Conservation of migratory Magellanic penguins requires marine zoning

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ABSTRACT

Conservation of migratory species requires an understanding of their migration path and pattern. We used band returns and satellite tracking to characterize the seasonal migration of Magellanic penguins breeding in southern Argentina, with the purpose of identifying an effective conservation approach for this species. Band returns show these penguins migrate annually to the coastal waters of northern Argentina, Uruguay, and southern Brazil, an average one-way distance of approximately 2000 km, and a modal distance of 2300–2400 km. Satellite data indicate that the penguins follow a migration corridor within 250 km of shore. Mean migration distance varied among years. Juveniles migrated farther on average than older birds, although migration distance of different age classes overlapped substantially. Mortality rates during migration were higher among younger birds, and juvenile mortality rate during migration was inversely correlated with cohort survival, indicating that mortality during migration is an important determinant of population recruitment. A minimum of 13% of the migration-period mortality we recorded resulted from fisheries bycatch and oil pollution. Because of the penguin's mode of travel (swimming at or near the surface), the large spatial extent of its migration, and the intensity of human use of the area, effective conservation through conventional coastal marine reserves is unlikely. Marine zoning is an alternative that could provide the spatial scale and flexibility necessary to accommodate both penguin migration and human activities. As the waters traversed by Magellanic penguins are among the most threatened in Latin America, zoning for protection of this wide-ranging and charismatic species can also protect regional biodiversity.

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1. Introduction

Migration poses a major challenge for conservation of many animal species (Robinson et al., 2009; Terborgh, 1989; Wilcove, 2008). Depending on favorable conditions in more than one seasonal habitat, as well as along the travel routes between those habitats, migratory species are vulnerable to human-caused environmental changes in multiple, often widely separated, locations (Martin et al., 2007; Primack, 2010; Reid and Miller, 1989). Furthermore, for species that migrate long distances, particularly top predators (Hooker et al., 2011), economic, political, and logistical factors make effective conservation difficult to achieve (Nevins et al., 2009).

These challenges notwithstanding, conservation efforts that do not address species' migration requirements are likely to fail (Martin et al., 2007; Webster et al., 2002). Successful conservation measures for migratory species must protect seasonal habitats as well as migration corridors; for many marine vertebrates, these measures must be large-scale and dynamic (Hyrenbach et al., 2000). Design of effective protections requires a comprehensive understanding of species' migratory routes – including the range of variation in those routes – to identify and effectively respond to points of conflict with human activities (Costa et al., 2012; Schofield et al., 2013).

The migrations of flying birds have long been the object of scientific study (Berthold, 2001); more recently recognized is the migratory nature of many flightless birds, among them, several species of penguins (Davis and Renner, 2003; García-Borboroglu and Boersma, 2013). Logistical constraints have prevented comprehensive monitoring of penguin migrations, however satellite and geolocation sensor tracking of small numbers of individuals has documented long distance seasonal movement in some species (e.g., Ballard et al., 2010; Boersma, 2012; Davis et al., 2001; Pütz et al., 2006; Trivelpiece et al., 2007).

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The Magellanic penguin (*Spheniscus magellanicus*) is a migratory upper trophic level predator that breeds along the coasts of southern Argentina and Chile and the Falkland/Malvinas Islands (Boersma et al., 1990, 2013). Although the species' overall population trend is uncertain (Boersma et al., 2013), it is declining at its largest breeding colony (Boersma, 2008) and is subject to increased mortality associated with human activities such as offshore petroleum extraction and transport (Boersma, 2012; Gandini et al., 1994; García-Borboroglu et al., 2006, 2008), commercial fishing (Boersma and Stokes, 1995; Cardoso et al., 2011), and perhaps climate change (Boersma, 2008; García-Borboroglu et al., 2010). As a result of these threats, the species is classified as "Near Threatened" on the IUCN Redlist (IUCN, 2012).

In the southwest Atlantic (southern Argentina and the Falkland/ Malvinas Islands), where the majority of the population occurs (Schiavini et al., 2005), Magellanic penguins are present at their colonies only during the breeding and molting periods (September– April; Boersma et al., 1990), and spend the rest of the year at sea (Boersma et al., 2013). Satellite tracking of adults departing colonies following the breeding season indicates initial annual northward movement (Pütz et al., 2000, 2007; Stokes et al., 1998); however their whereabouts during most of the non-breeding season are not known with precision. Results of a small banding study (Daciuk, 1977), discoveries of oiled birds (García-Borboroglu et al., 2006), and anecdotal evidence (see below) indicate that the penguins migrate north as far as the southern coast of Brazil and, rarely, as far as northern Brazil (Boersma et al., 1990; García-Borboroglu et al., 2010; Ramos da Silva et al., 2012). Given that the primary threats to the penguins occur in the marine environment, a more precise and comprehensive picture of their migration and wintering areas is needed to design conservation measures to protect them.

To investigate the migratory movements of Magellanic penguins, we used a 30 year record of band recoveries from a large (approximately 60,000 birds banded), long-term study at Punta Tombo, Argentina, the largest breeding colony of this species (approximately 20% of the Argentine population; Boersma et al., 2013). Carcasses of penguins that die at sea normally float and wash up on beaches (Gandini et al., 1994; pers. obs.), and live penguins tend to come ashore when sick or injured (García-Borboroglu et al., 2006; pers. obs.). As Magellanic penguins do not appear to frequent waters far from shore during the non-breeding season (Boersma, 2012; Stokes et al., 1998), the locations of penguins on beaches should correspond to their recent locations at sea. Because penguin carcasses persist on beaches for only a short time (Gandini et al., 1994), and because of our public information effort (see below) and a continuously inhabited coastline, the record of discoveries of banded birds on beaches should reflect the large-scale spatial and temporal patterns of penguin movement along the South American coast. To provide finer scale information about this movement, we complemented band return data with satellite tracking of migrating penguins departing Punta Tombo following the breeding season (Stokes et al., 1998; this study). While satellite data cannot cover the entire migratory period, they provide an independent and more precise record of penguin movement, including distance from shore, which is not available in the coarser-scale band return data.

We expected that our data would reveal both the general pattern and the variation in Magellanic penguin migratory behavior. In addition to individual variation within age classes, migration distance may be greater for juveniles and young adults than for breeding adults because younger age classes are not constrained by the colony attendance requirements of breeding and chick rearing. As prey conditions strongly influence Magellanic penguin foraging patterns (Boersma et al., 2009), penguin migratory activity may also vary by year due to inter-annual variation in prey location and abundance.

