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Original Investigation

At-sea behavior of South American fur seals: Influence of coastal hydrographic conditions and physiological implication

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ABSTRACT

At-sea behavior and effects of hydrographic conditions on the pelagic habitat use of South American fur seals (*Arctocephalus australis*) seasonally inhabiting the surrounding waters of shallow rocky reefs off Punta Mogotes (Mar del Plata, Argentina) were analyzed integrating geographic locations of fur seal groups (FSGs) with coastal hydrographic conditions and behavioral data in a Geographic Information System. Punta Mogotes rocky reefs represent a potentially high quality patch foraging area, crucial to a central place foraging species during their pelagic dispersion at sea. Fur seal behavior at-sea was strongly influenced by hydrographic conditions such us bathymetry, Beafourt sea state and sea surface current direction. Fur seals General Use Area (GUA) was associated with the 10 m isobaths, whereas Critical Use Area (CUA) was almost completely enclosed within the 5 m isobaths. A concentration-dispersion dynamic trend according to sea state was evident (GUA Beafourt $\leq$3 = 3.3 km^2 vs. GUA Beafourt >3 = 1.7 km^2), with a "use area displacement" according to sea surface current direction. A general prevalence of long, at-sea resting periods (*passive floating* was the most frequently performed behavior, and usually for long periods) and a differential occurrence of each behavior associated with Beafourt sea states were detected. During calm seas (Beafourt $\leq$3), fur seals exhibit *passive floating*, occupying extended areas, and drifting according to sea surface current direction. With increasing sea states (Beafourt sea state >3), fur seals tended to perform *shallow prolonged immersion* and *directional movements*, and concentrated in restricted areas weakly affected by currents. The importance of floating periods at-sea, probably associated with resting and digestion, was interpreted as an energy conserving strategy that would allow an increase overall foraging efficiency. Results suggested that the ability of fur seals to perform certain behaviors that will allow completing physiological process and ultimately determine reproduction and survival success, would be conditioned by the hydrographic regime at foraging areas. This last could be extrapolated to other fur seal species spending long times at-sea, both as part of migration movements or during typical long foraging round trips.

Introduction

Fur seals and sea lions are polygynous, gregarious and sexually dimorphic (Bartholomew 1970). As central place foragers, they alternate periods on land for mating, pup attendance, molting and resting with periods at sea for foraging and/or migration. At sea activities, which include swimming, diving, resting and grooming, represent a dual challenge to marine mammals. In the first place, the elevated energetic cost of these activities can potentially exceed the energy ingested, and ultimately affect overall foraging efficiency. In addition to this, heat loss in water is markedly higher than in air, and it can potentially lead to hypothermia (Hind and Gurvey 1997). A net positive energy balance during foraging at-sea result is crucial for Otariid reproduction and survival.

Marine mammals and birds usually concentrate their pelagic activity in focal areas of high interest, which may be relatively small and discrete (McConnell et al. 1999). The existence of small patches of high quality food can influence the foraging strategy throughout the non-breeding season, particularly in the case of animals with no pup attendance on land, such as males and pre-reproductive females. Minimizing the cost of swimming between scattered patches can contribute to the optimization of foraging strategies by reducing the energetic cost of foraging. Optimal foraging theory (Pyke 1984; MacArthur and Pianka 1966) predicts that foraging strategies maximize resource acquisition, while predators

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should adjust their movement behavior in relation to prey density and distribution (Charnov 1976).

