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Trans-equatorial migration, staging sites and wintering area of Sabine's Gulls *Larus sabini* in the Atlantic Ocean

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The migrations and winter distributions of most seabirds, particularly small pelagic species, remain poorly understood despite their potential as indicators of marine ecosystem health. Here we report the use of miniature archival light loggers (geolocators) to track the annual migration of Sabine's Gull *Larus sabini*, a small (*c*. 200 g) Arctic-breeding larid. We describe their migratory routes and identify previously unknown staging sites in the Atlantic Ocean, as well as their main Atlantic wintering area in the southern hemisphere. Sabine's Gulls breeding in northeast Greenland displayed an average annual migration of almost 32 000 km ($n = 6$), with the longest return journey spanning close to 39 000 km (not including local movements at staging sites or within the wintering area). On their southern migration, they spent an average of 45 days in the Bay of Biscay and Iberian Sea, off the coasts of France, Spain and Portugal. They all wintered in close association with the cold waters of the Benguela Upwelling, spending an average of 152 days in that area. On their return north, Sabine's Gulls staged off the west African coast (Morocco, Mauritania, Senegal), spending on average 19 days at this site. This leg of migration was particularly rapid, birds travelling an average of 813 km/day, assisted by the prevailing winds. Sabine's Gulls generally followed a similar path on their outbound and return migrations, and did not exhibit the broad figure-of-eight pattern (anti clockwise in the southern hemisphere and clockwise in the northern hemisphere) seen in other trans-equatorial seabirds in the Atlantic and Pacific oceans.

Keywords: annual cycle, Benguela Upwelling, geolocators, hotspots, *Larus sabini*, *Xema sabini*.

Many marine predators undertake long-distance migrations, sometimes thousands of kilometres, during their annual cycle (Phillips *et al.* 2005, González-Solís *et al.* 2007, Guilford *et al.* 2009, Egevang *et al.* 2010). Knowledge of these movements and the spatial use of marine habitats by predators can add considerably to our understanding of marine ecosystem dynamics, especially the interactions between predators and prey (Phillips *et al.* 2007). Mapping population distributions and identifying spatially overlapping uses and threats is also critically important in marine ecosystem management and conservation (González-Solís & Shaffer 2009). Threats to seabirds at sea include competition with fisheries and the associated widespread impacts of bycatch (Montevecchi 2002) and marine pollution, particularly from petroleum products (Burger & Gochfeld 2002). The risk of oiling has potentially increased in recent years with the development of deepwater drilling, while the rapidly increasing interest in harnessing offshore wind and wave energy in outer continental shelf regions of the world brings additional potential threats for seabirds, including habitat loss, disturbance and increased risk of collision (Croxall *et al.* 2005, Phillips *et al.* 2005, Hüppop *et al.* 2006, Grecian *et al.* 2010).

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Despite a long history of research interest, the long-distance migratory movements and behaviour of many seabird species remained poorly understood until recently, particularly for pelagic species. For some species, traditional ringing studies and at-sea surveys have provided basic information on general movements, but these methods do not provide details of the individual spatial and temporal dynamics of migration that are often necessary for effective conservation.

Over the last decade or so, advances in technology have increasingly opened windows into the lives of animals in the offshore marine environment that were previously beyond our reach. Initially, the heavy batteries required for tracking devices, such as satellite transmitters, restricted their deployment to large avian species, including penguins and albatrosses (generally > 2–3 kg). However, the size of satellite transmitters has decreased over time, and the range of birds studied has progressively shifted to smaller species. With the recent development of increasingly miniaturized archival data loggers that record light intensity, known as geolocators, it has become possible to track the long-distance migrations of smaller seabirds, such as shearwaters (< 1 kg, Shaffer *et al.* 2006, González-Solís *et al.* 2007, Guilford *et al.* 2009), puffins (< 0.5 kg, Harris *et al.* 2010) and terns (< 150 g, Egevang *et al.* 2010). Geolocators have quickly proved to be a valuable tool in describing the temporal changes in distribution and migration patterns of medium- to small-sized seabirds across vast distances (Burger & Shaffer 2008).

