

FINN SALOMONSEN

MIGRATORY MOVEMENTS
OF THE ARCTIC TERN
(*STERNA PARADISAEA* PONTOPPIDAN)
IN THE SOUTHERN OCEAN

Det Kongelige Danske Videnskabernes Selskab
Biologiske Meddelelser 24, 1



Kommissionær: Munksgaard
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Synopsis

The Arctic Tern (*Sterna paradisaea* Pontoppidan) breeds in the polar regions and winters in the antarctic zone, performing the most extensive migratory movements known in any bird. The crossing of the Antarctic Ocean, a flight of more than 3000 km, forms the most critical part of the long migration. It is demonstrated in the present paper that this oceanic passage follows the meridional cyclone trajectories, in which way the terns are aided in their flight by obtaining a considerable increase to their ground speed. The peculiar moulting system in the Arctic Tern is discussed, and it is shown that it must be explained as an adaptation to the extremely strenuous flight across the Antarctic Ocean. The winter range in the pack-ice zone and the flight routes during the autumn and spring migration across the Antarctic Ocean are outlined. Differences in the timing of the wing moult between adult and immature birds are pointed out, and it is demonstrated that a number of terns, particularly immature birds, are drifted eastwards by the strong winds. In this way the birds may perform a complete circumnavigation of the Antarctic Continent before they return to South Africa for the spring migration towards the north. Many one-year old birds spend the summer in the Humboldt Current, off South America, and do not continue to South Africa until the following spring. In such cases the circumnavigation takes two years. The regular drifting of young birds around the Antarctic Continent is a result of the special situation in the young birds, which are more liable than the adult birds to be caught by the wind. The circumnavigation is compared with similar movements in other antarctic sea birds. Evidently, it must be regarded as an advantageous adaptation of considerable survival value to the birds. An attempt is made to map the complicated migration pattern of the Arctic Tern within the antarctic zone (fig. 8).

The Arctic Tern has the longest migratory flight of any bird. It literally moves from pole to pole. It has its main breeding range in the Arctic region, where it is known to breed as far north as dry land extends, and has recently been found to breed at Cape Morris Jessup on 83°40'N, the northern point of Greenland (RØEN 1965, p. 128). On the other hand, it winters in the Antarctic region, where it has been recorded as far south as 74°S.

The migration route, leading from the Arctic to the Antarctic region has been described a number of times, most recently by KULLENBERG (1946, p. 58), FISHER and LOCKLEY (1954, p. 140) and DORST (1962, p. 175). The route is not known in detail and an exact analysis of the complete migration complex in this species has never been attempted. The ringing records, which have piled up in recent years, have never been treated in their entirety, but there are a number of special studies, like that of RADFORD (1961, p. 174) on recoveries of British specimens.

I do not intend to describe or comment on the migration between the breeding places and the southern subtropical zone, to which I cannot add anything new, but it is necessary to outline briefly this long movement, because it is fundamental to the understanding of the subsequent winter migration in the south polar region.

The great flight takes place along two, and only two, migratory routes, the first one along the continental shelf of Western Europe and southwards along West Africa, and the second one along western North and South America. The first route is the main one, while the latter is of lesser importance and is very little known. Somewhere in eastern Siberia and in northern Alaska a migratory divide must have developed, separating populations which migrate to the west from those migrating to the east. The

populations of the Bering Sea, Bering Straits, easternmost Siberia and westernmost Alaska move southwards along the west coast of America and part of them are said to winter in the Humboldt Current off Chile. The evidence for this, summarized by MURPHY (1936, vol. 2, p. 1100–1101), is very meagre, however. Virtually all observations refer to October–November records of migrating birds (the last date being 3. December) or to June–July records of summering one-year old non-breeders. It is safe to conclude that the migrants using this western American route usually continue across Drake Strait to the Antarctic zone.

The Arctic Terns breeding in Canada, Greenland, north-eastern United States, Northern Europe and the coasts of Northern Siberia (except the eastern parts) use the south-west European – west African migratory route. In order to reach S.W. European waters the Siberian populations must carry out an extensive westward migration along the coasts of the Polar Sea and south-west along the coasts of Norway and the British Isles. The populations of the nearctic region must carry out a transatlantic crossing in the zone between 60°N and 50°N . This long oceanic voyage takes place in a direction which is almost due east, but probably has a slight southern component, as the birds reach the European coastal waters in the area from Scotland to Western France. This has been demonstrated by a number of autumn (September–October) recoveries of birds ringed in Western Greenland, Labrador, and New Brunswick.

During the transatlantic flight the terns do not feed and do not attempt to rest by alighting on the surface of the sea. Before the flight the birds have accumulated ample fat resources (cf. SALOMONSEN 1951, p. 347), but nevertheless it is necessary to accomplish the oceanic crossing as fast as possible. In this period of the year the wing- and tail-feathers are comparatively worn, being more than half a year old. It is important, therefore, that the terns during the transatlantic flight are aided by the westerly winds which prevail over the boreal areas of the seas in the northern hemisphere (fig. 1) and which give them an almost constant tail wind and considerably add to their ground speed.