The South American fur seal (*Arctocephalus australis* Zimmermann, 1783) has an insular distribution that extends along the coast of South America from Southern Brazil to Central Perú (Vaz-Ferreira 1982). The main breeding area of this species in the Atlantic Ocean is constituted by six colonies in islands off the coast of Uruguay (Vaz-Ferreira 1982; Vaz-Ferreira and Ponce de León 1987; Bastida and Rodríguez 2003; Ponce de León and Pin 2006), separated by a hiatus of more than 2000 km to the nearest breeding colonies off Patagonia (Carrara 1952). Southbound foraging dispersion covers extensive areas of the northern Argentina continental shelf (Ximenez 1986; Rodriguez 1996), and groups of fur seals from the Uruguayan stock routinely haul out in shallow rocky reefs off Punta Mogotes (38°06′S, 57°30′W; Mar del Plata, Argentina) between mid May and late December each year (Bastida and Rodríguez, 1994). This dispersion is in clear correspondence with the non reproductive season at Uruguayan breeding colonies (Ximenez 1986).

The suitability of this area as a potential foraging habitat is indicated by the winter to spring presence of fur seal groups that has been documented for at least 30 years (Rodriguez 1996; Dassis 2005). The shallow and rocky reefs present both higher prey richness and a more predictable prey location than the surrounding sandy benthos, thus requiring a lower energetic demand for foraging. On the other hand, the lack of emerged areas for resting and the changing local oceanographic conditions requires that the animals remain at sea over the reefs, representing a potential highly energetic demanding scenario. Although these rocky reefs are located only 1000 m from the coastline, fur seals never settled along the nearest beaches. We hypothesize that while at sea, their behavior is influenced by short term oceanographic changes, and animals tend to balance their activity in order to minimize energy expenditure and maximize prey consumption.

The Punta Mogotes rocky reefs represent a long term and recurrent at-sea fur seal concentration and constitute a key place for the study of fur seal habitat use and behavior at sea, mainly due to their proximity to the coast that allows observations from land. The objectives of the present study were to characterize the at-sea behavior of South American fur seals in a coastal habitat of predictable food resources and evaluate how it is affected by hydrographic conditions. Considering the insular distribution of South American fur seals, the results obtained are of potential application to other foraging habitats for this species and to estimate its relation with normal physiological limitations of the at-sea behavior. In addition, the fact that many species of fur seals normally spend long periods at-sea, both as part of migration and/or long foraging round trips (Gentry and Kooyman 1986), results can be useful for understanding the ecology and physiology of other species of pinnipeds.

Material and methods

Study site

This study was conducted from May to December of 2002 and 2003 on Punta Mogotes reefs (38°06′S, 57°30′W), an area seasonally inhabited by 100–400 fur seals and located in the coastal region of Mar del Plata (Argentina). These late autumn to late spring periods represents the fur seals' pelagic dispersion at sea. The reefs are formed by three main underwater ridges not connected to the coastline, located about 1000 m offshore and extending for about 3000 m in SSE direction (Fig. 1). The two reefs closer to the shore are partially exposed only during spring tides, whereas the third one is always submerged. Fur seals do not come ashore along the coast, and the animals remain at sea on waters over these shallow reefs. Only adult males can occasionally haul out during short periods when some parts are exposed during low spring tides combined with strong land-based winds. The whole reef area is about 10–11 km^2, and surrounded by the 10 m isobath. The depth between reefs varies from 2 to 5 m whereas the sandy channel located between the shore and the first reef is shallower. The dynamics of the whole area is complex, with periods of strong currents. These bathymetrical and hydrological conditions make navigation in the area possible only to small recreational boats and under good sea conditions.

Abundance estimation and geographic location of fur seals

We used scan sampling to make direct counts of fur seals present off Punta Mogotes waters, which were made in the morning or noon once or twice a week, depending on meteorological conditions. The observations were made with wide-angle binoculars (Dione 12×50) and scopes (Bushnell Stalker) from a main coastal observation point at Punta Mogotes (38°05′52.0″S and 57°32′39.5″W), 1000 m from the reefs, because previous observations from other nearby coastal points (Punta Cantera, Playa Serena and Barranca de los Lobos; Fig. 1) showed this area to have the highest fur seal concentration (Dassis 2005). Due to poor visibility, no observations were made at Beafourt sea-state ≥6.

