$$

Where n = the number of whale observation days within each SSMU and k is 0.5 (i.e. equal probability of foraging or traveling). We drew 1000 draws from this null model to determine the expected deviation equal split given our sampling effort. If the observed value was outside the lower 5th or upper 95th of the null distribution, we considered our result different from random.

3. Results

Our analyzed data contained 29,346 observations from 33 individuals from 2013 to 2016. On average individuals had 11.95 tracks, with an average track duration of 80.9 h. The average number of observations per individual within our study area was 1187 (min = 31, max = 2731). Average deployment for each individual within our study area was 46.06 days (min = 1.75, max = 145.5). Average time between observations was 1 h and 5 min. Average distance between points was 824 m, although this does not include estimate Argos error ellipses, and should be seen as approximate measure. We witnessed 11 whales begin their migration northward from Antarctic waters (defined as north of − 60 latitude), ranging from March 22nd to July 17th (mean = May 25th). These migration events were assumed to relate to other life history functions (e.g. mating, calving) and were not included within this analysis.

Our behavioral model partitioned animal movement resulting from traveling and area-restricted search states. The traveling state was associated with high movement autocorrelation (mean $\gamma_1 = 0.91\ (0.88, 0.93)$), and the area-restricted state with low movement autocorrelation (mean $\gamma_1 = 0.05\ (0.03, 0.06)$). The mean probability of switching from traveling to area-restricted search was 9.9% (7.2%, 12.3%). The mean probability of switching from area-restricted search to traveling was 4.7% (3.4%, 6.2%). Transition probabilities must add to one, therefore the mean probability of remaining in the traveling state was 90.1% (87.7%, 92.8%), and the probability of remaining in the area-restricted search state was 95.3% (93.8%, 96.6%).

Overlaying the predicted behavioral state on our observed tracks showed strong concentrations of activity on the south side of Anvers Island, in the Gerlache Strait and along nearshore waters in Marguerite Bay (Fig. 3). Area-restricted search in the Bransfield Strait was restricted to the continental coastline, and away from the deep canyon south of Livingston Island. With the exception of one major feeding event on North side of Livingston Island in the late austral fall, no bouts of area-restricted search were seen north of the South Shetland Islands. We found no evidence of area-restricted search as whales crossed the Drake Passage and continued north towards tropical breeding grounds.

Table 1
Number of whale hours in each the CCAMLR small-scale management units (SSMUs) within Subarea 48.1. The duration of time was calculated by the time difference between the last observation and the first observation for each movement track for each animal. The sum value across animals is shown. We also included 'outside proposed units', which largely consists of observations west of Marguerite Bay (see Fig. 3). Ordered by total time in area-restricted search. Total krill catch is shown between 1980 and 2009 and 2009–2015, as well as the catch density per year, to account for difference in SSMU area.

Unit	Whale traveling (days)	Whale area-restricted search (days)	Krill catch (metric tons/year)		Catch Density (metric tons/km^2/year)	
			1980–2009	2009–2015	1980–2009	2009–2015
Antarctic Peninsula West	222.17	430.78	332	9335	0.01	0.25
Bransfield Strait West	61.33	193.68	13,486	55,688	0.06	2.47
Antarctic Peninsula Pelagic Area	122.82	134.54	2082	141	> 0.01	> 0.01
Drake Passage West	41.42	63.64	17,774	10,132	1.11	0.63
Outside Proposed Units	42.15	47.78	–	–	–	–
Bransfield Strait East	5.19	4.29	1357	11,044	0.05	0.40
Drake Passage East	6.53	5.32	6923	4882	0.42	0.30
Elephant Island	0.00	0.00	10,917	620	0.30	0.02
Antarctic Peninsula East	0.00	0.00	156	–	0.08	–

Partitioning our results by the CCAMLR small-scale management units (SSMUs), the majority of whale activity occurred in the Antarctic Peninsula West and Bransfield Strait West SSMUs (Table 1). This activity was disproportionately in the area-restricted search state. Only in the Bransfield Strait East and Drake Passage East units was there greater time spent in the traveling state. We recorded a total of 47 whale days in the area-restricted search state outside of the current SSMUs for the krill fishery, with the majority of this activity occurring southwest of Antarctic Pelagic Area SSMU boundary towards Marguerite Bay (Fig. 4).