A similar utilization of the westerly winds in the northern seas takes place in some other sea birds, primarily in the large shear-waters, such as *Puffinus gravis*, *P. griseus* and *P. tenuiro-*

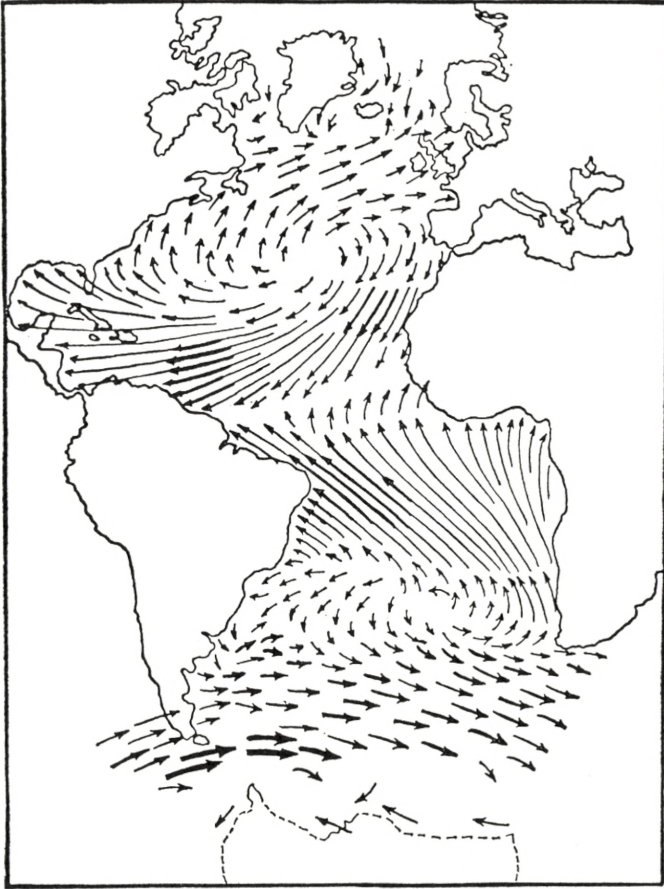


Fig. 1. Prevailing winds in the Atlantic Ocean in August. (After DORST 1962).

stris. Altogether, the use of wind as an aid during oceanic migrations is a wide-spread phenomenon among sea birds; cf. the excellent summary by DORST (1962, p. 181–199).

When on their return flight in the spring (latter half of April and May) the Arctic Terns are forced to make the transatlantic crossing against the westerly winds the force of the winds is as a rule much slighter. In addition, their wing- and tail-feathers are new and strong, their growth having been completed only one or two months previously.

Arrival in South Africa usually takes place in October or November, sometimes in September, but there is very little exact

information. One-year old birds summering in South African waters obscure the picture, making it difficult to ascertain when the migrants arrive in the autumn. Just as in Chile Arctic Terns may winter in South Africa, but by no means appear to be common as winter visitors. The species is "mainly a passage migrant" (CLANCEY 1965, p. 313), contrary to the Common Tern (*Sterna hirundo*), which is a "general visitor to all coasts" (CLANCEY, *loc. cit.*), where it is "fairly abundant" (SCLATER 1906, p. 441). This remarkable difference between the two species is borne out by the recoveries of ringed birds. The South African records of Arctic Terns include altogether nine birds, namely four British (Nov., Dec., two Jan.), one Swedish (Dec.), one Greenland (Oct.) and two Canadian birds (both Nov.), besides a one year old Faeroe bird summering there (Aug.). The European populations of the Common Tern are allohiemic, the British and West European populations wintering in tropical W. African waters and never reaching as far south as S. Africa (RADFORD 1961, p. 176), while the Scandinavian birds have their main winter quarters in S. Africa. There are altogether 20 recoveries of Scandinavian birds in S. Africa, namely one Danish, four Norwegian, eight Swedish and seven Finnish birds, from the period September—April, including a summering one-year old bird from May and June, respectively. These figures, which I have compiled from various lists of ringing recoveries (cf. SALOMONSEN 1967, p. 265), indicate that the Common Tern is the main contributor to the wintering tern population in S. Africa, while the Arctic Tern is a much more uncommon winter visitor. The situation of the Arctic Tern in S. Africa resembles somewhat that in Chile.

According to KULLENBERG (1946, p. 16) some of the Arctic Terns moving southwards during the autumn migration somewhere off West Africa branch off in a westerly direction, crossing the Atlantic in the zone of the doldrums and the southeastern trade winds (cf. fig. 1), reaching the coastal waters of S. America somewhere in southern Brazil. However, evidence for the existence of this migratory route is only indirect. There are, so far I know, no actual observations of terns migrating along this route. Records of Arctic Terns moving southward in October off Mar del Plata in Argentina (MURPHY 1936, vol. 2, p. 1101) tend to show, however, that an east-west crossing of the Atlantic does take place,

but this is probably carried out by only a small number of birds. During their Atlantic crossing the birds may benefit not only from the favourable wind conditions, but also from the large quantities of macroplankton in the border zones of the equatorial countercurrent, particularly at its northern boundary, brought about by the extensive upwelling of water from deeper layers in this area. It is a wellknown fact, of course, that upwelled water induces large amounts of nutrients (phosphates, nitrates, etc.) to the surface water layers, giving rise to a high organic production (cf. REDFIELD, KETCHUM and RICHARDS 1963, p. 65; WOOSTER and REID 1963, p. 276; LA FOND 1966, p. 957). It is doubtful, however, whether the Arctic Tern feeds at all during such a long oceanic crossing. A few terns, having finished the crossing and moved south along the eastern coast of Argentina, probably spend the winter in the waters off the Falkland Islands and southeastern Argentina, but the few records known are unsatisfactory and not quite certain.