The at-sea distribution of the fur seals was patchy, with individuals in groups of closely spaced animals. Therefore, a fur seal group (FSG) was visually defined as a concentration of animals in the water separated by less than 5 body lengths. In the case of single animals, they were considered as a FSG of $n = 1$ size. To prevent from re-sampling the same FSGs, we used the scan sampling method with instantaneous sampling (Altmann 1974; Martin and Bateson 1993) for recording the FSG composition and geographic location. Data was pooled because FSG mean size and frequency distribution were similar between years.

The geographic location of each FSG (considered at its central point) was estimated indirectly throughout field measurements of FSG-Magnetic North horizontal and FSG-observer location vertical angles. FSG relative coordinates were initially referred to a hypothetical observer by trigonometric calculation of the horizontal distance and the Azimuth relative to the observer GPS location, and converted into a lat/long format. Observer height above sea level (20 m) was measured with a theodolite (Nikon NT3a). Annual magnetic declination, used to estimate the Azimuth by correction of the FSG-Magnetic North angle, was extracted from the Nautical chart RADA H-250 (Servicio de Hidrografía Naval, Argentina, 2nd Ed., 2003). The nautical chart, used as a base map for plotting FSG locations, was digitized and geometrically transformed from its Mercator original projection to the plane coordinate Gauss Krüger system. FSG geographic locations, and all other data analyzed and maps were projected in this coordinate system. During the study (165 h of effective observation), a total of 365 FSGs were observed, 336 of which were geographically located. A mean 8.0 ± 7.8 FSG were positioned per day, representing an efficiency of $89.9 \pm 19.7\%$.

Fur seal behavior at sea

Four behavioral states were determined during this study: *passive floating* (*PF*), *shallow prolonged immersion* (*SPI*), *short and successive submergence* (*SSS*) and *directional movement* (*DM*). A single behavioral state was computed for each FSG when >75% of the group members performed the same behavior, which was the case for almost all the observations, and expressed as a percentage of the total number of groups observed daily.

PF was considered when the animals rested on the surface, in a belly up position and the flippers in a vertical position extending out of the water. This behavior was commonly performed for long

