Benthic foraging on seamounts: A specialized foraging behavior in a deep-diving pinniped

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In wide ranging marine animals, it is often difficult to record or observe the behaviors necessary to describe fine-scale or specialized foraging behaviors. These

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specialized behaviors may be rare, but are of importance because they may represent previously unknown predator–prey relationships or ecosystem interactions (Partridge and Green 1985, Estes *et al.* 2003). Seamounts are an example of an uncommon but relatively productive and predictable ocean habitat that can be exploited with specialized foraging behaviors. Researchers have demonstrated that a range of pelagic taxa including tuna, swordfish, whales, dolphins, sharks, marine turtles, and seabirds congregate at, or otherwise exploit, waters overlying seamounts (see Pitcher *et al.* 2007, Morato *et al.* 2008 for review). These species take advantage of increased primary productivity and elevated biomass associated with seamounts (Genin and Boehlert 1985, Klimley *et al.* 2003). Increased productivity results from turbulent upwelling that introduces deep-water nutrients into the photic zone as ocean currents are displaced by seamount bathymetry, resulting in elevated pelagic productivity, as well as productive benthic communities that are dominated by slow-growing sponges and corals (Boehlert 1988, Bograd *et al.* 1997, Roberts *et al.* 2006, Pitcher *et al.* 2007).

Several studies suggest the importance of seamounts to pelagic animals, and observations of large pelagic animals associating with seamounts have come from surface surveys, mark-recapture studies, satellite tracking instruments, and acoustic telemetry (Klimley *et al.* 1988, Itano and Holland 2000, Sibert *et al.* 2000, Sedberry and Loefer 2001, Cañadas *et al.* 2002, McDonald *et al.* 2009). Despite this, high-resolution observations of vertical and horizontal movements to determine whether foraging occurred on the seamount or in the water column above have only been made with bigeye tuna (*Thunnus obesus*). Musyl *et al.* (2003) determined that tuna were foraging in the water column above the seamount, but how other species might use seamounts to forage remains unknown.

Although pinnipeds have been observed near seamounts and similar abrupt to-pographies, our understanding of how pinnipeds use seamounts is limited. Using satellite telemetry, Nordøy *et al.* (1995) found crabeater seals (*Lobodon carcinopha-gus*) favored seamounts for pelagic foraging in the Antarctic, as did northern fur seals (*Callorhinus ursinus*) in the northwest Pacific (Baba *et al.* 2000). Using satellite-linked time-depth recorders (TDRs), researchers found that Hawaiian monk seals (*Monachus schauinslandi*) foraged on submarine ridges near haul-out sites in the Hawaiian archipelago (Parrish *et al.* 2002). Juvenile male southern elephant seals (*Mirounga leonina*) have also been observed concentrating their activity near seamounts, though details of dive behavior were not reported (Bornemann *et al.* 2000). Given their diverse foraging strategies and exceptional dive capabilities, ele-phant seals (*Mirounga* spp.) should be more capable of employing benthic foraging on seamounts than other pinnipeds (Hindell *et al.* 1991, Le Boeuf 1994, Simmons *et al.* 2007, Costa *et al.* 2010, McIntyre *et al.* 2010). Male northern elephant seals (*M. angu-stirostris*) are known to forage on benthic shelf-slope habitats along the Gulf of Alaska, while most females (approximately 85%) forage in the mesopelagic zone of the north-east Pacific (Le Boeuf and Crocker 1996; Costa *et al.,* unpublished data). Females may choose these oceanic habitats to avoid their primary predators, white sharks (*Carcharodon carcharias*) and killer whales (*Orcinus orca*) that are mainly coastal (Le Boeuf and Crocker 1996, Le Boeuf *et al.* 2000). Thus, seamounts may allow elephant seals to exploit benthic prey in isolated, lower risk oceanic environments.

To determine individual foraging behaviors involving North Pacific seamounts, at-sea behavior was examined in 179 northern elephant seals instrumented during the annual breeding (January–February) or molt (May–June) haul-outs. Animals were instrumented at two rookeries 1,100 km apart: Año Nuevo State Reserve, California,

between 2004 and 2009 (9 males, 150 females) or in the San Benito Archipelago in Baja California, Mexico (9 males, 11 females) between 2005 and 2006. Both satellite platform transmitter terminals (PTTs) and TDRs or Sea Mammal Research Unit Conductivity-Temperature-Depth Satellite Relay Data Loggers (SMRU CTD-SRDL, Sea Mammal Research Unit, St. Andrews, UK) were attached to each animal following deployment procedures described in Simmons *et al.* (2010).