KULLENBERG in his paper 1946 summarized the current ideas about the movements of the Arctic Tern in a map, shown in this paper as fig. 2. This map has formed the basis for most other maps on the subject in recent publications. It shows the migration

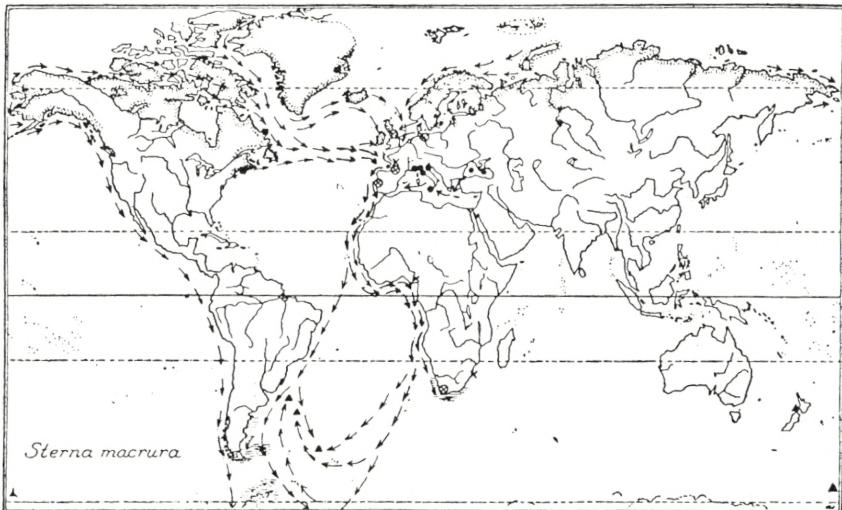


Fig. 2. The generally accepted view-points concerning breeding range, winter quarters and migratory routes of the Arctic Tern. Breeding range is dotted, winter quarter hatched, migratory routes shown by arrows. (After KULLENBERG 1946).

route of the Arctic Tern to form a loop, the birds heading southwest from S. Africa to the antarctic waters and then, in spring, northwest to the waters east of Argentina. This view is purely speculative, and quite apart from there not being a single observation to support it, it is evident at once that the theory cannot be correct. When leaving S. Africa for the south the terns are subject to the heavy storms and gales of "the Roaring Forties and the Shrieking Fifties", which constantly blow west to east (cf. fig. 1). It is quite out of the question that the terns should be able to fight these powerful forces, especially as the birds in this period of the year have extremely weak and worn wings. I had seen no better attempt to explain the movements of the Arctic Tern in winter until the map published by STORR (1958, p. 60), rendered here as fig. 6, which is much nearer the truth.

It can now be concluded, however, that the Arctic Terns wintering in the waters around southern S. America and off S. Africa constitute only a small fraction of the whole population of this species. The main wintering areas are situated in the Antarctic pack-ice zone, where hundreds of thousands of individuals spend the winter. Recent expeditions and collectings have shown this to be the case, but it is noteworthy that the existence of this winter quarter was completely unknown until quite recently. Although specimens were collected in the Antarctic zone by several expeditions in the 19th century and some of them identified by the expert on *Laridae* HOWARD SAUNDERS (1896, p. 66), the occurrences of the species in the Antarctic were regarded as mere exceptions by most students, even by MURPHY as late as 1936 (MURPHY 1936, vol. 2, p. 1102). In the subsequent year FALLA (1937) published the results of the Australasian Antarctic Expedition 1911-14 and the B.A.N.Z. Antarctic Research Expedition 1929-31, and demonstrated with a wealth of facts that the Arctic Tern was numerous in the Antarctic zone in winter. Mainly because of FALLA's results MURPHY (1938, p. 7) changed his mind, and since then almost every Antarctic expedition has added to our knowledge about the south-polar winter quarters of the Arctic Tern.

When leaving S. African waters for the final stage of the autumn migration towards the Antarctic pack-ice zone the terns face a gloomy situation. Not only have they exhausted their resources and their strength during the long journey already

carried out, but their efficiency of flight is considerably reduced owing to the weak and worn-out condition of their wing-feathers. Before them is a stretch of more than 3000 km of open ocean which they are forced to traverse before they can start moulting the flight-feathers. The possibilities for resting (on islands or icebergs) under the long and strenuous ocean crossing are extremely slight, and it is necessary, therefore, to get through the flight as fast as possible. All evidence tends to show that the terns are in a great hurry, and even if they should happen to pass an island they do not remain there for any length of time (cf. DOWNES 1952, p. 307). The same must hold good of encounters with icebergs; these are as huge as islands, but very scattered. They occur in the Atlantic northwards to about 40°S (cf. fig. 7). During the overseas voyage the terns are exposed to incessant westerly storms, against which they cannot possibly fight, owing to their present debility. It is unavoidable, therefore, that they are carried more or less to the east by the wind before they reach the border zone of the pack-ice, which constitutes their winter quarters. The birds which, for some reason, lag behind on their southward journey along West Africa will arrive so late in South Africa that they will not have time enough for the journey to the Antarctic before the moult commences. Consequently, they must remain in the South African waters. The majority of the Arctic Terns wintering there probably belong to such belated rear parties. Recoveries of ringed birds have demonstrated that odd birds may winter as far north as the Ivory Coast (December) and Ghana (February) in tropical West Africa.

It is appropriate here to insert some remarks on the moult of the flight-feathers, which has not been properly understood until quite recently. STRESEMANN (1966, p. 254) in his excellent monograph on the avian moult has demonstrated that the moult of the flight-feathers in the *adult* individuals of the Arctic Tern begins in the last days of December and is finished before the end of February, *i. e.* in a period of about 60 days. The flight feathers are only moulted once a year in this species.

The moulting processes of the Arctic Tern differ considerably from those of its allies (*Sterna hirundo*, *S. albifrons*, *S. sandvicensis*, *Chlidonias leucoptera*, *C. nigra*), which move from Europe to the coasts (or fresh-waters) of West and South Africa, but do not continue across the southern ocean to the Antarctic region. In

these species the migration takes place in a more leisurely way and is not impeded by the very slow moult, which takes place at the same time and which continues without interruption from July–August to April–May, *i. e.* the entire non-breeding period. These species can afford to moult the flight-feathers twice a year, and some of the innermost primaries even three times a year, in the lengthy moulting period they have at their disposal (STRESEMANN 1966, p. 247–268).