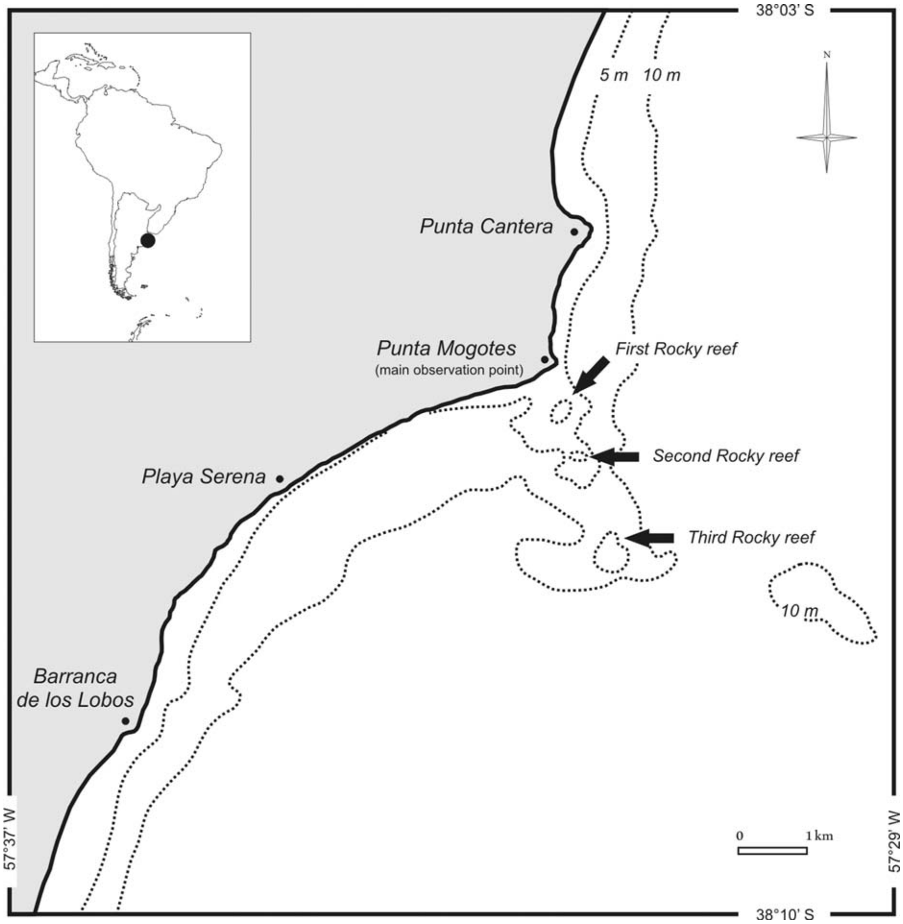

Fig. 1. Location of the shallow rocky reefs off Punta Mogotes (Mar del Plata, Argentina) and the position of the observation points.

periods, from one to more than 3 h. *DM* occurred when the animals swam in a defined direction and, with a few exceptions, moved against the surface current. *SSS* occurred when animals performed short dives (0.5–2.0 min) within a restricted area. On two occasions, fur seals were seen chewing fishes at the surface immediately after the submergence, which confirmed the association of this activity with feeding. During the *SPI* the animals stay with most of the body submerged below the surface for long periods (minutes to hours), alternating with rapid emerging of the head for breathing.

Habitat use analysis and influence of hydrographic conditions

Habitat use was analyzed by integrating the geographic location of FSGs with coastal hydrographic conditions and behavioral data in a Geographic Information System (ArcView 3.2; Environmental System Research Institute, ESRI, CA, USA). Complementary data for bathymetry, Beafourt sea state, sea surface current direction and fur seals behavior was combined to each FSG position. Beafourt sea state and wind-driven sea surface current direction were classified by direct observation according to standardized scale (Celemin 1984). Bathymetry was extracted from the Nautical Chart RADA H-250 (Servicio de Hidrografía Naval, Argentina, 2nd Ed., 2003).

The study area was divided into 200 m × 200 m (0.04 km^2) cells, and an Areal Use Index (AUI), defined as the proportion of the days each cell was used, was calculated as follows:

$$AUI_i = \frac{Seals_i}{Surveys_i} \times 100$$

where $Seals_i$ is the number of days with presence of seals in the cell, and $Surveys_i$ is the number of days in which cell i was surveyed to detect the presence of FSGs.

Fur seals' maximum distributional range or General Use Area (GUA) was defined as the area occupied by all FSG positions during the study, and was estimated by applying the Minimum Convex Polygon method (MCP; Mohr 1947) with CALHOME software (California Home Range; Kie et al. 1996). MCP is one of the commonly reported methods to estimate use areas and individual home ranges of many species of marine and terrestrial mammals (Gubbins 2002; Heide-Jørgensen et al. 2002; Takekawa et al. 2002; Flores and Bazzalo 2004; Pike and Reeder 2006; Wedekin et al. 2007; Volampeno et al. 2011). The most intensively used area or Critical Use Area (CUA) was defined as the area where the 50% of the FSG were concentrated, and estimated with the 50% locations MCP method, also with CALHOME software. The size ratio between CUA and GUA was used to estimate which proportion of the general area was most intensively used.

GUA and CUA (100% and 50% of the locations in MCPs, respectively) were calculated for each environmental variable and behavior. FSGs were grouped according to the hydrographical conditions and behavior in which they were positioned, and 100% and 50% MCPs were generated for each group. To evaluate the effects of these variables on habitat use and distribution, MCP size and overlap were compared. MCP size was used as an indicator of FSG "concentration-dispersion dynamics". Because the MCP method is highly sensitive to sample size, bootstrap analyses were performed to check that differences in the polygon size were not caused by differences in the number of locations used to calculate each polygon.