Discovered in Greenland in 1818 (Sabine 1819), Sabine's Gull *Larus sabini* exhibits a circumpolar breeding distribution, and loose colonies are found in the Arctic and sub-Arctic regions of the northern hemisphere (Day *et al.* 2001). Their wintering areas remained a mystery for well over 100 years; even as recently as the 1950s it was thought that they might spend the winter months off the coasts of France and Spain, in the Bay of Biscay (Fisher & Lockley 1954) and it was not until the 1960s that this far northern breeder was confirmed to cross the equator and winter in the southern hemisphere (Zoutendyk 1965, 1968, Chapman 1969). Recent studies have concentrated on various aspects of the breeding behaviour and ecology of Sabine's Gull (Forchhammer & Maagaard 1991, Stenhouse *et al.* 2001, 2004, 2005a, 2005b, Stenhouse 2003, Stenhouse & Robertson 2005, Levermann & Tøttrup 2007, Smith *et al.* 2007). Until now, very little was known about their general ecology during the non-breeding period or their migration routes, and nothing about stopover areas or staging sites (Day *et al.* 2001). In Greenland, the species breeds only in close association with Arctic Terns *Sterna paradisaea* (Boertmann 1994), although this is not the case elsewhere in the range (Day *et al.* 2001). Between 1975 and 2001, 46 Sabine's Gulls were ringed in Greenland, but none of them was ever recovered (Lyngs 2003). Although considered of least concern (LC) globally (IUCN 2011), Sabine's Gull is listed as near threatened (NT) in Greenland, due to the small population (100–500 pairs) breeding there (Boertmann 2008).

In this study, we used miniature archival light loggers (geolocators) to track the migration patterns of Sabine's Gulls breeding in Greenland and to explore their broad-scale winter habitat use. Specifically, we tracked the entire annual migration of Sabine's Gulls from their breeding colony in northeast Greenland to their South Atlantic wintering area and back. Our aims were (1) to investigate and describe in detail the timing of migration and route(s) used by Sabine's Gulls in the Atlantic Ocean, (2) to identify and characterize their destination wintering area(s), and (3) to highlight any significant staging areas where management actions may contribute to the conservation of this species.

METHODS

Study site

Fieldwork was conducted from mid-July to late August in 2007 and 2008 at Sand Island (74°43′N, 20°27′W), Young Sound, Northeast Greenland. Sand Island (*c.* 0.22 km^2) peaks at only 2.5 m above sea level at high tide. The substrate consists mainly of fine sand and gravel, but a slightly raised section in the centre of the island has sparse vegetation, mostly Arctic willow (*Salix* sp.). The island supports a breeding population of 700–1000 pairs of Arctic Terns, 60–65 pairs of Sabine's Gulls (Egevang & Stenhouse 2007) and, in some years, 80–100 nesting Common Eiders *Somateria mollissima* (Egevang *et al.* 2008). Breeding success at this colony is dependent largely on the timing of sea-ice break-up; birds may be forced to abandon breeding in late spring when Arctic Foxes *Alopex lagopus* can gain access to the island via intact or densely packed ice (Levermann & Tøttrup 2007, Egevang & Frederiksen 2011).

Logger deployment

Adult breeding Sabine's Gulls were captured at Sand Island by placing a self-triggered wire mesh drop trap over their nests (see Koopman & Hulscher 1976). On their initial capture in 2007, biometrics (weight, wing length, tarsus, head and bill) were recorded, they were ringed, and a blood sample and a cloacal swab were taken. In total, 30 adults were fitted with miniature archival light loggers (Mk14 geolocators, 1.4 g; British Antarctic Survey, Cambridge, UK) attached to plastic (darvic) leg rings. The total weight of the logger, attachment (tape and cable tie) and ring was 2.0 g, *c.* 1% of adult body mass. A small amount of picric acid was used to dye the plumage of the nape area immediately below the dark grey hood, or the white spots on the otherwise black outer primaries, so that birds with loggers could be easily identified on the nest and their attendance behaviour closely observed throughout the remainder of the breeding season. Handling time was kept to a minimum (*c.* 10–15 min), although birds were held in cotton bags to allow the dye to dry, adding another 15–20 min to the overall processing time. In 2008, all Sabine's Gull nests on Sand Island were observed for attendance by tagged individuals, which were recaptured using the same drop traps. Upon capture, weight was recorded, the logger was removed, and their legs were examined for any wear or damage. Again, handling time was kept to a minimum (< 10 min).