All tracks were fit with a behaviorally discriminating state-space model (SSM) to both handle Argos error and infer behavioral state. SSMs directly address Argos error by coupling a model for observation error with a mechanistic model of animal movement and solving the models together. Behavior can also be inferred from the mode and was discriminated into two states (nominally referred to as "foraging" and "transiting") based upon the autocorrelation of consecutive displacements and turn angle between those displacements (Jonsen *et al.* 2005, 2007; Breed *et al.* 2009). The model was fit in WinBUGS using a Bayesian Markov Chain Monte Carlo (MCMC) simulation. In the SSM, the behavioral state estimate is described by a binary distribution, and as in Breed *et al.* (2009), the ratio of MCMC samples was used as a measure of certainty of the behavioral state. At each location, the MCMC samples describing behavioral state needed to be at least two to one to be considered in a given state. Locations with smaller ratios were considered uncertain in their behavioral classification.

To assess the level of opportunities elephant seals have to forage on seamounts in the North Pacific, we plotted satellite tracks of all 179 elephant seals against North Pacific seamounts using ArcMap (Version 9.1, ESRI, Redlands, CA). We used the Earth Topography 2 min cell resolution (ETOPO2) seamount data set by Kitchingman and Lai (2004) that applied two algorithms to determine global seamount locations. Seamount depths were extracted for a rectangular region encompassing all 179 tracks. We determined the percent of seamounts within 1,600 m of the surface, or seamounts within northern elephant seal diving capacity, and also those within 400 m, or shallower than the average elephant seal dive depth (Le Boeuf 1994).

Seamount foraging behavior was determined by visually locating positions during an individual's track on or near seamounts using MamVisAD (Beta Release version, Sea Mammal Research Unit, University of St. Andrews) or Instrument Helper (Version 1.0.0.5, Wildlife Computers Inc., Redmond, WA) depending on the type of TDR used. Once dates and locations were determined, we inspected TDR records at the dates of interest to look for benthic foraging behavior according to profiles described by Hassrick *et al.* (2007). Animals displaying benthic dive profiles near seamounts were noted and used in further analyses.

To determine foraging success while at sea, body condition estimates were determined for animals instrumented at Año Nuevo using mass and ultrasound measurements. Similar measurements were not taken on animals tagged in the San Benito Archipelago due to logistical constraints. Dorsal, lateral, and ventral blubber thickness, length and girth were measured at six locations along the length of the seal's body and body condition was estimated using the truncated cones method following methods described by Gales and Burton (1987). As most females spent time on shore post deployment and/or before recovery of instruments, corrections were necessary to estimate mass at departure and arrival. This correction was based on equations derived from serial mass measurements of fasting female seals from previous studies (mass change [kg/d] = $0.51 + 0.0076 \times$ mass, $n = 27$, $r^2 = 0.79$, $P < 0.01$; Simmons *et al.* 2010). All measurements were taken at both instrument deployment and recovery following the foraging trip. Body condition of animals found

exploiting seamounts was compared to all seals instrumented over the same foraging trip.

Of North Pacific seamounts in the ETOPO2 database, 39 of 1,024 (3.8%) seamounts extend close enough to the water surface to be within the range of the average dive depth of northern elephant seals and 84 seamounts (8.2%) are within range of the maximum recorded dive depth. Of the 179 animals for which complete satellite tracks and dive data were available, three animals (one Año Nuevo female [M627, fitted with MK9 TDR and SPOT4 PTT, Wildlife Computers Inc.], one San Benito female [Ana, fitted with MK9 TDR and SPOT4 PTT], and one San Benito male [Chepo2, fitted with a SMRU CTD-SRDL]) showed evidence of benthic foraging on isolated undersea ridges or seamounts (Table 1). Both of the San Benito animals focused on Cortez Bank, a shallow undersea ridge peaking at 20 m below sea level approximately 190 km northwest of San Diego, California. SSM results revealed that Chepo2 spent 68.8% of his trip in foraging mode with 100% of foraging time spent on or near Cortez Bank (Fig. 1A) performing many benthic dives (Fig. 2A). Similarly, Ana spent 82.7% of her trip in foraging mode with 100% of foraging time largely employing benthic foraging on Cortez Bank (Fig. 1A). In the 2005 postbreeding trip, M627 traveled to the central Pacific to forage along the Bowie–Kodiak Seamount chain (Fig. 1B). SSM results revealed that she spent 17.5% of her time in foraging mode and 100% of this time was spent performing many benthic dives over Welker and Pratt Seamounts, two isolated and deep seamounts (depths 618 and 710 m) (Fig. 2B). This animal was instrumented again following the 2006 breeding season. She returned to the same region of the North Pacific, but utilized pelagic foraging, performing only seven benthic dives to depths of 1,200 m over 4 h on Denson Seamount in the Bowie–Kodiak chain during the 73 d trip.