The moulting conditions in the five species of terns mentioned above demonstrate that a performance of a flight from Europe to South Africa is compatible with a coinciding wing-moult. The Arctic Tern is the only species which postpones the wing-moult until the arrival in the winter-quarters, and at the same time is the only species which continues the migration from South Africa across the Antarctic Ocean. The aberrant moulting condition in the Arctic Tern must be explained, therefore, as an adaptation to the extremely strenuous and demanding flight across the stormy seas from South Africa to the Antarctic, which can be carried out successfully only under special conditions. Selection will soon eliminate individuals unable to stand the iron test. As already said, the birds are in a rather poor physical state when they start the south-polar journey. The wings are very worn and the conditions for building up new fat resources during the stay in South African waters are not too good. Nevertheless, the strength of the wings is very heavily taxed during the south-polar flight, and it must be an absolute condition that all remiges and rectrices are functioning perfectly and not weakened by growth or shedding processes. This requirement holds good both for the autumn and spring passage. Consequently, the moult has to be restricted to the comparatively short resting period in the winter quarters. This implies that the moult must be speeded up at a considerable rate when compared with conditions in all other species of terns. All observers agree that the flight of the Arctic Tern in the winter quarters is considerably hampered by the poor condition of the heavily moulting birds, which causes a lack of endurance against strong winds. The weak and awkward flight and the reluctance to rise from the safe ground has been noticed even by early observers, but was for a long time held to be a character of the Antarctic Tern (*Sterna vittata*) (*e. g.* by MURPHY (*loc. cit.*) and

KULLENBERG (*loc. cit.*)), until FALLA (1937, p. 252) rightly ascribed it to the Arctic Tern. FALLA adds that in February the terns are more frequently on the wing than earlier, by then showing signs of recovery from the extreme conditions of moult. This agrees with the examination of skins made by STRESEMANN (1966, p. 257), who found that in five adult February birds three had completed the wing moult and two had almost finished it, only the outermost primary still showing growth. A single specimen from 25. February examined by FRIEDMANN (1945, p. 312) likewise had only the outermost primary still in growth. The body moult continues until about the middle of March, when the nuptial plumage is completely established. Shortly before this the adult birds start on the northward spring migration towards the breeding places.

A parallel development has taken place in the Great Shearwater (*Puffinus gravis*), which crosses the equator during its migration from the southern hemisphere and spends the southern winter in the North Atlantic. Just like the Arctic Tern it postpones the moult of the flight-feathers (but not of the body-feathers) until arrival in the winter quarters. By far the majority of the population moult the flight-feathers off the coast of S. W. Greenland, usually in August, while gathered in large flocks. During this wing-moult the Great Shearwater "although not completely unable to fly, can only rise with difficulty from the surface in calm weather" (SALOMONSEN 1951, p. 43). The largest flock of moulting birds I ever saw in Greenland was met with on the 22. August 1954 about one mile off the west-coast at 61°N. I estimated the flock to comprise about 30,000 individuals. The birds, which dotted the surface of the sea for about 9 miles, were very reluctant to rise when I passed the area onboard a steamer. MARSHALL and SERVENTY (1956, p. 943) found the same postponement of the wing-moult in the related species *Puffinus griseus* and *P. tenuirostris*, which migrate to the oceans of the northern hemisphere, just like *P. gravis*. STORR (1958, p. 61) has already drawn attention to the parallel development in wing-moult in the Arctic Tern and in the said shearwaters.

The moult of the *young* Arctic Terns differs in some important points from that of the adult birds, but strangely enough this has escaped the notice of STRESEMANN. In *Sterna hirundo* and other

related species the young birds in their first winter do not start the moult of the juvenal remiges until January, *i. e.* about half a year later than the adult birds. The moult is not finished until August, but the next wing moult starts already in September and continues to May, when the now two year old birds arrive in the areas around the breeding places, although usually not yet breeding (STRESEMANN 1966, p. 250). The young Arctic Terns have developed a similar postponement of the wing moult, but the delay compared with the situation in the adult birds is of about two month's duration only. STRESEMANN (*loc. cit.*, p. 256) has examined a young bird from 1. March with the two outer primaries still in growth, and another specimen from 16. March still in possession of two old primaries, not yet shed. These stages correspond to those in two adult individuals captured 15. January and 22. January, respectively (STRESEMANN, *loc. cit.*, p. 257), *i. e.* about two months previously. On the other hand, three young birds from 10., 12., and 19. January, respectively, had not yet started the wing-moult (STRESEMANN, *loc. cit.*, p. 255). FALLA (1937, p. 251) has examined 10 specimens captured in the period from 17. January to 6. February. Among these were seven adult birds, all of which were in wing-moult, while the remaining three specimens were young birds, all obtained on the 25. January, which had not yet started the wing moult, but were still in possession of the old remiges "much faded and worn". This tends to show that the young birds do not usually start the moult of flight feathers until the end of January and that they are still in full moult in the middle of March, when the adult birds have had new flight feathers for about a fortnight.

It is noteworthy that the ornithologists of the Willem Barendsz Expedition 1946-47 and 1947-48, who daily encountered Arctic Terns in the Weddell Sea area from 25. December, did not observe moulting birds (with moulting holes in the wings) until 31. January and then continued to see moulting birds until 27. March (BIERMAN and VOOUS 1950, p. 112). I strongly suspect that the majority of these birds must have been individuals in their first or second winter.

It is not possible to state when the wing moult of the young birds is completed. Probably it happens sometimes in April, but the moult may occasionally draw out until June. MURPHY (1936,

vol. 2, p. 1101) examined a one year old specimen, captured 26. June, which was spending its second summer in Chilean waters, with "new quills appearing in wings and tail". All other specimens from May–June examined by MURPHY had finished the moult. The main point is, however, that the period in which the wings are weak and the flight impeded is considerably protracted in the young birds.

The departure from South Africa for the south-polar flight takes place from the latter part of October to the first part of January, the adult birds probably leaving earlier than the young ones. The latter start the moult later and are, therefore, not so pressed for time. Evidently the greater part of the migrants start from the leeward areas east of the Cape, but they are soon exposed to the full force of the western storms.