The description of the penguin's migratory behavior that emerges from our data can be used to identify the parameters of effective conservation for this species in its marine environment. As a large and mobile predator, the Magellanic penguin is unlikely to be protected by small fixed-location coastal marine reserves, and larger-scale approaches, such as marine zoning, may be more appropriate (Boersma and Parrish, 1999; García-Borboroglu et al., 2008). Such approaches require detailed and comprehensive information on the spatial and temporal dimensions of the species' habitat use and movements (Costa et al., 2012; Hooker et al., 2011). Thorough understanding of the Magellanic penguin's migratory movements and winter range, along with its nesting and foraging patterns during the breeding season (Boersma et al., 1990, 2007; Boersma and Rebstock, 2009a), can provide the informational basis for an effective conservation plan for this species.

2. Methods

2.1. Band return study

As part of a breeding biology study of Magellanic penguins, we banded 58,232 penguins at the largest colony of the species, Punta Tombo, Argentina (44° 02′S, 65° 11′W), from 1983 to 2010 (see Boersma et al., 1990). We also banded approximately 2000 penguins at colonies farther south along the Argentine coast. At the time of banding we recorded each bird's location and age class (chick, juvenile, adult). We banded chicks at their natal colony just before they fledged, and juveniles (fledged the previous year) at colony beaches where they congregate before or during their molt to adult plumage; hence these birds were of known-age. Birds banded as adults were of unknown age, but nearly all were banded as breeders, meaning they were at least four years old, the earliest age at which Magellanic penguins typically breed (Boersma and Rebstock, 2009b; Rafferty et al., 2005).

Bands were stainless steel (Lambournes-Porzana, East Sussex, UK). Each was custom fitted to the base of the penguin's left flipper, with the side of the band bearing an identifying number visible to an observer (Boersma and Rebstock, 2010). On the inside of the band was a message in Spanish: "Send to the Natural Science Museum, Buenos Aires, Argentina." In 1983 and 1984, the office of Tourism of the Province of Chubut, Argentina, distributed posters to government offices, museums, and individuals in coastal areas, asking people to look for and report banded penguins on beaches.

Nearly all (99%; *n* = 298) reports of band recoveries we received included the band itself or a written record of the band number, which allowed us to reference our banding records to determine the penguin's colony of origin, age at banding, and the date on which it was banded. Most reports (86%; *n* = 258) also included the date the penguin was found. Those that did not include at least the month and year (*n* = 42) were assigned the date the report was mailed to the museum. All reports included a location, and most of these were specific (a town, point, beach, etc.). For reports (*n* = 22; 7%) that merely indicated a substantial stretch (*ca* 100–500 km) of coastline (e.g., Rocha, a province in Uruguay with a 170 km coastline), we assigned the midpoint of the identified coastline as the recovery location. Many reports included additional information on the condition of the bird, e.g., whether it was alive, had petroleum on its feathers, was in a fishing net, etc. Because we were interested in penguin locations during migration, we excluded reports of bands recovered at breeding colonies.

To determine survivorship of birds across years, we searched for banded birds throughout the colony at Punta Tombo every breeding season (September to March) and at other colonies when we were able to visit them. We also searched beaches at Punta Tombo at times of year when large numbers of juveniles and other

non-breeders congregate (Boersma et al., 1990). Observations over 30 years at Punta Tombo indicate that returning breeding adults nearly always nest in the same area of the colony where they nested previously, and chicks that survive to breeding age nearly always return to breed at their natal colony (Boersma, unpubl. data). Thus, we assumed that adults and fledglings not seen again at the colony over a period of 10 years had died. Juveniles, following their first migration, sometimes molt to adult plumage at a location other than their natal colony, and are present at non-natal colonies more commonly than other age classes (Boersma, unpubl. data). Therefore, we made no assumptions about the natal colony of birds banded as molting juveniles nor about the fate of these birds if they were not seen after banding.

2.2. Analysis of band returns

We defined the migration period as the time when penguins are typically absent from the colony. This varies by age and breeding status (Fig. 1). Juveniles (fledglings of the most recent breeding season) have the longest migratory period, departing the colony in mid-January to mid-February and coming ashore again the following November through February. Breeding adults have the shortest migration period. Successful breeders attend the colony from early-to-late September, when they claim nest sites, until they finish their molt in early-to-late April. Failed breeders attend the colony less consistently following loss of nest contents, but most return to their nest site during the breeding season, and many molt in their nest in late February to mid-April. Pre-breeding adults (two and three year olds in adult plumage) are present at the colony more sporadically and for a shorter period than breeders, arriving later and leaving earlier.

We assigned each bird found during migration to one of these three age groups (juvenile, pre-breeding adult, breeding adult), depending on the date it was found relative to its age at banding. Those found during the migration period following the season they fledged until they molted into adult plumage the following January or February were classified as juveniles, those found during the first or second migrations after molting to adult plumage (i.e., two and three year-olds) were classified as pre-breeding adults, and those four years or older were classified as breeding adults. Although many adults do not breed until they are more than four years old (Boersma and Rebstock, 2009b; Boersma et al., 2013), most exhibit breeding behaviors such as occupying a nest and pairing with a prospective mate, and therefore have colony attendance patterns resembling those of breeders.

Most (61%; $n = 184$) of the band recoveries we received were from juveniles. Because of the small numbers of recoveries in the other age classes, some of our analyses include only juveniles. Birds banded as molting juveniles (following their first migration) did
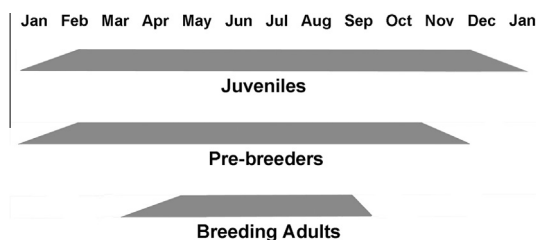
not necessarily originate from Punta Tombo, and therefore we excluded them from analyses of migration distance and timing. Most band recoveries were from birds banded in the 1984–1993 period, when we banded large numbers of fledglings each year ($\bar{x} = 3349$ banded, $sd = 646$, $n = 10$ years), and our inter-year comparisons of migration distances include only those years.