Changes in body condition were calculated for M627 during both the 2005 and 2006 trips (Table 2). M627 was more successful in 2005 than in 2006, gaining 11.8% more mass and accruing 2.9 MJ/d more energy during the year she foraged on seamounts. In 2005, M627 foraged extensively over the Bowie–Kodiak seamounts, gaining 83.3 kg over 91 d at sea with a 26.7% mass gain, 2.7% more mass than the average female, and more mass than half of the sampled population ($n = 18$) at Año Nuevo for the 2005 postbreeding trip (Table 2). In 2006, M627 returned to the same region of the North Pacific but employed pelagic foraging. She gained only 55.1 kg over the 73 d trip, a 14.9% mass gain, 6.7% less mass than the average female, and less mass than 87.5% of the sampled population ($n = 17$) in the 2006 postbreeding foraging trip (Table 2).

This study documents that, although rare, northern elephant seals forage benthically on the top of seamounts, and it is the first study to show benthic foraging on seamounts by a large pelagic animal. In this study, we also incorporated dive data to show that foraging occurred on the surface of the seamount and not in the water column above it. Surface movement data in conjunction with dive data have been used to identify other specialized foraging behaviors such as benthic foraging along the continental shelf or in association with mesoscale eddies (Campagna *et al.* 2006, Simmons *et al.* 2007). This is one example of a specialized foraging behavior, and additional foraging behaviors can be detected in elephant seals and other marine mammals using depth recorders, cameras, accelerometers, jaw movement tags, fatty acid analysis, and land-based observations (Bradshaw *et al.* 2003, Estes *et al.* 2003, Watanabe *et al.* 2006, Tinker *et al.* 2007, Naito *et al.* 2010, Viviant *et al.* 2010).

Table 1. Summary information for three northern elephant seals (*Mirounga angustirostris*) that displayed benthic foraging over seamounts.