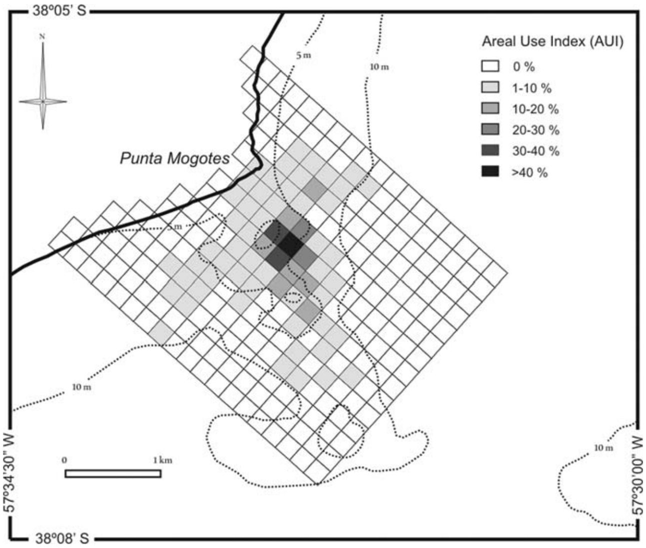

Fig. 2. Fur seal Areal Use Index (AUI) off Punta Mogotes, distributed in 200 m × 200 m cells.

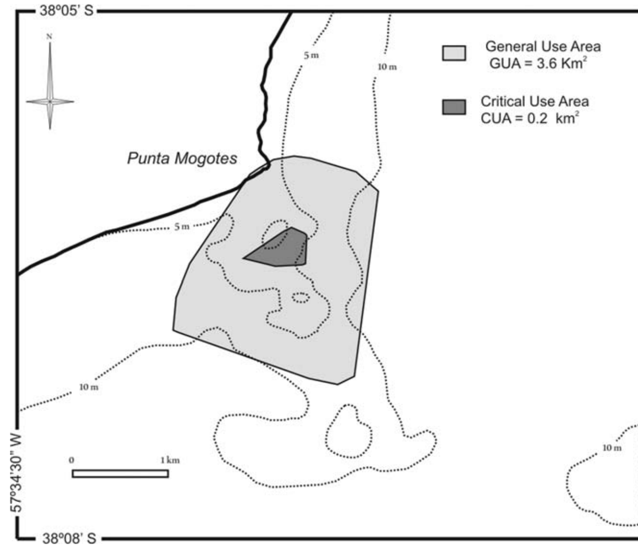

Fig. 3. Fur seal General Use Area (GUA) and Critical Use Area (CUA), estimated with the MCP method, with 100% and 50% of locations, respectively.

GUA and CUA sample sizes were within the asymptotic range of bootstrap curves in all cases, confirming that they were not biased. MCP overlaps were considered inverse indicators of "displacement effect" caused by the variable change. A low degree of overlap (quantified as percentage) was assumed as a high "displacement effect" over the use area and vice versa.

The effects of both "concentration-dispersion dynamic" and "displacement effect" were additionally compared between the two more frequently performed behaviors (*PF* and *SPI*).

Results

Fur seal abundance, general distribution and group size

Fur seal maximum daily abundance ranged from 60 to 300 animals, and FSGs were observed in Punta Mogotes reefs' in 90% of observation days, with only a minor proportion (12.5–19.4%) in nearby areas. Considering FSGs with and without geographic location, the mean FSG size was 3.3 ± 4.2 fur seals ($n = 365$) with 2–5 animals the group size most frequently recorded (44.2%) followed by solitary animals (42.2%) and decreasing FSG size therein (9.2% and 4.4% for 6–10 and >10 fur seals per group, respectively).