We determined the latitude and longitude of the locations where banded penguins were found using United States Defense Mapping Agency charts and coastal directions (USDMA, 1986). When the reported location did not appear in the USDMA charts, we used national maps and assigned latitude and longitude values to the nearest five minutes. Locations were plotted, and distances calculated using ArcView geographic information software (ESRI, 1991–1999). Statistical methods follow Zar (1999), and were carried out using SPSS statistics software (SPSS, 2009).

2.3. Satellite tracking

In early April 2000 we attached satellite transmitters to four recently molted male penguins that had bred at Punta Tombo earlier in the season. All birds appeared healthy, with a post-molt weight of at least 3.3 kg ($\bar{x} = 3.63$ kg, $sd = 0.32$). Transmitter units were equipped with ST-10 transmitters (Telonics, Mesa, AZ) packed in a pressure-resistant hydrodynamically shaped epoxy housing (Sirtrack Ltd., Havelock, New Zealand). The devices had a total weight of 96 g and cross sectional area of 6.5 cm^2, and were attached following the protocols used when tracking four male penguins departing from Punta Tombo in 1996 (see Stokes et al., 1998). To conserve battery life, the devices were set to transmit every 45 s for six hours per day. The Service Argos satellite system (ARGOS, 1996) reported locations.

For mapping the movement of tracked birds and to calculate travel distances and speeds, we used ArcView geographic information software (ESRI, 1991–1999). To calculate travel speeds we used only locations for which one standard deviation of estimated location error < 1.5 km (location class 1 or better; 122 locations; Argos, 1996). Duration of tracked migration (from the bird's departure from the colony to the last class 1 or better location) ranged from 43 to 50 days ($\bar{x} = 47.8$ d $sd = 3.2$). We re-sampled our 1996 satellite tracking data (Stokes et al., 1998) using only class 1 or better data to allow comparison with the 2000 data.

3. Results

3.1. Band recoveries

We received 300 reports of banded penguins at locations other than the colonies where they were banded. Of these, 286 birds were banded at Punta Tombo and 12 were banded at colonies farther south on the Argentine coast, 10 at Cabo Vírgenes (52° 20′ S 68° 21′ W), and one each on Isla Chaffers and Isla de los Pájaros, near Puerto Deseado (47° 45′ S 65° 54′ W). Colony of origin could not be determined for two returns because no band number was reported. Most of the birds found (94%, $n = 281$) were dead or dying.

Of the returns from birds banded at Punta Tombo, 82% ($n = 234$) were found outside of penguin colonies during the migration period for the bird's age class (Fig. 1) or beyond the maximum foraging distance from the colony (>600 km; see Boersma and Rebstock, 2009a; Stokes and Boersma, 1999), and the birds were presumed to be migrating prior to their discovery. The remainder ($n = 10$ juveniles, 9 pre-breeders, 33 breeding adults) were found outside their migratory period and within foraging range of the colony.

Most (93%, $n = 214$) of the migrating birds were banded as fledglings or breeding adults at Punta Tombo. Except for one

Fig. 1. Generalized migration periods for three age classes of Magellanic penguins at Punta Tombo, Argentina. Gray band indicates period when the age class is typically absent from the colony (i.e., the migration and wintering period). Angle regions indicate periods of arrival and departure. Birds are considered juveniles from their departure from the colony following fledging until they molt to adult plumage the following summer. Pre-breeders are more than one year old and less than four. Breeding adults are four years or older.

juvenile found 290 km south of Punta Tombo, all penguins found during the migration period were north of their colony of origin. Band recoveries were concentrated near the Golfo San Matías and Mar del Plata (Argentina), the east coast of Uruguay, and the southern coast of Brazil, with the latter area having the greatest representation for all age classes (Fig. 2).

Petroleum was reported on the plumage of 7% of the birds recovered ($n = 21$), and 6% ($n = 18$) were reported killed in fishing nets (three additional birds were reported to have survived capture in fishing nets and were released). As this information resulted only from observers who both recognized evidence of oil or fishing net capture and reported it without prompting, these values represent minimum estimates of oil and bycatch mortality. Among the five reports of capture in fishing nets that included depth of capture, birds were caught at an average depth of 53.4 m ($sd = 25.1$, max = 90). The two reports that included latitude and longitude indicated capture locations 71 and 121 km off the coast of southern Brazil.

3.2. Migration distances

Banded penguins from Punta Tombo that were found during the height of the migration period for their age class (i.e., juveniles, July–December; pre-breeders, July–October; breeders, July–August), when birds are expected to be near the northern limit of their migration, were found an average of 1959 km ($sd = 692$, $n = 140$) from the colony. Juveniles were found an average of 2041 km ($sd = 656$, $n = 112$) from the colony, with a modal distance (in 100 km increments) from the colony of 2300–2400 km ($n = 23$ birds; Fig. 2), and a maximum distance of 3171 km for a bird found near Rio de Janeiro (22° 54′S 43° 10′W). The greatest distance from colony of origin among all returns was a juvenile from Cabo Vírgenes recovered on the southern Brazil coast (26° 49′S 48° 37′W), a distance of 3326 km.

Band recoveries from juveniles from Punta Tombo during their first migration indicate the temporal pattern of migratory movement (Fig. 3). For the first months after departing, birds remained relatively close to the colony ($\bar{x} = 624$ km, $sd = 378$, $n = 40$). In May and June they moved rapidly northeastward and then continued at a slower pace through August, remaining in their wintering area far from the colony until December. A similar pattern was seen among the six band returns from juveniles banded at Cabo Vírgenes. All traveled north along the Atlantic coast, with the two that were recovered early in migration (February and May) relatively close (684 km, $sd = 40$) to their natal colony, and the four recovered during the height of migration an average of 2641 km ($sd = 638$) from the colony.

Despite substantial overlap among age classes (Fig. 2), distance traveled from the colony during migration differed significantly by age, with juveniles migrating farther on average than pre-breeders and adults. Band recoveries from the middle of the migratory period for breeding adults, showed that juveniles were significantly farther from the colony than older birds at this time (Fig. 4a). The greater distance of juveniles was not merely a result of age-related difference in timing of migration; distance from the colony at the height of migration for each age class was also greater for juveniles than older birds (Fig. 4b).