The shortest distance to the pack-ice zone is found in a due south direction, but the westerly winds will carry the birds more or less to the east, and the resulting flight direction will be E.S.E. or S.E. I do not think that this direction is achieved by a passive drifting to the east of birds which aim at a southern direction. It is more reasonable to suppose that the flight direction is genetically fixed, and that selection has favoured this direction because of its superior survival value for the migrants. By following this direction the birds are aided by the wind without being led too far away from their destination.

The S.E. direction of the flight over the Antarctic Ocean exactly corresponds with the course of the cyclone trajectories leading across the sea to the Antarctic continent, and I do not hesitate to conclude that the migration of the terns is intimately connected with these air movements. This is an important point. The terns need all support for the crossing, which forms the most dangerous part of their long journey, and following the cyclones downwind they can achieve an increase to their ground speed of no less than 20–60 km/hr, with a mean of 34 km/hr. (ASTAPENKO 1964, table 7, p. 69). It is doubtful whether the birds could accomplish the ocean crossing with their worn wings and unfit physical condition without the support of these air movements. Altogether, the whole migration system in this species, the routes chosen (along southwestern South America and South Africa), the absence of the species in the Pacific, the situation of the winter

quarters as outlined below, appear to be one large scale consequence of the drastic dependence on the cyclones during the last and crucial part of the migration. The terns can depend on the presence of these cyclones, for in the migration time (October–December) they occur virtually every day. Nevertheless, it must happen rather frequently that the terns are overcome by the hardships of the oversea flight, judging from the comparatively great number of cases in which exhausted and dying birds have been caught onboard ships or washed ashore during migration. Elsewhere such phenomena occur very rarely among such good flyers as terns, and bearing in mind the small number of observations made on tern migration in the antarctic and subantarctic zone, the number of records of exhausted birds is remarkable. There are two records from the “Valdivia” Expedition (cf. p. 23), one described by MÖRZER BRUYNs and VOOUS (cf. p. 19), and a number of records from Australia, during autumn migration (p. 20) as well as spring migration (p. 34).

It is possible now to give a satisfactory description of the said air movements owing to the considerable advances in Antarctic meteorology in recent years. Atmospheric disturbances continuously develop in the region of the strong temperature gradient of the subtropical convergence zone, fluctuating around 45°S and called the polar front by meteorologists. These disturbances give rise to cyclonic systems which move with the westerly winds in a zonal (annular) pattern and may even cross from one ocean to the other. Owing to circulation obstructions, which are usually blocking-anticyclones of south-polar origin, or more rarely orographic barriers, polar front depressions are also deflected to the south, forming meridional cyclones. On reaching the antarctic front they divide into an eastern and a western branch. The trajectories of these meridional cyclones in the antarctic summer are shown in fig. 3. The whole system is fairly staple and is fundamental for the elucidation of the tern migration.

When leaving S. Africa the majority of the Arctic Terns, moving in a southeasterly direction, assumably will reach the area of the Kerguelen trajectory and arrive at the pack-ice belt at localities situated from about 50°E to 110°E . A minority of birds, leaving South Africa at more western longitudes, follow the South African trajectory. Another minority, following the east-

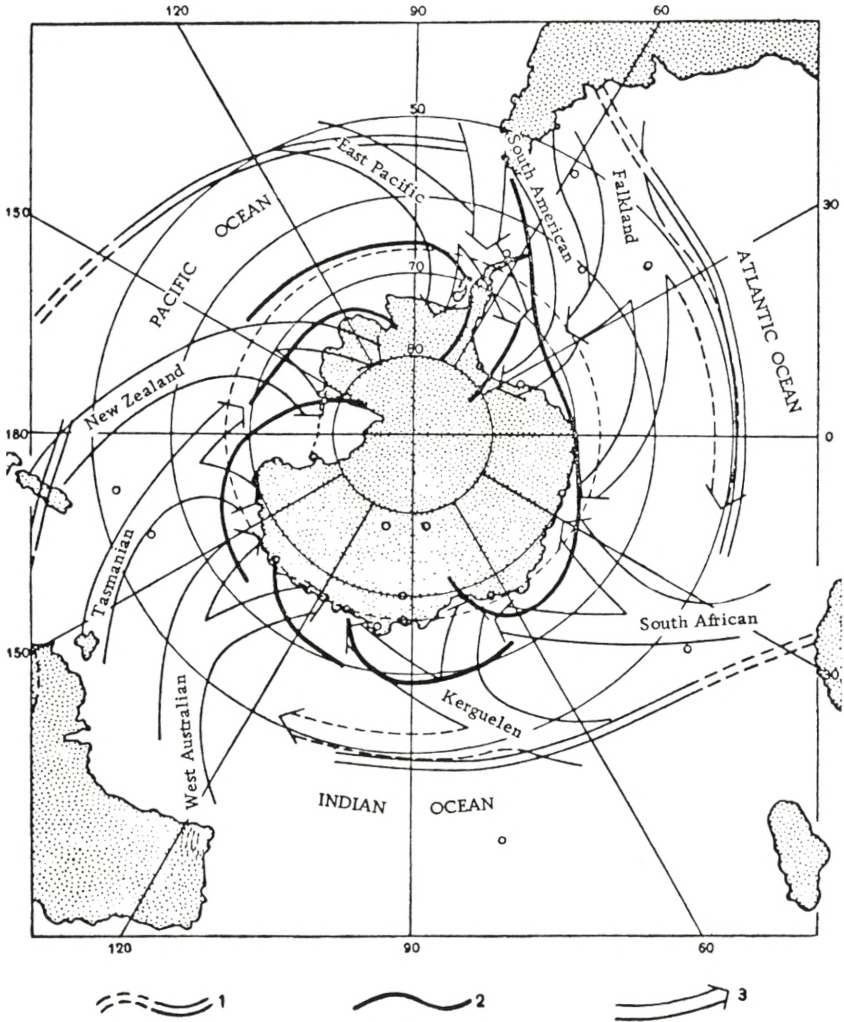


Fig. 3. Cyclone trajectories over the Antarctic Ocean and position of major fronts in the southern summer. 1. Polar front, 2. Antarctic front (tentative), 3. Meridional cyclone trajectories. (After ASTAPENKO 1964).

ward zonal branch of the Kerguelen system (cf. fig. 3) will reach the West Australian trajectory and follow it to the south. Altogether the entire tern population starting from S. Africa will reach the pack-ice in the area from about 30° E to 150° E, with the greatest concentration in the central parts.