Geolocators and analysis of light data

The geolocators measured the intensity of visible light every 60 s and recorded the maximum reading (truncated at saturation) within each 10-min interval. Light data were processed following the approach of Phillips *et al.* (2004). The timing of sunrise and sunset was calculated from light records and converted to location estimates (two per day) using TRANSEDIT and BIRDTRACKER (British Antarctic Survey) using thresholds of 10, an angle of elevation of −4.7°, and applying the compensation for movement. Transitions associated with obvious interruptions to light curves were noted during processing, and resulting locations were subsequently excluded from analyses, as appropriate. Latitudes could not be calculated during equinox periods, and locations were also unavailable from very high latitudes due to 24-h daylight. A straight-line path was assumed between the preceding and succeeding valid fix around periods when locations were unavailable. The only exceptions were movements between the breeding colony and 60°N, the latitude at which it becomes impossible to calculate locations because of 24-h daylight, where the projected route was altered to follow the coast. As positions obtained from geolocators exhibit a relatively low accuracy, *c.* 185 km in flying seabirds (Phillips *et al.* 2004), we used a conservative approach when calculating distances and speed. Furthermore, local movements at staging sites and within the wintering area were not included in the calculation of overall migration distances, so values presented here are minimum estimates. Great-circle distances were calculated using the mean of the two daily positions, interpolating between valid locations across periods when data were unavailable (see above). Staging sites were identified following the approach of Guilford *et al.* (2009) where latitudinal movements were < 0.8° over a 0.5-day period, and smoothed over 3 days. A kernel density map (Fig. 1) was generated in a WGS 1984 projection in ARCGIS using Hawth's Tools (Beyer 2004), with a cell size of 1 km and a search radius of 200 km.

RESULTS

Of the 30 birds fitted with geolocators in 2007, > 18 (> 60%) were observed at the colony in 2008, although many proved impossible to recapture and only 11 loggers (37%) were retrieved. Compared with untagged birds at the same colony, the nest attendance and general reproductive behaviours of tagged birds appeared to be unaffected by the presence of the logger, and most of the tagged birds are known to have successfully raised young in 2008 without any obvious sign of their abilities being compromised. We closely examined the legs and feet of all recaptured individuals at the time of logger removal and saw no physical signs of harm. Neither was there a difference in the body mass of individuals with loggers between years (2007 = 176.1 ± 10.83 g; 2008 = 177.7 ± 11.29 g, $t = 0.29$, $P = 0.769$, df = 8, $n = 9$). In 2008, birds with loggers nested 5–150 m from nest-sites used in the previous year, which is well within the normal range of movement for this

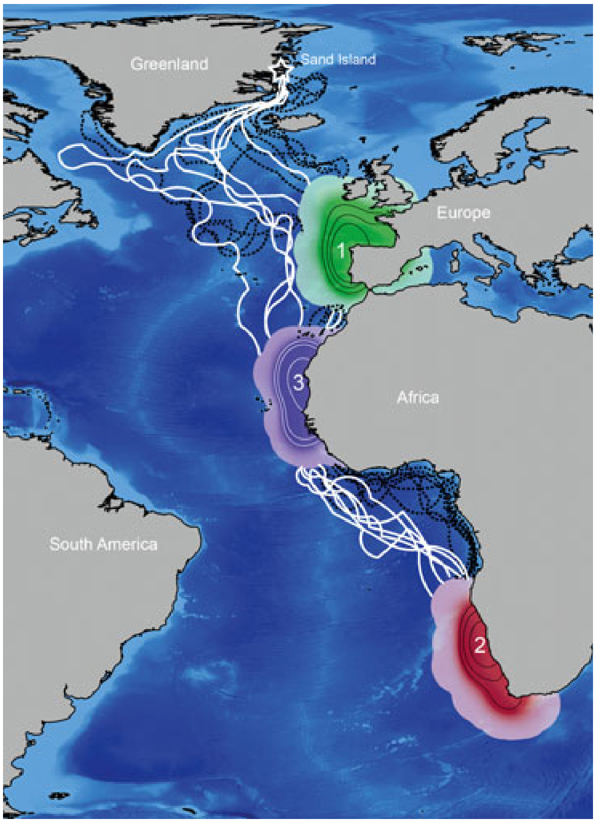

Figure 1. Interpolated migratory pathways, staging sites and wintering area of Sabine's Gulls (n = 10) tracked from a colony in northeast Greenland (star). Dashed black lines = southbound autumn migrations; 1 = autumn staging site; 2 = wintering area; solid white lines = northbound spring migrations; and 3 = spring staging site (see Table 2 for periods spent at each staging site). Contour lines within the density kernels indicate the 50th (inner), 70th (mid) and 90th (outer) percentiles of the distribution of positions within each of the identified areas. Periods when logger data are unreliable (i.e. around equinoxes) are absorbed within the kernels on this map, thus there are no gaps in the tracks displayed.

species (Stenhouse *et al.* 2001, Stenhouse & Robertson 2005). Six of the retrieved loggers contained a full year of migration data, four contained partial data and one logger failed to download (Table 1). All migrations were characterized by very well-defined phases of movement, from breeding colony to autumn staging site, autumn staging site to wintering area, wintering area to spring staging site, and eventual return to the colony.