Although the general pattern of migratory movement was consistent across years, distance migrated varied (Fig. 5). In the six years in which more than five juveniles were recovered during the high migration period (July–December), mean distance from Punta Tombo ranged from 1029 km in 1986 to 2259 in 1984. Mean and maximum distance in 1986 were significantly shorter than in three of the other five years ($p < 0.05$). We could not analyze annual migration distances after 1992 because of small sample size ($n = 23$ band returns in 19 years). However, the mean distance from Punta Tombo of juveniles found out of foraging range of the colony in July–December from 1993–2012 ($\bar{x} = 2282$ km, $n = 16$) was similar to the mean value for the 1984–1992 period ($\bar{x} = 2151$, $n = 88$; t-test, $t = 1.023$, d$f = 102$, $p > 0.25$).

3.3. Juvenile survival

Annual mortality rate of juveniles during migration, as indicated by proportion of banded juveniles recovered during migration, was inversely correlated with cohort recruitment to the
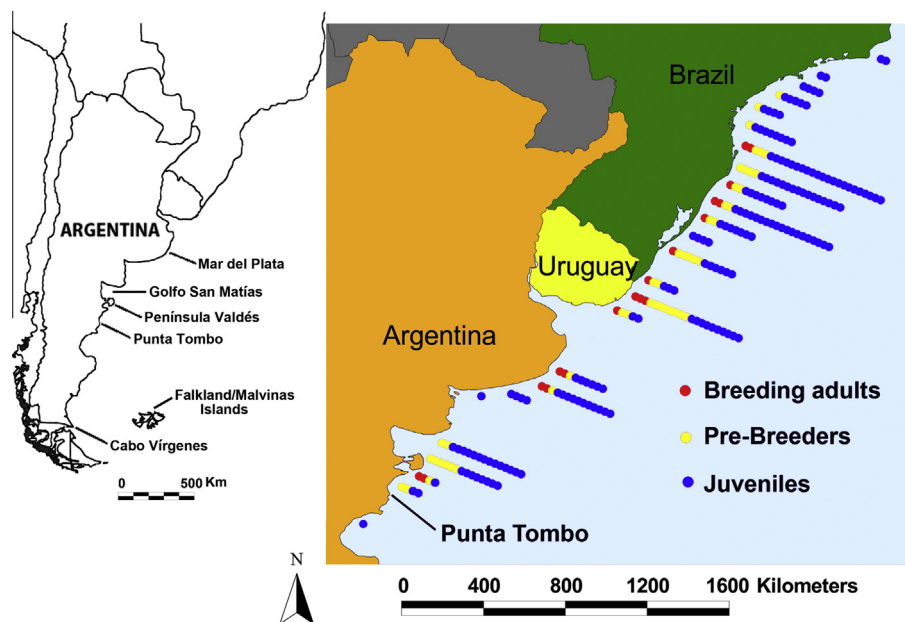

Fig. 2. Locations along the South American coast of all band recoveries from migrating and wintering penguins banded at Punta Tombo, grouped in 100 km intervals. Age class refers to age of bird when the band was recovered. Birds were considered to be migrating or wintering if they were found during the usual period of absence from the colony for their age class (Fig. 1) or were beyond the maximum foraging range (600 km) from Punta Tombo during the breeding season ($n = 234$). Inset map shows locations of penguin colonies at Punta Tombo and Cabo Vírgenes and prominent coastal features. Magellanic penguin breeding colonies occur along the Argentine coast south of Golfo San Matías, as well as many locations in the Falkland/Malvinas Islands.
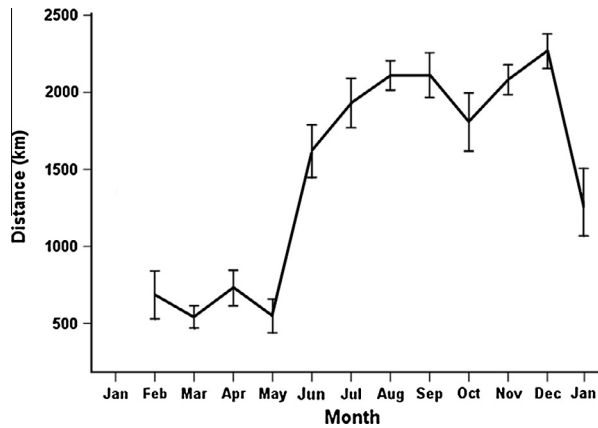
Fig. 3. Mean distance from the colony of band recoveries from juveniles banded as fledglings at Punta Tombo, Argentina, by month reported, 1984–2010 (*n* = 176). Whiskers indicate standard error. No juveniles were found away from the colony in January of the season they fledged.

breeding colony (Fig. 6), suggesting that survival of first migration is a significant regulator of population dynamics. Among the years in which we banded large numbers (>1700) of fledglings (1984–1993), the proportions of those birds that were known to have survived their first migration (i.e., were re-sighted at the colony) varied widely among years, with more than 10% surviving in 1985, 1989, and 1993, and less than 3% in all other years. Younger penguins were more likely to die during migration than older birds. Over the 1984–1993 period, the proportion of juveniles recovered during their first migration (0.45%) was nearly twice the proportion of pre-breeding adults; (0.23%; *n* = 4339) recovered during their first migration as pre-breeders, and nearly eight times the proportion of breeding adults (0.06%) recovered per migration (total migrations of breeding adults estimated at 33,513 over the period; Boersma, unpubl. data).

3.4. Satellite tracking

The eight adult penguins we tracked during the first two months of migration in 1996 and 2000 traveled northeast along the coast (Table 1, Fig. 7). The birds took similar routes in the two years, and showed similar patterns of movement, initially traveling rapidly, and then slowing. In both years, one of the four birds entered Golfo San Matías, a large gulf centered approximately 350 km north of Punta Tombo. In 1996, bird #1 remained there until signals ceased, a period of 29 d. In 2000, bird #6 remained in the gulf for at least 18 days and then moved to an area approximately 100 km north of Punta Tombo.

The other three penguins tracked in each of the two years continued northeastward beyond the gulf at a similar rate; the five for which date of departure was precisely known were 700–841 km northeast of the colony at the 20th day of their migration (Table 1). All but one of the six (#8) continued to move northeastward until signals ceased. Bird #8 reached a maximum distance from the colony of 1124 km, but backtracked approximately 350 km to the southwest over the last two weeks signals were received.