Trajectories situated further east (Tasmanian, New Zealand)

are only utilized by the terns on rare exceptions. It is noteworthy that no meridional cyclones develop in the greater part of the Pacific, which probably explains why the Arctic Tern does not migrate south in the eastern and central Pacific.

The Arctic Terns leaving South America will follow the South American and the Falkland trajectories and end up in the eastern Weddell Sea. A smaller number will go further east, until about 30°E , where they meet the more eastern birds, of South African origin. The trajectory shown in fig. 3 to move almost due south west of Cape Horn leading towards the west coast of Palmer Peninsula is probably used by a few birds moving south far out to sea, *i. e.* several hundred miles off the Chilean coast, but it cannot possibly be a much frequented route. The westerly winds in northern Drake Strait are extremely strong and will usually cause the birds to drift farther east, through the strait. In November, the main migration month, only 5 per cent of 888 observations showed quiet or almost calm weather, while no less than 40 per cent showed storms or gales from N.W., W. or S.W. with a force of 7–12 on the Beaufort Scale, *i. e.* a velocity higher than 28 knots (Oceanographic Atlas 1957, fig. 50, p. 42).

The migration routes outlined above are purely theoretical, but the few observations of terns during their ocean crossing agree very well with the theory. On 26. October 1929 one individual was observed on 40°S , 28°E and the following day another individual on 41°S , 31°E , *i. e.* southeast of S. Africa (FALLA 1937, p. 253).

Very interesting observations have been made on Heard Island (53°S , $73^{\circ}30'\text{E}$) by DOWNES (1952, p. 306); cf. fig. 4 for this and other geographical localities. This island is situated in the Kerguelen cyclone trajectory. In November–December Arctic Terns were seen daily in small bands, the first birds observed as early as 22. October, the last in the first week of January. The passage of terns past the island was fairly continuous, and apparently the individual terns did not remain more than one day throughout the time they were seen. It was easy to distinguish the Arctic Tern from the Antarctic Tern in the month of December, because by this time the Antarctic Tern had acquired its breeding plumage with black cap and red bill, whereas the Arctic Tern was in winter plumage with white forehead and blackish bill.

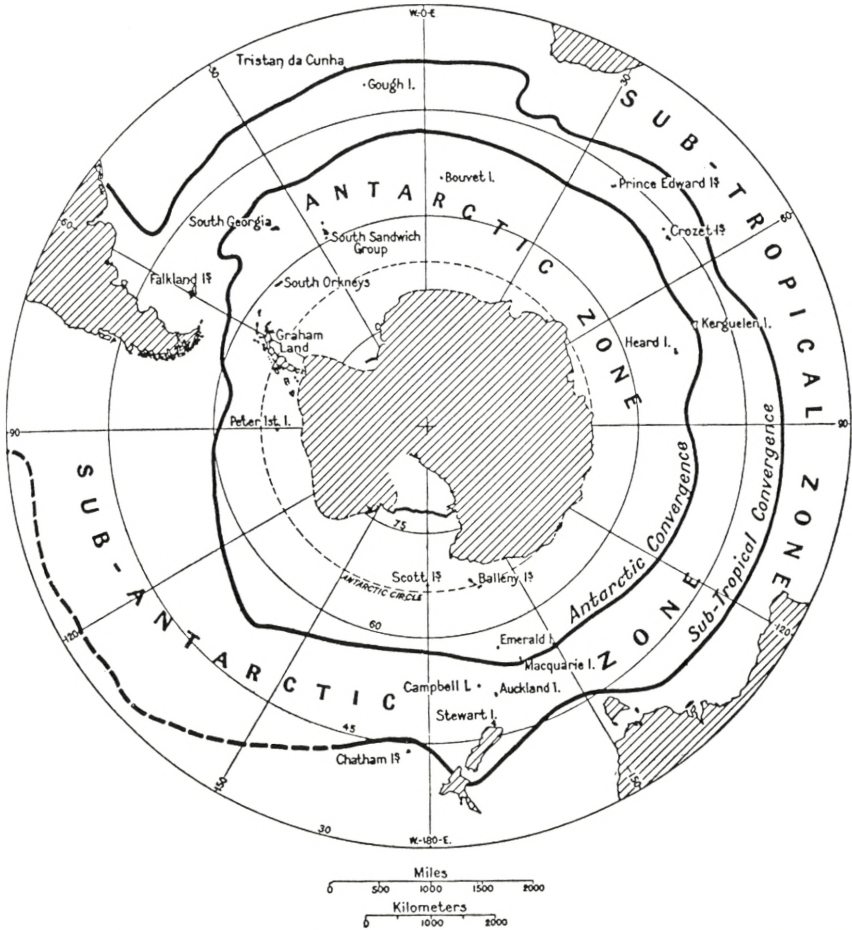


Fig. 4. The Antarctic Continent and the surrounding ocean, in south-polar projection, showing the zones of surface water and their convergences. (After MURPHY 1936).