| Animal (year; tag model)	Sex	Tagging location	Total track length (d)	Seamount name(s)	Seamount location(s)	Shallowest seamount depth(s) (m)	Percent of "foraging" mode over seamounts (% mode uncertain)
M627 (2005; MK9, SPOT4)	Female	Año Nuevo	89.7	Pratt; Welker	56.25°N, 142.64°W; 56.25°N, 140.44°W	710; 618	17.5 (0.4)
M627 (2006; MK9, SPOT4)	Female	Año Nuevo	73	Denson	54.12°N, 137.33°W	993	0.0 (4.1)
Chepo2 (2006; SMRU CTD-SRDL)	Male	San Benitos	112.0	Cortez Bank	32.45°N, 119.14°W	20	68.8 (5.0)
Ana (2005; MK9, SPOT4)	Female	San Benitos	79.0	Cortez Bank	32.45°N, 119.14°W	20	82.7 (4.2)
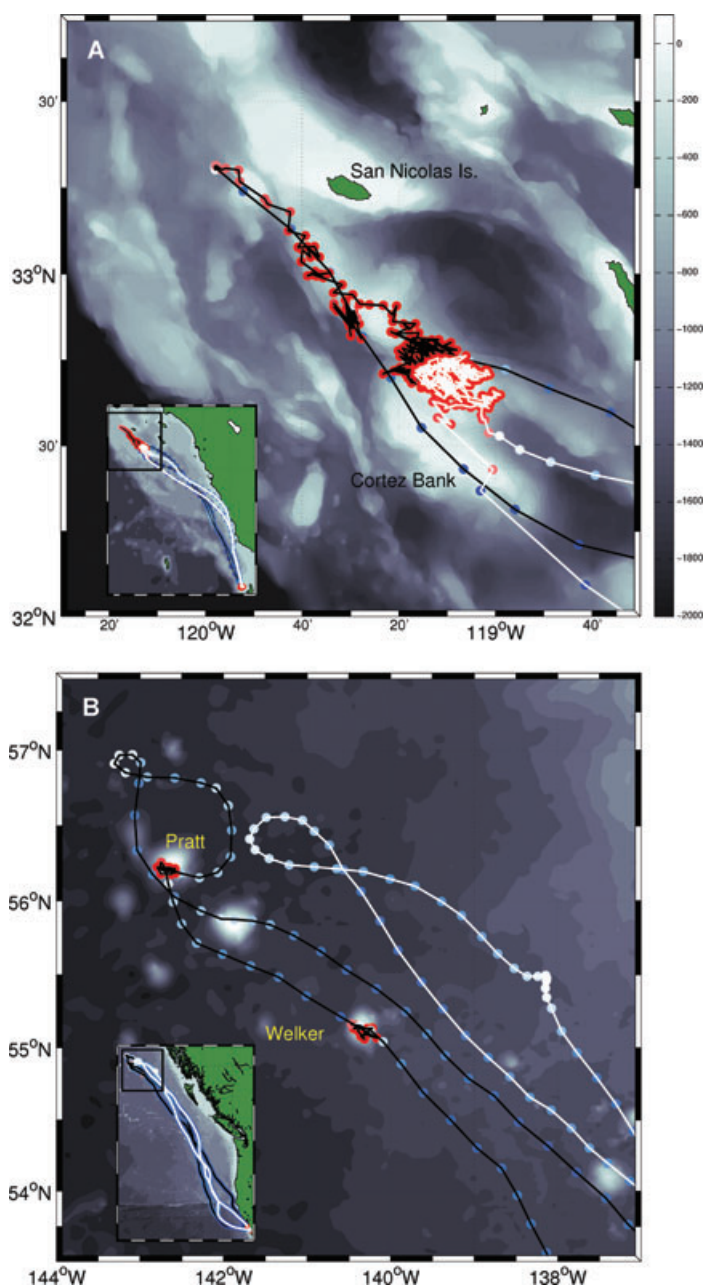
Figure 1. State-space modeled tracks of (A) male elephant seal (*Mirounga angustirostris*) (Chepo2; black line) and female elephant seal (Ana; white line) foraging on Cortez Bank off the coast of southern California and (B) female elephant seal (M627) foraging on Pratt and Welker Seamounts in 2005 (black line) and 2006 (white line) in the northeast Pacific. Red dots indicate model inferred foraging behavior; blue dots indicate model inferred transiting behavior. Background shading represents depth contours in meters.
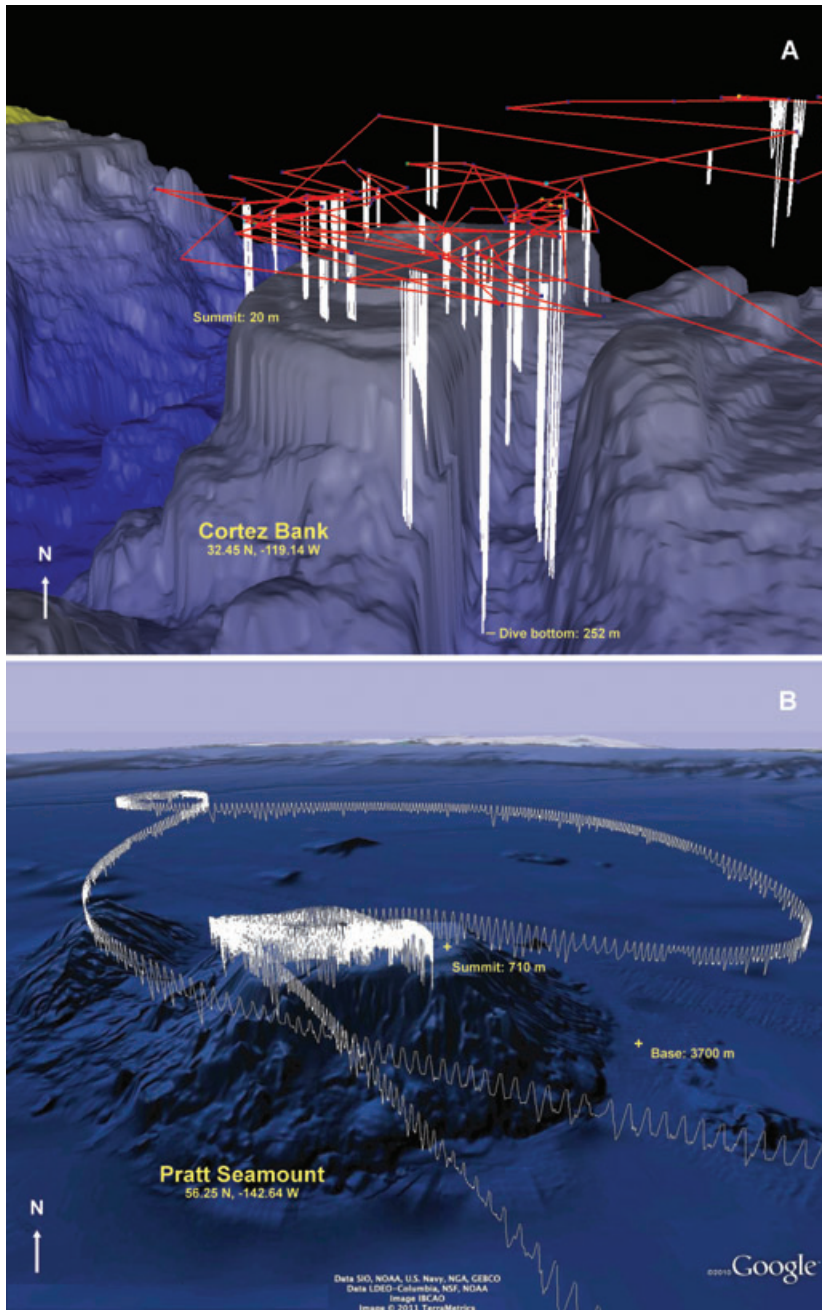
Figure 2. (A) Telemetry track (red) and dives (white) of a male elephant seal (*Mirounga angustirostris*) (Chepo2) foraging on Cortez Bank off the coast of southern California and (B) dives of a female elephant seal (M627) foraging on Pratt Seamount in the northeast Pacific.