The locations of the six birds that traveled past Golfo San Matías were concentrated in a path 40–240 km from shore, well inside shelf break (Fig. 7). The average width of the migration path (i.e., maximum spread of locations perpendicular to direction of travel) of these birds was 42.5 km (*sd* = 30.4, *n* = 23 transects at 50 km intervals), with a narrower average width in each year separately (1996: $\bar{x}$ = 26.1 km, *sd* = 33.6, *n* = 11 transects; 2000: $\bar{x}$ = 30.3 km, *sd* = 23.5, *n* = 22 transects). Over the portion of the route north of Península Valdés that three penguins traveled in
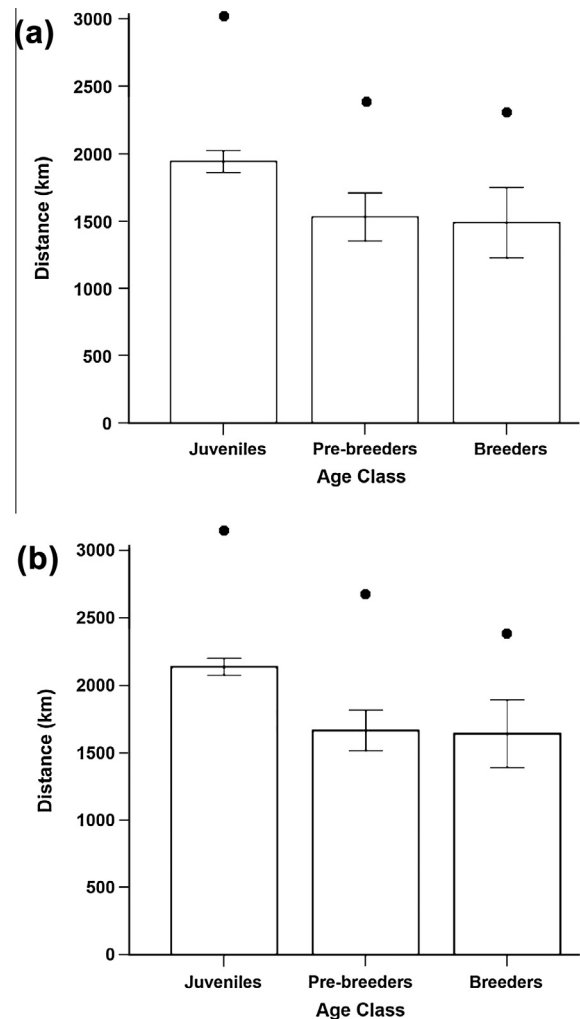

Fig. 4. Mean, standard error (whiskers) and maximum (dots) distance from Punta Tombo, Argentina, of juveniles, pre-breeders, and breeding-age adults banded at Punta Tombo and found outside of the breeding season, 1984–2012. (a) Recoveries of juveniles (*n* = 62), pre-breeders (*n* = 19), and breeding adults (*n* = 9) during the mid-migration/wintering period for breeders (June–August); Oneway ANOVA $F_{2,87}$ = 3.75, *p* < 0.05. (b) Recoveries during the period of maximum distance from the colony for each age class (juveniles, *n* = 104, July–December; pre-breeders, *n* = 23, July–October; breeding adults, *n* = 7, July–August; $F_{2,131}$ = 6.01, *p* < 0.01). To avoid inclusion of birds that died while attending the colony during the breeding season, band recoveries within foraging range (<600 km) of Punta Tombo are excluded for all age classes (*n* = 8 juveniles, 7 pre-breeders, 1 adult).

both years, mean path width was 60.4 km (*sd* = 29.5); width did not differ between years (*t*-test: *t* = 0.89, d*f* = 4, *p* > 0.25, *n* = 11 transects).

4. Discussion

4.1. Magellanic penguin migration

Band returns and satellite tracking data provide a consistent record of the annual long-distance migration of Magellanic penguins. The birds leave their breeding colonies in southern Argentina in the austral summer or fall and move north to winter off the coasts of northern Argentina, Uruguay, and southern Brazil, returning to their colonies in spring or summer, depending on their age. The average one-way migration distance, as indicated by band recoveries, is approximately 2000 km, with some records exceeding 3000 km. Because band recoveries include those from penguins
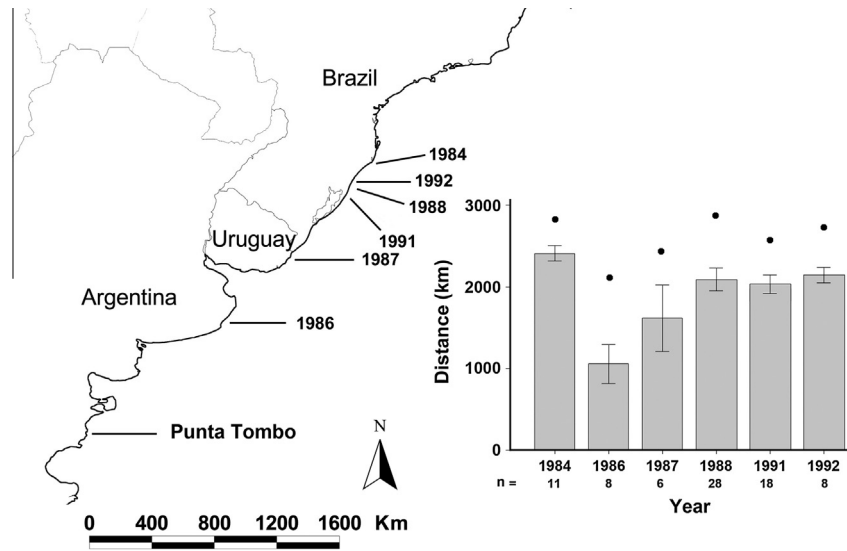
Fig. 5. Mean distance and location north of Punta Tombo of band recoveries by year (years with > 5 recoveries) for juveniles recovered during their first migration/wintering season, July–December. Oneway ANOVA $F_{5,73}$ = 4.98, p < 0.001. Post-hoc contrasts indicate 1986 distance differed significantly from 1984, 1988, and 1991 (p < 0.05, Scheffé's comparison). Whiskers indicate standard error, dots indicate maximum.
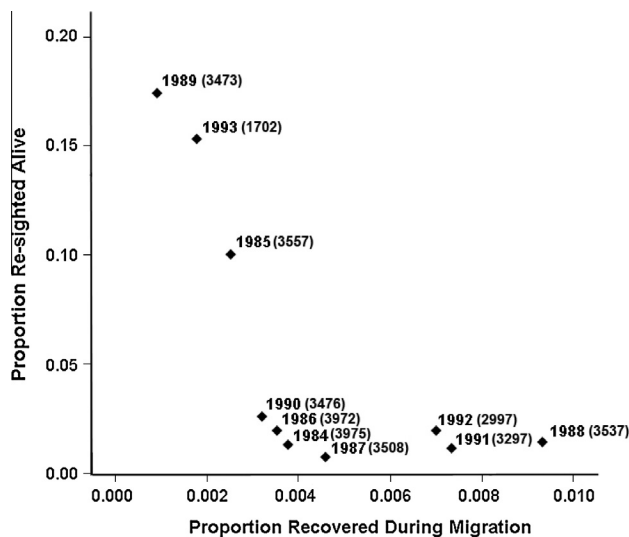