Autumn migration

After breeding, all tagged birds headed south down the eastern coast of Greenland. Approximately half of the birds turned sharply southeast, taking them west of Iceland and Ireland, directly towards the western coast of mainland Europe. The other birds travelled further west into the central part of the North Atlantic Ocean before bearing sharply east, one bird venturing round Cape Farewell to western Greenland before heading south and east (Fig. 1). All tagged birds eventually reached the Bay of Biscay and Iberian Sea, off the coasts of France, Spain and Portugal (Fig. 1). Individuals arrived at this staging site in mid-August to mid-September (median arrival date: 31 August), and remained there for an average of 45 days (range: 35–53 days; Table 2). By the end of October, all tagged birds had left this area and headed south (median departure date: 15 October), travelling close to the west African coast and crossing the equator to arrive in their primary wintering area from late October to late November (median arrival date: 12 November).

Wintering area

All birds wintered in close association with the Benguela Upwelling, where they spent an average of 152 days (range: 125–180 days; Table 2). Seven of the eight birds for which data are available remained throughout this time within a geographically restricted area (between 20° and 30°S), with just one bird (SAGU_035) wintering further south, between 31° and 37°S.

Spring migration

Tagged birds departed on their return migration in late March to early May (median departure date: 19 April), and moved quickly and directly north to a different staging site off the west African coast (Morocco, Mauritania, Senegal), between 27° and 9°N. This leg of the migration was particularly rapid, birds covering a distance of 5890 km (±261 km) in 6–9 days (7.4 ± 0.45 days), an average flight speed of 813 km/day. On average, tagged birds spent 19 days (range: 13–25 days, Table 2) at the spring staging site, much shorter than the time spent around the Bay of Biscay on the migration south. By the end of May, all tagged birds had left the spring staging site and headed north (median departure date: 17 May), with most bearing fairly directly north across the North Atlantic to the southeast coast of Greenland and continuing up the east coast to the breeding colony at Sand

Table 1. Distances travelled by Sabine's Gulls from their breeding colony in northeast Greenland to the autumn staging site (off Portugal), their wintering area (the Benguela Upwelling) and the spring staging site (off Senegal), the average distances travelled between these areas, and the total distance travelled by each bird. Local movements at staging sites and the wintering area are not included.

Bird ID	Breeding colony to autumn staging (km)	Autumn staging to wintering area (km)	Wintering area to spring staging (km)	Spring staging to breeding colony (km)	Total (km)
SAGU_010	8382	11 219	9485	9781	38 867
SAGU_011	5279	10 333	7902	8792	32 306
SAGU_034	6038	10 214	7505	7127	30 883
SAGU_035	5329	10 618	7493	6736	30 175
SAGU_027	4500	10 533	6547	7974	29 554
SAGU_014	5837	10 019	7053	6338	29 247
SAGU_013[a]	8049	10 060	7477	–	–
SAGU_020[b]	10 849	11 453	–	–	–
SAGU_016[c]	5016	–	–	–	–
SAGU_018[d]	5364	–	–	–	–
Average (±se)	6464 (598.7)	10 556 (174.5)	7637 (322.0)	7791 (490.5)	31 839 (1346.1)

Partial data; tag stopped logging on [a]3 May 2008, [b]14 March 2008, [c]31 August 2007, [d]6 September 2007.

Island. Two birds, however, travelled west as far as Cape Farewell, one reaching as far as the Labrador Sea, before returning to eastern Greenland and making their way up the coast to the breeding colony (Fig. 1).

On average, tagged individuals travelled an estimated 31 839 km (±1346 km, $n = 6$) in total during their annual migration, with a maximum distance of close to 39 000 km (Table 1).