Influence of hydrographic conditions in the patterns of habitat use

The highest AUI value (>40%) was restricted to a unique cell located in the central reef area with a gradual decrease to the periphery (Fig. 2). AUI less than 10% was dispersed to the north, south and west, with unused cells (AUI = 0) in deeper areas to the east.

The fur seal maximum distributional range or General Use Area (GUA) was 3.6 km^2 ($n = 336$ locations), while the Central Use Area (CUA) was 0.2 km^2 ($n = 168$ locations) (Fig. 3). CUA was 5.5% of GUA, also confirming a trend of fur seal concentration between the two first reefs.

Area use was strongly influenced by bathymetry, Beafourt sea-state and wind-driven sea surface current direction. The external limits of GUA and CUA were highly coincident with the 10 and 5 m isobaths, respectively (Fig. 3). Most of the FSG locations were concentrated within the 5 m isobaths (72.3%), whereas 27.4% were between 5 and 10 m isobaths; only 0.3% of locations were outside the 10 m isobaths.

Beafourt sea-state strongly affected the size of the GUA, resulting in a dispersion-concentration pattern. GUA at Beafourt ≤3 was higher than for Beafourt >3 (3.34 km^2 versus 1.72 km^2,) but, in contrast, the CUAs were of similar size independent of sea state (0.15 km^2 versus 0.13 km^2).

The sea surface current displaced the GUA in the direction of the current, with a more pronounced effect on the N–S axis than on the NW–SE axis, with a higher overlap in the latter (Fig. 4).

Fur seal behavior at-sea and its relation with hydrographic conditions

The most frequent behavioral state was *PF*, with a mean frequency of 42.2 ± 37.3%, followed by *SPI* at 38.2 ± 35.6%. *DM* and *SSS* were comparatively less important (13.9 ± 26.8% and 5.8 ± 16.3%, respectively).

Fur seal behavior frequency depended on Beaufort sea state ($Chi^2 = 110.21$, df = 12 and $p < 0.001$). *PF* frequency progressively decreased with increasing sea-states, whereas *DM* and *SPI* increased their frequency in rough seas (Fig. 5). *SSS* was too infrequent to determine its relation with Beaufort sea state.

No differential use areas or evident spatial restrictions were recorded among behaviors, although fur seals in *PF* occupied larger and deeper areas than those in *SPI* (3.5 km^2 versus 1.7 km^2). Fur seals on *PF* were more displaced by surface currents than *SPI*, resulting in a significantly higher overlap between different axes (10.1 ± 14.5% versus 31.9 ± 18.6%; *T* test, $t = -2.54$, df = 10 and $p = 0.03$; arcsin transformed (Zar 1984)).

Discussion

South American fur seal distribution along the Mar del Plata coast was restricted to the rocky reefs waters off Punta Mogotes, with no utilization of the nearby coastal area and almost no dispersion to adjacent areas of soft benthos. The focal concentration of fur seals in this rocky habitat for approximately seven months and the permanent occurrence of marine birds (Kelp, Orlog and brown-hooded gulls and terns) suggest the presence of abundant prey.

Habitat use within the Punta Mogotes area was concentrated around the reefs, and the most intensively used area (CUA) represented only 5% of the total used area (GUA), and was located in the central and more shallow part of the reefs. As most species of ter-