Fig. 6. Rate of survival of each cohort of juveniles fledged at Punta Tombo, Argentina for their first migration/wintering season 1984–1993, as indicated by % re-sighted alive at the colony subsequent to that initial season, by migration/wintering mortality, as indicated by proportion of the cohort found dead during their initial migration/wintering period (r^2 = 0.504, $F_{1,8}$ = 8.14, p < 0.05). Number of birds banded in each cohort shown in parentheses. Years after 1993 are excluded because fewer birds were banded (<1500 per year).

that died before reaching maximum migration distance or during the return trip, modal distance of band recoveries (2300–2400 km for juveniles, corresponding to a latitude of 29° S off the coast of southern Brazil) is likely to better represent the typical migration distance and location of wintering grounds (Fig. 2).

Migration pattern was broadly consistent across years, although average annual migration distance varied. We found no evidence of a long-term shift in migration distance over the 30 years of the study, as the average distance indicated by band recoveries in the first 10 years of the study was similar to that of subsequent years. Birds of different age classes overlapped substantially in their migration route and wintering locations. However, juveniles and pre-breeders migrated farther on average than breeding adults, and were away from the colony nearly an entire year, approximately twice the duration of the breeders' absence. In some

cases, non-breeders may remain on their wintering grounds for the entire breeding season (Boersma, 2012).

These results are consistent with numerous popular and scientific accounts of Magellanic penguins along the coasts of northern Argentina, Uruguay, and southern Brazil during the non-breeding season (e.g., Narosky and Yzurieta, 2003; Schiavini et al., 2005; Vooren and Brusque, 1999; Ramos da Silva et al., 2012), some of which reported small numbers of penguins known to have originated at colonies in southern Argentina (Boswall and MacIver, 1975; Daciuk, 1977).

Our small sample of recoveries of juveniles from Cabo Vírgenes, suggests that penguins from colonies all along the Argentine coast may migrate and winter in the same general areas. Mean distance north of Punta Tombo of juveniles from Cabo Vírgenes (approximately 900 km south of Punta Tombo) was within 250 km of the mean for juveniles from Punta Tombo. Satellite tracking of Magellanic penguins from the southernmost colonies of the species in Argentina (Pütz et al., 2007) and in the Falkland/Malvinas Islands (Pütz et al., 2000) during the initial months following breeding also shows long-distance northward movement along the Argentine coast, suggesting that the entire South Atlantic population (Bouzat et al., 2009) of this species may follow a similar migratory route.

The location and timing of migratory movement of penguins from Punta Tombo broadly correspond to the seasonal movement of anchovy *Engraulis anchoita*, a small schooling fish that is the penguin's primary prey in the northern part of its Atlantic breeding range (Boersma et al., 2013; Frere et al., 1996; Wilson et al., 2005). Anchovy spawning activity moves from Patagonian coastal waters in spring and summer, northward to coastal Brazil in winter (Bakun and Parrish, 1991; Sanchez and de Ciechomski, 1995; Viñas and Ramírez, 1996). Inter-year variability in distance of northward movement of migrating penguins may reflect year-to-year differences in prey abundance and distribution due to oceanographic conditions (Boersma et al., 2009; García-Borboroglu et al., 2010; Ramos da Silva et al., 2012). Annual variation in migration distance in our sample and occasional reports of large numbers of penguins farther north than usual (e.g., Bellos, 2001) – as far as northern Brazil in rare cases (García-Borboroglu et al., 2010) – suggest that while migration as far as southern Brazil is the norm, there is substantial variability in the northward extent of migration.

Table 1
Summary satellite tracking data for eight male Magellanic Penguins departing from Punta Tombo, Argentina in April 1996 (see Stokes et al., 1998) and April 2000. For both years only locations of class 1 or better (one standard deviation of estimated location error < 1.5 km) were used to calculate travel speed. Distance was also calculated from class 1 locations except for bird #6, for which we received no class 1 or better locations (distances in parentheses). Maximum distance from colony is the minimum (straight line) swimming distance; actual distance traveled was greater. Initial travel speed is the average speed for the first week following departure. Subsequent travel speed is the average for the remainder of the trip to date of last signal.

Bird	Last date at colony	Date of last location	No. of locations (classes 1, 2, 3)	Max. distance from colony (km)	Dist. from colony at last location (km)	Dist. from colony at day 20 (km)	Max. dist. from shore (km)	Travel speed (km/d)	
								Initial	Subsequent
1996									
#1	15 April	20 May	28	444	412	431	46	61.3	11.6
#2	14 April	4 May	20	702	704	700	197	55.7	31.9
#3	15 April	7 May	31	743	739	721	187	60.2	31.3
#4	⩾15 April	1 May	3	726	724	–	238	–	–
2000									
#5	10 April	29 May	68	1246	1246	742	211	49.1	29.3
#6	11 April	24 May	0[a]	(390)	(101)	(356)	(94)	–	–
#7	10 April	30 May	28	1289	1243	841	199	55.9	24.5
#8	11 April	30 May	26	1124	786	791	201	60.1	33.2