The Antarctic Tern does not breed on Heard Island until the Arctic Terns have left in early January. This may be due to interspecific competition for food between the two species. Further north, in Kerguelen Island, where the Arctic Tern does not occur, the endemic Kerguelen Tern (*Sterna virgata*) breeds in November and the Antarctic Tern in January–February (FALLA 1937, p. 255 and p. 259; PAULIAN 1953, p. 213 and p. 215), which tends to show that the interspecific competition between these closely related birds must be an important factor. Still further north, on

Amsterdam Island, where neither the Arctic Tern nor the Kerguelen Tern occurs, the Antarctic Tern breeds in October–November (PAULIAN, *loc. cit.*, p. 215).

Heard Island, situated rather far north in the Antarctic zone, forms the northern boundary of the migratory area of the Arctic Tern. On Kerguelen Island, which is situated almost on the Antarctic convergence, the Arctic Tern has never been met with. PAULIAN (*loc. cit.*, p. 218) who spent November–December on the island expressly states that he did not see it, adding, however, that other work prevented him from concentrating on sea birds in this period.

On the other hand, it is possible that the Arctic Tern appears on Macquarie Island ($54^{\circ}30'S$, $159^{\circ}E$, situated on the Tasmanian cyclone trajectory; cf. fig. 3–4) during autumn migration. FALLA (1937, p. 261) noticed “white-capped terns” at this island in the beginning of December, holding them to be Antarctic Terns, but since this species has usually acquired its black-capped breeding plumage by this time DOWNES (1952, p. 309) is inclined to think that the birds observed by FALLA actually were Arctic Terns. If this is correct, the Arctic Terns passing Macquarie Island must belong to populations wintering farther east than hitherto known. Heading towards the pack-ice belt along the Tasmanian cyclone trajectory the terns could not reach their destination until east of $150^{\circ}E$, and in these regions the Arctic Tern appears to be a very rare winter visitor. I do not think, therefore, that Macquarie Island is situated on the regular autumn migration route of the Arctic Tern.

A minority of the Arctic Terns leaving South African waters are carried away by strong westerly gales and drifting across the southern Indian Ocean in due eastern direction in the subtropical zone between $30^{\circ}S$ and $40^{\circ}S$ and in extreme cases reaching the western and southern coasts of Australia and Tasmania and even New Zealand. The prevalence of the western winds is as pronounced at these latitudes as further south in the “roaring forties”, which distinctly appears from a comparison between the wind directions on Amsterdam Island and Kerguelen Island (fig. 5). The long eastward drift of the terns is undoubtedly due to strong zonal cyclones along the polar front; cf. fig. 3. It must be remarked that the polar front is situated considerably higher to the

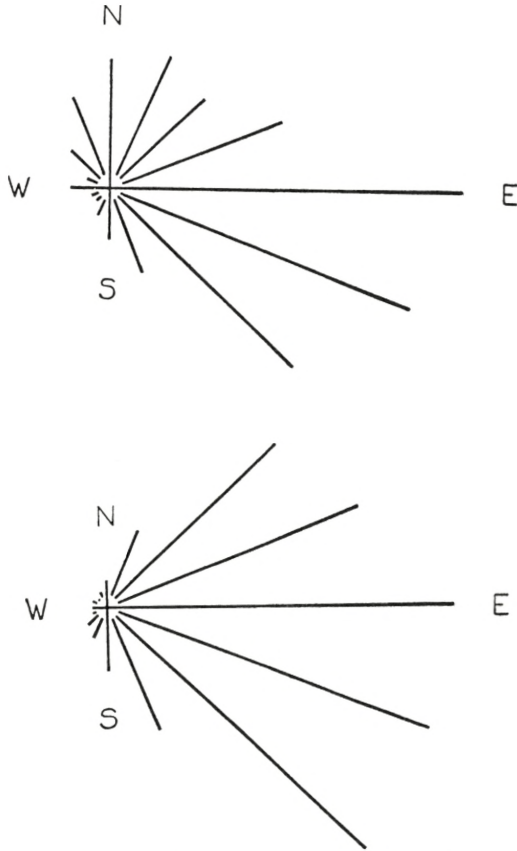


Fig. 5. Frequency of wind directions at Amsterdam Island (above) and Kerguelen Island (below), based on observations in 1952. (After PAULIAN 1954).

north in the migration time (October–November) than shown on the map fig. 3, which gives the condition in summer (January–February).

As there is a considerable amount of shipping in the northern parts of the Antarctic Ocean these areas are better known from an ornithological point of view than the areas further south. The following observations of Arctic Terns in these areas have been published (enumerated in a west-to-east direction):

33°41'S, 40°38'E, 21. November 1961, one "found on deck of the ship in a very exhausted state", in first winter plumage, feathers very worn, wing moult not started (MÖRZER BRUYNS and VOOUS 1964, p. 117).

- 37°S, 57°18'E, 23. October, ♂ "vix ad.", collected during the voyage of the yacht "Venus" (SAUNDERS 1896, p. 66).
- 30°S, 60°E, 3. October 1929, five observed flying south (FALLA 1930, p. 178).
- Amsterdam Island (39°S, 78°E), 29. November 1951, one collected, "probablement pas adulte" (PAULIAN 1953, p. 217).
- From 33°30'S, 41°E to 37°30'S, 79°30'E, 21.-26. November 1961, one or two observed each day (except 25. November) (MÖRZER BRUYNs and Voous 1964, p. 117).
- Australia: Six specimens collected, all found dead, washed ashore, or in a weak condition, with worn plumage and old faded wing feathers; three records are from S.W. Australia, two from the south coast and one from Tasmania, two of the specimens collected in October (one as early as 10. October), three in November and one in December (STORR 1958, p. 59; HINDWOOD 1958, p. 259).
- New Zealand: One specimen collected in December and a few others without date (FLEMING 1953, p. 51).