Aggregating the krill catch effort by SSMU showed uneven spatial catch by the krill fishery (Table 1) (Fig. 2). The Bransfield Strait West and the Drake Passage West units had the most catch between 1980 and 2009. Since 2009, the Drake Passage West unit has been used less frequently, but remains the 2nd most used unit by area. In contrast, the catch in the Bransfield Strait West unit increased dramatically during this period. Smaller increases were seen in Antarctic Peninsula West and Bransfield Strait East units. The temporal trend in krill fishery distribution is moving towards nearshore areas, with a decrease in the reported catch from the Elephant Island unit, and the lack of reported catch in the Antarctic East unit since 2009.

We asked whether whales used SSMUs non-randomly, given the differences in size of the management units. Compared to a random model of distribution, whales used the Bransfield Strait West, Drake Passage West, and Antarctic Peninsula West units more frequently than expected (Fig. 5a). The greatest number of observation days was within the Antarctic Peninsula West management unit. While several of the management units had less whale days than expected by random chance, we refrained from overly interpreting this finding (see discussion).

Our second randomization asked whether whales behaved non-randomly, given their presence in each of the SSMU (Fig. 5b). We found we had sufficient sampling to differentiate the observed behavior from random in the Drake Passage West, Antarctic Peninsula West, and Bransfield Strait West units. In all three units, we found a greater proportion of the area-restricted search state than expected. For the remaining units where we had whale observations, there was insufficient sampling to differentiate the observed allocation of behaviors from random.

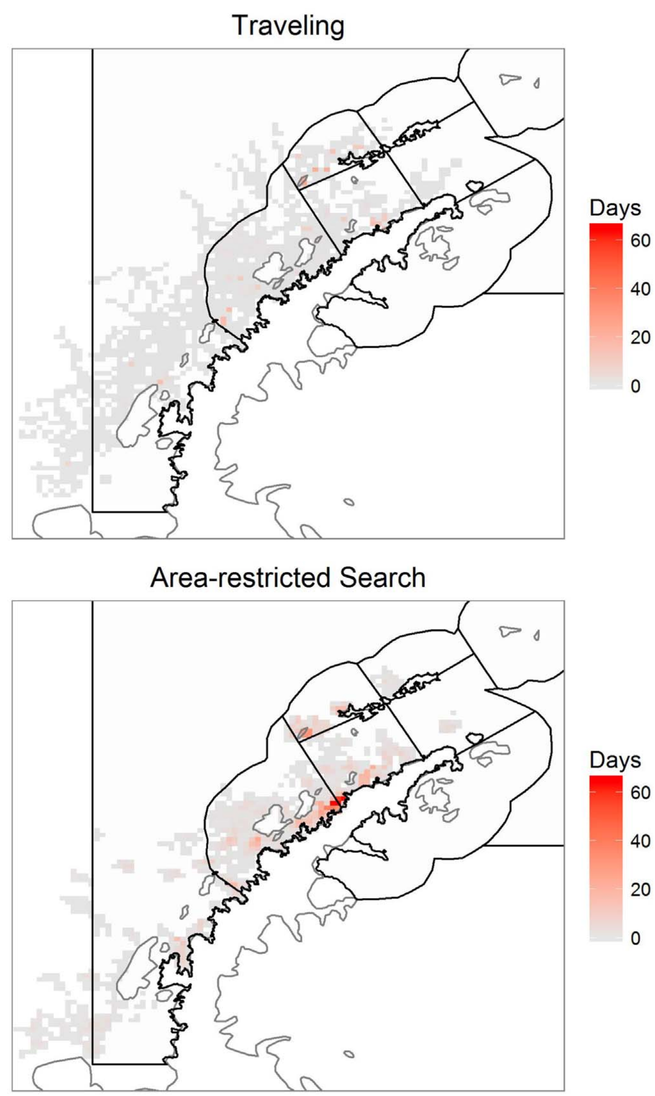

Fig. 4. Total whale days for each behavior state. Using our state-space model to estimate the movement process we divided locations as belonging to traveling or area restricted search states. We then calculated the total time each whale spent in each state at each grid cell. Combining the results for all individuals we mapped the distribution of behavioral states across the waters surrounding the West Antarctic Peninsula.