[a] No locations of class 1 or better received; all values based on locations of class 0 (*n* = 18).
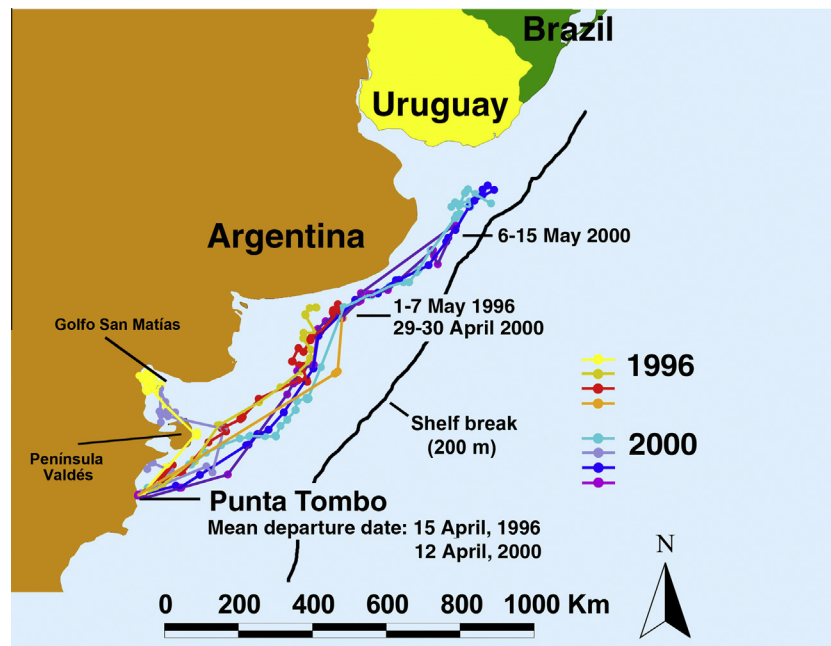

Fig. 7. Initial migration routes of adult penguins from Punta Tombo, 1996 (*n* = 4) and 2000 (*n* = 4), as determined by satellite tracking.

Our two years of satellite tracking data indicate that the northward penguin movement follows the coast in a relatively narrow migration corridor within 250 km of shore. Tracking of rehabilitated oiled penguins released in northern Argentina suggests a nearshore return (southward) migration path as well (Boersma, 2012). This is consistent with the locations of penguin captures reported by fishing operations off the coast of Brazil (this study; Cardoso et al., 2011), and with results of studies of Magellanic penguin foraging and diet, which indicate that the penguins forage at relatively shallow depths (<100 m; Walker and Boersma, 2003) for small schooling fish that inhabit waters over the continental shelf (Lima and Costello, 1995). Notwithstanding the consistency of the travel pattern across individuals and years, our satellite data also show individual variation in migratory movement (Fig. 7), perhaps the result of opportunistic responses to local variation in prey availability, as penguins are opportunistic foragers (Davis and Renner, 2003; García-Borboroglu and Boersma, 2013; Williams, 1995).

With little mortality of post-fledging Magellanic penguins occurring at breeding colonies (Boersma, unpubl. data), most mortality occurs during the non-breeding season, and survival of migration by young birds appears to be an important determinant of recruitment to the breeding population (Fig. 6). Substantial Magellanic penguin mortality due to oil pollution and fisheries bycatch has been documented in coastal areas of southern Brazil (Cardoso et al., 2011; Mäder et al., 2010; Petry et al., 2004). The significant, and likely under-reported, proportion of band reports we received indicating oiling or capture in fishing nets during migration suggests that these causes of mortality, along with depletion of prey species caused by commercial fisheries, as observed in African penguins *S. demersus* (Pichegru et al., 2012), are important anthropogenic threats to this species (Boersma, 1997, 2008; Schiavini et al., 2005).

While the broad outlines of Magellanic penguin migration emerge clearly from our data and its consistency with the reports of others, limitations inherent in band return data indicate the need for further research. In particular, the small number of band returns in some years, raises the possibility that annual differences identified here, though significant in our sample, may not be

broadly representative. In addition, the influence of ocean currents – highly complex and variable (Lima et al., 1996; Souza and Robinson, 2004) in this region – on locations of beached penguins is unknown. Expanded satellite or geolocation tracking efforts targeting all stages of migration and wintering are needed to produce finer scale characterizations of penguin migration and its variability, independent of ocean current effects and the vagaries of band return rates.

4.2. Conservation of penguins and their migration habitat

The importance of the non-breeding period for Magellanic penguin survivorship and recruitment means that an effective conservation program for this species must address the threats in the marine environment where it winters and through which it migrates. Currently, this habitat is largely unprotected. The southern Brazil coastal region is one of the most threatened marine environments in South America because of human activities, including hydrocarbon development, marine transport, and fisheries (Chatwin and Rybock, 2007), all of which are likely to negatively affect migrating penguins and other marine species. The proportion of the area included in marine protected areas is very small (<5%; Chatwin and Rybock, 2007); no-take protected areas are even more limited, and are non-existent farther south along the coasts of Uruguay and northern Argentina (Guarderas et al., 2008). Because of the small number and limited size (median area = 26 km^2) of protected areas in the region, the average distance between protected areas ranges from 100s to over 1000 km (Guarderas et al., 2008).

In response to the dearth of marine protections in the region, The Nature Conservancy recommended increasing marine protected areas to as much as 13% of some areas of coastal southern Brazil (Chatwin and Rybock, 2007). However, designation of marine protected areas, particularly no-take reserves, is controversial (Diegues, 2008), and establishment of large protected areas has been particularly difficult in coastal areas that are populous and heavily used by humans (Spalding et al., 2010), conditions that characterize northern Argentina, Uruguay, and southern Brazil (Chatwin and Rybock, 2007).

Furthermore, even if expanded as recommended, these protected areas would be inadequate for migrating Magellanic penguins. Traveling for thousands of kilometers at and just below the water's surface, migrating penguins are particularly vulnerable to anthropogenic threats such as net fisheries and oil pollution (Adams, 1994; García-Borboroglu et al., 2008), and require large-scale and continuous protection. We estimate that a continuous protected area encompassing the Magellanic penguin's foraging and migration habitat in the southwest Atlantic would exceed 500,000 km^2, more than twice the total area of all marine protected areas in Latin America and the Caribbean combined (Guarderas et al., 2008). Given these spatial requirements and the diversity and intensity of human activity in the area, a strictly regulated (e.g., no-take) marine reserve is unlikely to be feasible (Lascelles et al., 2012; Yorio, 2009).

A more promising mechanism for conserving this species is marine zoning (Agardy, 2011; Crowder et al., 2006; Halpern et al., 2008). An international conservation and management zone based on the marine habitat requirements of the Magellanic penguin would extend from the southern limit of penguin breeding colonies to the northern limit of the penguin's seasonal migration, and from the shore to the edge of the continental shelf, or to 250 km where shelf width exceeds that distance (Fig. 8). The zone would consist of management areas with seasonal regulations of human activities timed to correspond to the use of the areas by penguins. Types of regulations could include, for example, localized shifting seasonal regulation of net fisheries that target small schooling fish, and seasonal operations rules, safety requirements, and shipping lane locations for petroleum extraction and transport (García-Borboroglu et al., 2008). The penguin migration route is entirely within the Exclusive Economic Zones of Argentina, Uruguay, Brazil, and the UK, facilitating the regulation of these activities by each nation.