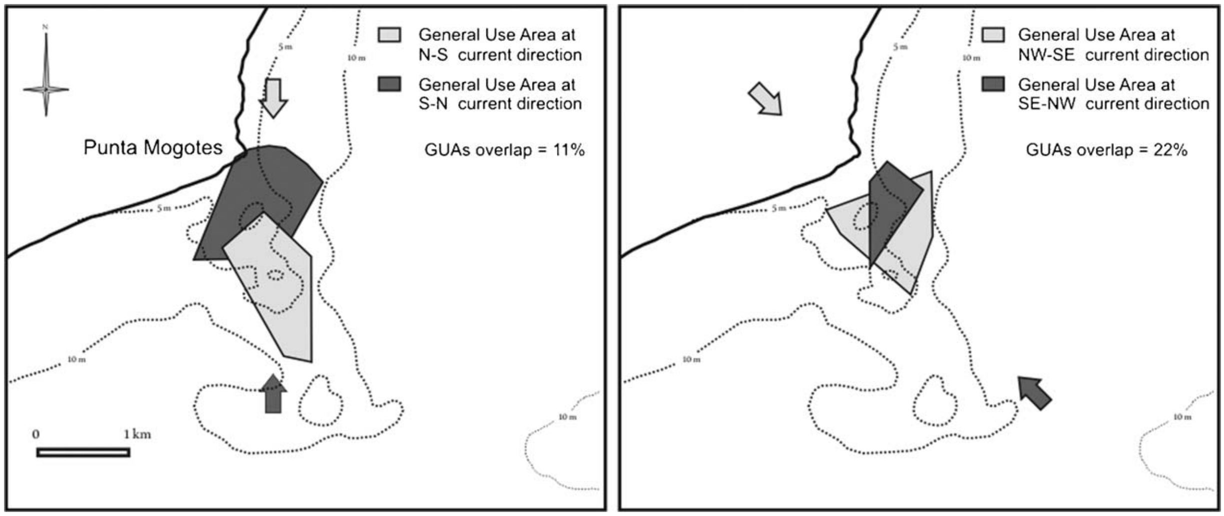

Fig. 4. Fur seal General Use Area (GUA) displacement according to the wind-driven sea surface current direction (represented by arrows) across N–S and NE–SW axis, and the corresponding GUAs overlap (%).

ritorial animals, fur seals do not use their entire distribution range with equal intensity, and tend to concentrate their activity in particular areas. This differential use of a specific areas has been described in birds and mammals (Dixon and Chapman 1980; Samuel et al. 1985), and reported several times for marine mammals (Gubbins 2002; Ingram and Rogan 2002; Te Wong et al. 2004; Wedekin et al. 2007).

Fur seals in Punta Mogotes actively concentrate on reduced areas on turbulent sea conditions that would naturally favor dispersion. This could be interpreted as a behavioral strategy to maintain specific locations in preferred focal patches, as both *SPI* and *DM* were the preferred activities. CUA location and the concentric distribution of AUI values confirms that the central zone of the reefs could provide some advantages over surrounding areas, such as greater food availability, reduced human disturbance and a clear topographic reference. The potential protection against predators could also be considered, as an active concentration in the central reef area was reported in the presence of killer whales (Dassis 2005).

Fur seal behavior at-sea was strongly influenced by hydrographic conditions such as Beafourt sea-state, wind-driven sea surface current direction and bathymetry. Fur seals showed a general preference for shallower waters, a concentration-dispersion dynamic trend according to rough-calm seas, a "use area displacement" according to sea surface current direction and a differential occurrence of particular behaviors, also associated to Beafourt sea states. During calm seas (Beafourt ≤3), fur seals were preferentially on *PF*, occupying more extended areas, and drifting according to sea surface current direction. With increasing sea states (Beafourt sea state >3), fur seals exhibited *SPI* and *DM*, concentrated in restricted areas weakly affected by currents. As a general conclusion, we interpret that the ability of fur seals to use a potential high quality prey area such as the Punta Mogotes reefs, which can influence reproductive success and survival, is most likely constricted by hydrographic factors.