4. Discussion

Understanding the spatial distribution of krill predator foraging is imperative to manage the Antarctic Krill fishery. Humpback whales are the largest krill predator commonly found in the waters near the West Antarctic Peninsula. The unknown effects of a warming climate on krill stock (Atkinson et al., 2004), combined with the slowly recovering cetacean community, suggest that precautionary management of krill fishery is required (Constable et al., 2000). We found that while humpbacks traverse the length of the entire western side of the Antarctic Peninsula, foraging areas are highly spatially clustered with

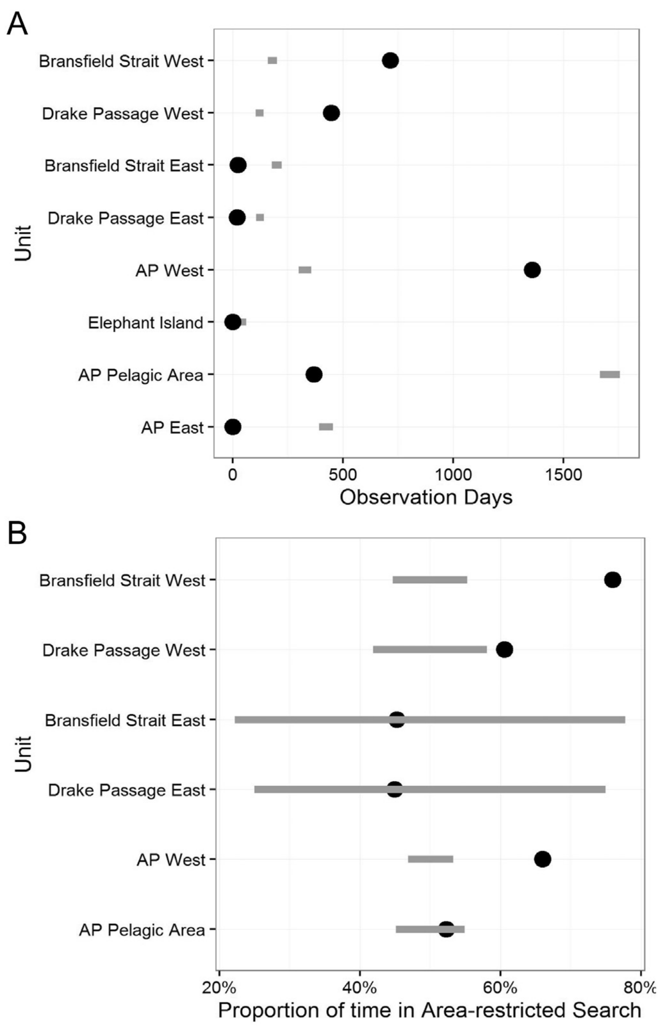

Fig. 5. Randomization tests for the occurrence and behavior within CCAMLR small-scale management units (SSMUs): **A**) Do whales use SSMUs non-randomly? We compared the observed duration of whale presence (in days) for each SSMU with a null expectation based on equal probability of occurrence in all cells. Black dots are the observed total days in each of the SSMUs. Grey bars are the lower 5th and upper 95th of the null distribution. Points to the right of the grey bars indicate that whales spent more time in a SSMU than expected. Points to the left of the grey bars indicate whales spent less time in a SSMU than expected at random. **B**): Do whales behave non-randomly within SSMUs? Using our movement model, we calculated the percentage of time in area-restricted search in each the SSMUs and compared it to a null distribution of foraging given the total number of observations. Black points are the observed proportion, grey bars are the lower 5th and upper 95th of the null distribution. Black points to the right of the grey bar indicate a greater proportion of area-restricted search than expected given the level of sampling within a SSMU.

respect to the CCAMLR small-scale management units (SSMUs). Whales used the Antarctic Peninsula West, Bransfield Strait West, and Drake Passage West SSMUs more often than expected. Within these units, whales spent more time in the area-restricted search state. Similarly, the krill fishery catch effort was spatially uneven, and has increasingly moved south and towards nearshore areas (Nicol and Foster, 2016). This finer scale information on humpback presence suggests that the uniform krill catch limit for all SSMUs in the Antarctic Peninsula Subarea 48.1 is overly broad and ignores important variation in humpback distribution and critical foraging areas. Resolving the disparity between the preference for specific areas by humpback whales and the uniform nature of the krill catch limits is critical in minimizing the potential conflict between whales and the fishery.