DISCUSSION

There have been few published tracking studies of gulls (Muzaffar *et al.* 2008, Pütz *et al.* 2008, Gilg *et al.* 2010, Bogdanova *et al.* 2011, González-Solís *et al.* 2011), and none that has described a migration that is even close to the minimum distance of 30–40 000 km travelled by Sabine's Gulls in this study, which we assume to be the longest migration of any gull. The habitats of Sabine's Gulls ranged from the Arctic seasonal ice zone during breeding to the subtropical waters of the Benguela Current system during winter. The only two other small Arctic-breeding gulls, the Ivory Gull *Pagophila eburnea* and the Ross's Gull *Rhodostethia rosea*, restrict themselves to the northern hemisphere year-round and exhibit relatively short-distance migrations (Blomqvist & Elander 1981). Ivory Gulls generally move only as far as the ice edge in the North Atlantic and North Pacific oceans (Gilg *et al.* 2010), while Ross's Gulls actually move north from their main Siberian breeding grounds, apparently wintering around the Arctic Ocean (Blomqvist & Elander 1981). The only other North American gull to exhibit regular long-distance, trans-equatorial migration is the Franklin's Gull *Larus pipixcan*, which breeds in northern interior regions of North America and primarily winters along the Pacific Coast of South America off Peru and Chile (Burger & Gochfeld 1994, Olsen & Larsson 2004). That area is also the only other known migration destination for Sabine's Gulls, most likely those breeding in colonies in western Canada, Alaska and eastern Russia (Day *et al.* 2001). A few other charadriiform seabirds also make long-distance, trans-equatorial migrations, including the Long-tailed Skua *Stercorarius longicaudus*, Pomarine Skua *Stercorarius pomarinus* and Arctic Skua *Stercorarius parasiticus*, which breed as far north as the high Arctic and winter off southern Africa, South America, or in the Southern Ocean, and the South Polar Skua *Catharacta maccormicki*, which breeds on the Antarctic continent and winters as far north as the North Atlantic or North Pacific oceans (Olsen & Larsson 1997, Kopp *et al.* 2011). The Arctic Tern has the longest known migration of any animal, with an average annual return journey of over 70 000 km/year (Egevang *et al.* 2010).

On their southerly migrations, both Arctic Terns and Long-tailed Skuas breeding in Greenland stage

Table 2. The timing of migration in Sabine's Gulls breeding at Sand Island, Northeast Greenland, 2007–2008.

	Median arrival/departure date or mean duration of stay (range)	n[a]
Arrival at autumn staging site	31 Aug (17 Aug–15 Sep)	9
Time spent at autumn staging site	45 days (35–53 days)	7
Departure from autumn staging site	15 Oct (4–30 Oct)	7
Arrival at wintering area	12 Nov (21 Oct–30 Nov)	8
Time spent at wintering area	152 days (125–180 days)	7
Departure from wintering area	19 Apr (25 Mar–3 May)	7
Arrival at spring staging site	26 Apr (9 Apr–11 May)	7
Time spent at spring staging site	19 days (13–25 days)	7
Departure from spring staging site	17 May (23 Apr–24 May)	7

[a]Number of individual birds included in the dataset.

in an area of high productivity in the central North Atlantic, east of the Newfoundland Grand Banks (Radi & de Vernal 2008, Egevang *et al.* 2010, Sittler *et al.* 2011), an area which has only recently come to light as a potential 'hot-spot' for migratory seabirds. Interestingly, few Sabine's Gulls breeding in Greenland ventured near that area and the Gulls did not appear to stage there, instead largely travelling southeast to the productive waters of the Bay of Biscay, the cold upwelling region off the Portuguese coast, the Galician Bank and the Celtic Sea (Sousa *et al.* 2008).

Most studies of migratory seabirds show considerable variation among individuals from the same breeding colony in the areas used during the non-breeding period (Phillips *et al.* 2005, González-Solís *et al.* 2007, Harris *et al.* 2010, Kubetzki *et al.* 2009). In contrast, Sabine's Gulls breeding in northeast Greenland appear to depend on a single, highly restricted wintering area in the South Atlantic. This result should be considered a preliminary one, due to the small number of birds ($n = 8$) tracked from a single colony over 1 year, but the Benguela region is thought to be the wintering destination for Sabine's Gulls from breeding colonies across all of eastern Canada, Greenland and Spitsbergen, and possibly western Russia (Day *et al.* 2001). This pattern, therefore, more closely resembles that apparent in two other trans-equatorial migrants from the North Atlantic, the Manx Shearwater *Puffinus puffinus* and the Arctic Tern, in which all individuals winter in broadly the same region (Guilford *et al.* 2009, Egevang *et al.* 2010).