Table 2. Body condition calculations for elephant seal (*Mirounga angustirostris*) M627, compared with mean body condition of all seals instrumented in each season. For season means, values are means with standard deviation in parentheses.

| Year | Days at sea | | Mass gain (kg) | | Percent mass gain | | Energy gain (MJ/d) | |
	M627	Season mean	M627	Season mean	M627	Season mean	M627	Season mean
2005 (*n* = 18)	91	78.1 (7.9)	83.3	78.2 (21.4)	26.7	24 (7.5)	16.5	15.3 (6.8)
2006 (*n* = 17)	73	77.5 (11.1)	55.1	68.3 (24.8)	14.9	21.6 (9.0)	13.9	14.3 (7.5)

In addition to showing benthic foraging by northern elephant seals, this study further finds that repeated instrumentation of the same animal shows that this female maintains plasticity in her foraging behavior. It is unclear as to how this animal managed the remarkable feat of returning to this same seamount chain in the huge featureless patches of the North Pacific Ocean. The single set of benthic dives located over the Denson Seamount in 2006, however, indicates she relocated the seamount chain, but did not persist in benthic foraging despite her success in benthic foraging in 2005. This suggests that M627 did not find adequate foraging resources in her seven dives, or that she failed to relocate the shallower seamounts in the chain in 2006. Diving to depths of 1,200 m may have represented too great of an energetic cost, causing her to shift to relatively more profitable pelagic foraging behavior, despite well-documented deep-sea coral communities present on these seamounts (Baco 2007, Stone and Shotwell 2007, Etnoyer 2008). In addition, it is possible that the benthic communities of this seamount chain had been depleted by the foraging activities of other predators, or by human fishers (Hughes 1981, Palacios *et al.* 2006, Clark and Koslow 2007). Chepo2 and Ana also exploited the profitability of benthic foraging on Cortez Bank. This shallow bank allowed seals to reach the seafloor easily, and possibly exploit otherwise inaccessible benthic prey such as rockfish (*Sebastes* spp.), which are known to be abundant at Cortez Bank (Lewbel *et al.* 1981, Yoklavich *et al.* 2007).

Studies in other ocean basins may additionally show the importance of benthic seamount environments to large pelagic animals, further highlighting seamounts as ecosystems of conservation concern (Probert *et al.* 2007). The North Pacific contains relatively few shallow seamounts available for benthic foraging (only 84 seamounts within maximum dive depth range of elephant seals). Thus, the low number of seals we observed using this foraging behavior is not surprising, though this study shows the capability of elephant seals in relocating isolated areas in the ocean. In the Southern Ocean, shallow seamounts are more abundant (3,072, 19.22%) seamounts or knolls shallower than 1,500 m in the Southern Ocean *vs.* 272 (7.03%) in the northeast Pacific (Yesson *et al.* 2011) and southern elephant seals are frequently associated with them (D. Costa and L. Huckstadt, unpublished data). The northeast Atlantic and west-central Pacific Oceans also contain relatively large numbers of shallow seamounts (seamounts and knolls shallower than 1,500 m accounting for 22.68% and 21.17% of the total number of seamounts, respectively; Yesson *et al.* 2011); deep-diving pelagic animals in these regions may forage on the surface of seamounts to a greater degree than observed in this study. A better understanding of both the vertical and horizontal behavior of large pelagic animals is key to

understanding the role seamounts and other bathymetric features play in ocean ecosystems and to determining specialized foraging behaviors.

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