Our analysis identified key areas for humpback whale foraging, as represented by the area-restricted search state. Foremost, the Gerlache strait, in the Antarctic Peninsula West SSMU, had the greatest number of whale days in the area-restricted search state. While fishing effort is comparatively low in this SSMU, it is critical that CCAMLR proactively minimize conflict with foraging whales as the fishery shifts farther south, especially given the potential seasonal implications for whale life history. During the austral fall, krill that are distributed along the continental shelf move inshore towards areas that will be soon covered by sea-ice (Brierley, 2002). As humpbacks follow krill inshore, they congregate in greater densities and have reduced foraging space (Curtice et al., 2015 Nowacek et al., 2011). The shift towards krill fishing later in the austral fall (CCAMLR, 2015) coincides with a lack of ice-free areas outside the Gerlache and Bransfield straits during this period (Friedlaender et al., 2011), highlighting the potential for negative impacts from the fishery on concentrated whale aggregations. Given the relatively low use of the Antarctic Peninsula West SSMU by the krill fishery, we advocate for a closure of this area, especially during the austral fall, as a preventative measure to preempt conflict between the fishery and marine predators.

In contrast to the Antarctic Peninsula West Unit, the adjoining Bransfield Strait West unit is the most used SSMU by the krill fishery. We found significant presence of humpbacks in this unit, especially in the nearshore areas south of Trinity Island. The spatial overlap between whale presence and concentrated fishing activities has negative implications for whale mortality due to the potential for ship-strikes and long-term effects on resource competition between the fishery and prey base. Given the dominance of this unit in the overall fisheries catch, it is unlikely that member nations will agree to large-scale catch limits. Nearby anecdotal observations suggest that whales move closer to shore in the austral fall (Nowacek et al., 2011), and further work must focus on the seasonal patterns of whale movement to determine whether distance to shore restrictions would reduce the potential overlap between fishing vessels and whales.

To differentiate observed patterns of whale distribution and behavior from random expectation, we used randomization tests to account for the different sizes of the SSMUs and our overall sampling effort. One remaining question is whether tagging location could have influenced our results. We believe that this effect is likely to be small. Rather than stay near tagging locations, whales traveled widely, covering the full breadth of the Antarctic Peninsula throughout the summer. This means that the importance of the initial location of tagging quickly diminished over time. *Re*-analyzing our map of area-restricted search days after removing the first week of observations showed the same spatial pattern as our full dataset (Fig. S2). Ship-board surveys along the north end of the Antarctic Peninsula have previously highlighted deep water areas in the Bransfield Strait (Santora et al., 2010 Santora and Veit, 2013), and Dalla Rosa et al. (2008) documented two cases of resightings of tagged humpbacks returning to the Gerlache Strait, underlining the importance of this area. While our dataset is larger than most cetacean movement studies, it would be inappropriate to conflate the lack of presence with inferred absence. We focus on where whales were observed, and our results should not be interpreted as dismissing the conservation potential of other areas within the study region.

The distribution of humpback whales may provide insights into the recovery of other krill foraging species. Humpbacks travel widely throughout the peninsula, and are not tied to breeding colonies or haul-out locations that limit the mobility of other krill predators, such as penguins and seals. The presence of humpback whales may therefore be a strong indicator of krill abundance, and our distribution patterns may represent important foraging areas for other krill predators along the West Antarctic Peninsula. For cetaceans, the SSMUs with the highest krill catch rates also overlap with areas that historically had high numbers of fin and blue whales (Kemp and Bennett, 1932). These species yet to recover from historic whaling, when at least 11,927 fin and 6628 blue whales were killed in this region during the 1920′s (Kemp and Bennett, 1932). Current distribution information is sparse, but observations of fin whales, which are few, are largely restricted to the Bransfield Strait East unit (e.g. Herr et al., 2016). Observations of blue whales are limited in the continental shelf waters of the West Antarctic Peninsula. As these animals repatriate the region, precaution must be taken to ensure that populations recover unhindered from diminished prey availability due to commercial harvest. We still lack information on the consumption rates and energetic demands of baleen whales (Goldbogen et al., 2015 Hazen et al., 2009), and a loss of food base has been shown to have negative demographic effects in cetaceans (Leaper et al., 2006), as well as other Antarctic marine wildlife (Croxall et al., 1999).

We highlight the concentrated space use of humpback whales in the Antarctic West, and Bransfield Strait West CCAMLR small-scale management units. To avoid conflict with the krill fishery, additional management action is needed to refine the spatial scale of catch limits, and provide ecologically informed guidelines for near-shore restrictions. Given the potential influence of global climate change to allow both whales and ships to stay longer in the Antarctic, regulations must also consider the temporal timing of krill movement and habitat availability in reducing competition for ice-free areas during the austral fall.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.04.014.

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