In general, trans-equatorial migrant seabirds of the North Atlantic follow distinctly different outward and return migration routes, suggesting a considerable reliance on the prevailing winds associated with the North Atlantic and South Atlantic gyres to facilitate speedy and energy-efficient migrations (Felicísimo *et al.* 2008, González-Solís *et al.* 2009, Guilford *et al.* 2009, Egevang *et al.* 2010). Sabine's Gulls appeared to exploit the prevailing winds around the South Atlantic gyre, as indicated by their extremely rapid movement between the wintering area and the spring staging site. Although high (> 800 km/day), this is well within the observed and theoretical ranges reported for other similar-sized migratory seabirds (Gudmundsson *et al.* 1992, Guilford *et al.* 2009, Egevang *et al.* 2010). However, they did not follow the broad figure-of-eight pattern (anticlockwise in the southern hemisphere and clockwise in the northern hemisphere) exhibited by Arctic Terns and Cory's Shearwaters *Calonectris diomedea* in the Atlantic Ocean (González-Solís *et al.* 2007, Felicísimo *et al.* 2008, Egevang *et al.* 2010), Sooty Shearwaters *Puffinus griseus* in the Pacific Ocean (Shaffer *et al.* 2006) or South Polar Skuas in both oceans (Kopp *et al.* 2011).

There have been few studies on the foraging habits of Sabine's Gulls, especially during migration and in winter, but they are known to have a relatively diverse diet (Day *et al.* 2001), including small fish and zooplankton (Duffy 1989) and are commonly attracted to discards from fishing vessels (Wahl & Heinemann 1979, Valeiras 2003). Like many other migratory seabirds (see Phillips *et al.* 2005, Shaffer *et al.* 2006, González-Solís *et al.* 2007, Kubetzki *et al.* 2009), however, Sabine's Gulls clearly target and exploit marine regions of high and relatively predictable productivity in their choice of wintering area and both migratory staging sites. The wintering area, the Benguela Current, off the west coasts of Namibia and South Africa, exhibits the strongest marine upwellings in the world and, as a result, is one of the world's most productive marine ecosystems (Shannon & Field 1985). Strong winds, a complex current system and a narrow continental shelf produce an intense upwelling of cold, nutrient-rich waters along this coast. This enhances primary and secondary production (Heileman & O'Toole 2008), which supports abundant populations of epipelagic fishes, such as Anchovy *Engraulis encrasicolus* and Sardine *Sardinops sagax*. These forage fish species are targeted throughout the year by a diverse community of predators, as well as intensive commercial fisheries (Shannon 1985, Grémillet *et al.* 2008). A documented depletion of forage fish species by commercial fisheries has had dramatic effects on seabirds that breed on the coast of Namibia and South Africa (Crawford 1991, Crawford & Dyer 1995, Crawford *et al.* 2007). However, the effect of competition with commercial fisheries may be less severe for non-breeding seabirds that visit the area, as they are not restricted to central place foraging and are free to follow ephemeral prey patches. Numerous migrant seabirds visit this region year-round, including species that breed in the Mediterranean Sea, North and South Atlantic, and Indian and Southern oceans (Phillips *et al.* 2005, González-Solís *et al.* 2007, Péron *et al.* 2010, this study).

High productivity and intense commercial fisheries are also characteristic of the staging sites on both legs of the Sabine's Gull migration. The autumn staging site, the Bay of Biscay, Iberian and Celtic seas, off the coasts of France, Spain and Portugal, is a moderately to highly productive area, with upwelling mainly over the Iberian Shelf section (Aquarone *et al.* 2008a, 2008b). The area is rich in small pelagic fishes, including Sardine, Anchovy and Mackerel *Scomber scombrus*. Many species are intensively fished in this region and overall landings have declined rapidly in recent decades (OSPAR 2000), with recent closures in the Anchovy fishery (OSPAR 2010). The spring staging site, the Canary Current, off the coasts of Morocco, Mauritania and Senegal, is another highly productive upwelling system (Heileman & Tanstad 2008). This area is also rich in small pelagic fishes (Rodríguez *et al.* 2004). Prolonged and intense fisheries in this region have led to a marked decline in commercial harvest in recent decades (Christensen *et al.* 2004).

Understanding the spatial and temporal details of migration in pelagic seabirds contributes to their conservation (1) by highlighting areas of critical habitat and hotspots of high marine biodiversity, (2) by identifying potential overlapping anthropogenic uses and/or threats to populations, and (3) by facilitating the identification marine Important Bird Areas (IBAs) and/or Marine Protected Areas (MPAs).

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