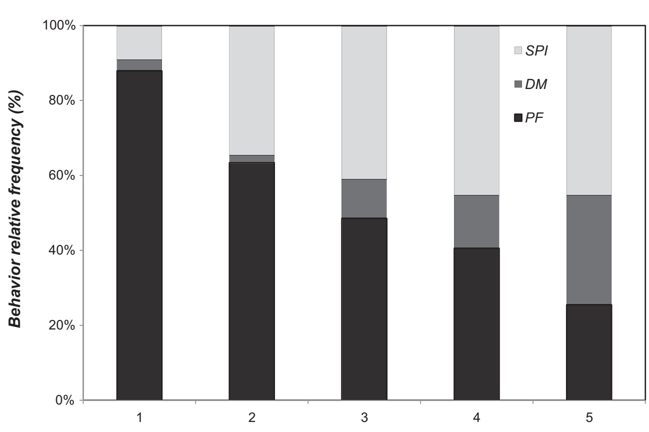

Fig. 5. Fur seal behavioral state frequencies [*Passive floating* (*PF*), *shallow prolonged immersion* (*SPI*), and *directional movement* (*DM*)] in relation to Beafourt sea-states.

Considering that several fur seal species spend prolonged periods at sea (Gentry and Kooyman 1986), inferences from our results could be extrapolated to other species and other regions. Coastal areas play a key role in adult females during early lactation stages (i.e., Thompson et al. 2003), and Beaufort sea-states and local currents could probably affect the foraging behavior.

In relation to physiological limitations that normally constrict at sea behavior, time dedicated to resting is one of the critical factors that can affect overall foraging efficiency (Costa et al. 1989). Swimming is energetically demanding for most of marine mammals (Williams et al. 2000), therefore, resting represents one of the most critical activities during long periods at sea. *PF*, a probably resting behavior, could be an energy saving strategy for fur seals during the prolonged presence off Punta Mogotes. Costa et al. (1989) suggested that differences in at-sea resting behavior could be associated with foraging efficiency in subpolar fur seals (*Arctocephalus gazella* and *Callorhinus ursinus*). Although prolonged resting at-sea has been interpreted as a thermoregulation challenge (Liwanag et al. 2009), it can provide an extended period for grooming. The maintenance of the insulative properties of the underfur is known to be necessary for fur bearing marine mammals during long periods at sea (Kooyman et al. 1976). The presence of South American fur seals off Punta Mogotes area is coincident with the period of lowest sea surface temperature (Martos et al. 2004), and maintaining the fur insulation could be strategic during austral summer. *PF* probably was also related to digestion due to a natural metabolic conflict between two energetically demanding activities that affect energy allocation into locomotion and decrease overall energetic efficiency of foraging (Rosen et al. 2007).

SSS and *SPI* were the main behaviors associated with foraging. Fur seals had been observed chewing fishes at surface after *SSS*, independent of hydrographic conditions. *SPI* was mainly performed in very shallow waters, and seems to be associated with prey detection and capture. South American fur seal diet include both coastal (inshore squids, rough scad, chub Mackerel, American harvestfish, croackers, weakfish) and shelf species (anchovies, shortfin squids, hairtails; Vaz-Ferreira 1982; Vaz-Ferreira and Ponce de León 1987; Ponce de León and Pin 2006; Naya et al. 2002). The sharp accumulation of mercury and cadmium after weaning in fur seals off Punta Mogotes is an indication of early predation also on local fish and squid (Gerpe et al. 2009), emphasizing the importance of the coastal areas of northern Argentina as potential foraging grounds for *Arctocephalus australis* during non-breeding season. The ability of fur seals to switch between different types of preys has been previously reported by Costa et al. (1989).

We reported that changes in coastal hydrographic conditions directly affect the at-sea behavior and pelagic habitat use in South American fur seals, mainly influencing their ability to complete physiological process through different behaviors. Although Punta Mogotes rocky reefs are a focal area of seasonal use, they may constitute an important concentration area during the pelagic dispersion after breeding. The results are of special interest to elucidate fur seal physiological, ecological and behavioral aspects during the pelagic phase of their life cycle, and also to design conservation management strategies for South American fur seals at a local scale. Geographic localization of areas of main use may help in defining future spatial restrictions to human activities off Punta Mogotes. The uniqueness and ecological importance of these reefs may help in identifying this site as a candidate for further marine protected area.

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