In addition to being expansive and continuous, such a zoning approach can be flexible and dynamic, with the capacity to respond to inter-year variability in oceanographic conditions. While Magellanic penguin migration patterns are broadly predictable, the annual variation shown here and more occasional and extreme variation reported elsewhere (García-Borboroglu et al., 2010; Ramos da Silva et al., 2012) indicate that management flexibility is important.

For greatest conservation effectiveness and likelihood of success, the penguin management zone would constitute one element of a regional comprehensive marine spatial planning (MSP) process (Douvere and Ehler, 2009), which allows holistic ecosystem management and explicitly addresses human uses and engages diverse stakeholders. This approach is particularly appropriate in areas where conflicting uses must be balanced (De Santo, 2013; Douvere and Ehler, 2009), such as coastal waters (White et al., 2012). Zoning in an MSP framework is used successfully in Australia's Great Barrier Reef Marine Park (GBRMP). The GBRMP comprises a large (344,400 km^2) network of sub-areas zoned for a variety of uses that range from purely conservation to resource exploitation (e.g., fishing) with protections (Kenchington and Day, 2011). The GBRMP has proven to have a flexible management system that can adapt to improve conservation effectiveness, for example, by altering zoning regimes to include more no-take areas when new information indicated that existing protections were inadequate (Fernandes et al., 2005).

A substantial challenge to the penguin conservation zone and MSP in the region is that unlike the GBRMP, an international scope is required. To date, MSP in coastal areas has been limited to the national level (e.g., Belgium, Netherlands, Germany, UK; Douvere and Ehler, 2009) or lower (e.g., the state of Massachusetts [USA]; White et al., 2012). This highlights one of the limitations of the current piecemeal approach to ocean management and governance, which is at odds with the large-scale, connected, and continuous nature of marine ecosystems (Crowder et al., 2006). However, existing international agreements have the potential to drive international MSP (e.g., the Convention on Biological Diversity and the Convention for the Conservation of Migratory Species; Douvere and Ehler, 2009; Yorio, 2009), although this potential is as yet unrealized. A four-party convention among the nations of Argentina, Uruguay, Brazil, and the UK could also provide a mechanism for international MSP.

The challenge of international action notwithstanding, a penguin conservation zone has several important practical advantages. First, it coincides with some of the most threatened coastal ecosystems in South America, along with the ranges of diverse marine species of conservation concern (Yorio, 2009). Thus, broader conservation goals would be accomplished through management of threats such as bycatch and oil pollution that affect many species in the region. Second, penguins are effective environmental indicators (Boersma, 2008; Hooker and Gerber, 2004). They are upper level predators that can be tractably monitored through current technology both on land and at sea, allowing them to provide the informational basis for highly responsive adaptive management, important for marine systems, which are dynamic and poorly understood. By monitoring penguin movements in real time, for example, through satellite tracking of migration and colony-based monitoring of foraging trip-length (Boersma and Rebstock, 2009a; Boersma et al., 2007), managers could respond to variation in the marine environment and penguin at-sea behavior (e.g., annual differences in migration distance). Expanded tracking of migrating
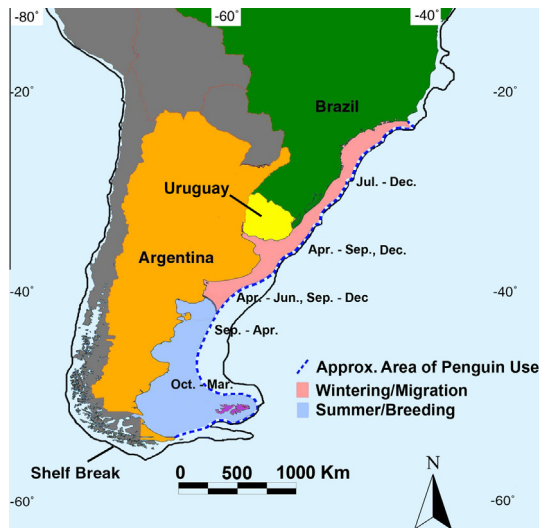
Fig. 8. Generalized spatial and temporal parameters of a South Atlantic Magellanic penguin marine conservation management zone. Zone would extend from the southern extent of breeding to the northern extent of migration, and from shore to shelf break or to 250 km where shelf break is farther offshore. Months shown indicate periods of penguin presence, when regulation of fishing and oil pollution-producing activities is needed. Southern extent of conservation zone is based on colony locations (Boersma et al., 2013) and foraging ranges as determined by satellite telemetry and penguin-borne data loggers (Boersma et al., 2002; Wilson et al., 2005).

penguins in the future also could allow refinement of the proposed conservation zone by more precisely delineating the width of the penguins' migration corridor, the timing of movements, and the most critical areas for protection. Finally, as an animal with wide appeal for people (Boersma, 2008; Stokes, 2007), the Magellanic penguin can serve as a flagship species (Leader-Williams and Dublin, 2000), providing a unifying focus, as well as popular and political support that will be essential for both the conservation zone and a more comprehensive MSP initiative, which will necessarily involve regulation of human activities. These practical and management-related advantages of the proposed conservation zone – the capacity of penguins to simultaneously serve umbrella, indicator, and flagship functions (Hooker and Gerber, 2004) – substantially increase the likelihood of conservation success.

Large-scale, international, marine zoning is an ambitious goal. However, the extensive spatial requirements of the Magellanic penguin mean that small scale coastal reserves will be inadequate for conservation of this species. Conservation policy must reflect scientific understanding to achieve effective protection for imperiled species and their ecosystems.

5. Conclusion

Because of the Magellanic penguin's long-distance seasonal migration and the significance of human-caused penguin mortality during migration, large scale protections are needed to conserve this species in its marine environment. Marine zoning is a conservation approach that can accommodate the spatial scale, temporal pattern, and variability of the penguin's migratory behavior, as well as the conflicting uses of the marine environment by humans. While the large scale and international scope of the required conservation measures present undeniable challenges, the marine zoning approach proposed here offers a practical way to conserve Magellanic penguins and the threatened coastal ecosystems through which they migrate without ignoring human interests.

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