This list of records, although short, shows that the oceanic observations soon thin out when moving from west to east. The majority was made between 40°E and 60°E, a few between 60°E and 80°E, but none further east. This shows that the birds blown eastward by the wind steadily attempt to break through to the south, penetrating the wind barrier in order to reach the Antarctic zone; cf. the observation on 30°S, 60°E of five birds "flying south". Sooner or later most of them succeed in doing so, although many of them probably succumb. At any rate, east of 80°E the Arctic Tern must be extremely rare on these northern latitudes, but odd specimens, nevertheless, are blown as far east as Australia and New Zealand.

STORR (1958, p. 60) has given a correct picture of the migration route of the Arctic Terns which are drifted eastwards to Australia. His illustration is given here as fig. 6. It must be kept in mind, however, that this route represents the exception, not the rule.

The Arctic Tern spends the winter in the border zone of the pack-ice. The water temperature here is rarely above 0°C, which corresponds to the conditions in summer in the high-arctic region in the northern hemisphere. The terns are mostly seen resting on ice-floes or fishing in leads among the pack. In the period of strong wing moult (late December and all of January in adult birds) they keep to the resting places, even clinging to powdered

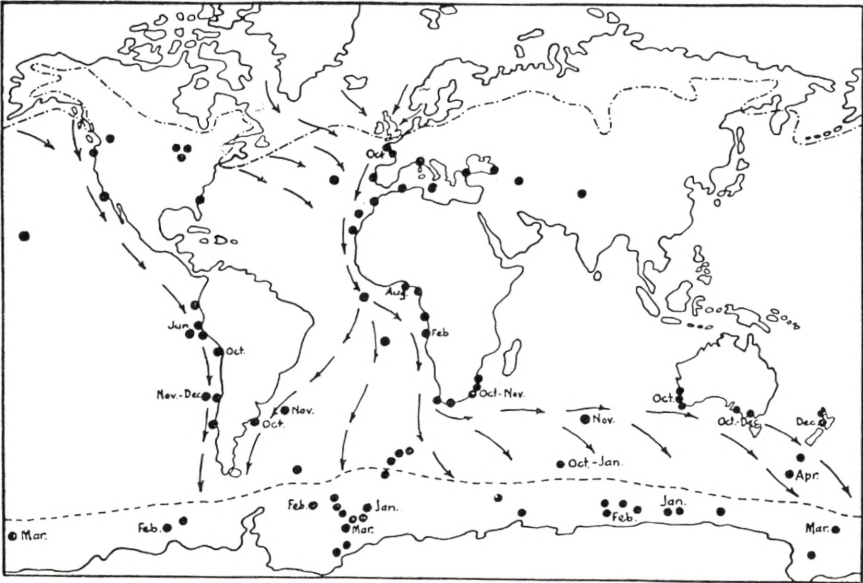


Fig. 6. Autumn migration and eastward drift towards Australia and New Zealand of the Arctic Tern, indicated by arrows. Solid circles show records of the species outside of the breeding ground (not complete); - - - southern limit of breeding range; - - - northern limit of Antarctic pack-ice belt. (After STORR 1958).

brash rather than taking to the wing, but in between they do some fishing in the narrow creeks between the floes, or occasionally undertake a short communal flight. They occur in flocks of varying size, from a dozen or less up to several thousand. Particularly large congregations appear when strong gales have pressed large areas of ice floes together into a congested mass. The birds then concentrate in enormous flocks which at a distance may appear as dark patches on the ice. The terns are virtually absent from the areas of open water, they appear at most a few miles away from the ice-edge, but never at considerable distances from the pack (FALLA 1937, p. 253; ROUTH 1949, p. 590; BIERMAN and VOOUS 1950, p. 109; v. OORDT and KRUIJT 1954, p. 278; HØLGERSEN 1957, p. 68). The food conditions at the ice-edge are particularly favourable for the terns. Macroplankton, the so-called "krill", appears here in large masses, as a consequence of the immense upwelling of deep sea water along the south-polar continent (cf. above, p. 7).

Keeping to the ice-edge and its immediate surroundings the

Arctic Tern in its winter range is restricted to a rather narrow zone, usually only a few miles wide. Generally, the ice-edge forms a solid line, with minor indentations only, and ships attempting to force their way through are soon barred from further progress. Sometimes there may be a transition from isolated stream of ice to close pack, but this is not a usual condition. Open water may of course lie to the south of the ice-edge, but generally there is much more ice than open water between the ice-edge and the shores of the Antarctic continent (MACKINTOSH and HERDMAN 1940, p. 290). Patches of open water within the ice-fields as well as the open land water may also be frequented by the Arctic Tern, but apparently it does not occur in particularly large numbers here (FALLA 1937, p. 252).

The geographical distribution of the Arctic Tern in the south-polar zone roughly coincides with the East Antarctic. This was to be expected on the basis of the migration routes outlined above. The postulated arrival area of the migrating terns was said above (p. 15) to extend from the eastern Weddell Sea to about 150°E , and the terns apparently do not move much outside this hypothetical range. The eastern limit of the winter quarters runs about 170°E , *i. e.* at the west coast of Ross Sea, but the terns are irregular and scarce east of 150°E . As early as 11. December (in 1930) FALLA (1937, p. 253) while making observations at the ice-edge at 63°S , 166°E saw a single bird flying S.E., *i. e.* heading towards Ross Sea.

The greatest concentrations of terns, totalling hundred of thousands of birds, are found between 150°E and westwards to at least Enderby Land (about 55°E), according to FALLA's careful investigations. The only south-polar recovery of a ringed Arctic Tern has been made in the central parts of these areas, namely an adult bird ringed on the nest on Saltholm Island, Denmark, 22. May 1958, recovered in the pack-ice off Wilkes Land at $65^{\circ}08'\text{S}$, $111^{\circ}15'\text{E}$ on 4. February 1959 (JOHANSEN 1959, p. 40). In the pack-ice belt at about 90°E Arctic Terns were daily observed "singly or in small flocks" between 18. February and 28. March 1903 by the German South-polar Expedition (VAN-HÖFFEN 1905, p. 507). In the same area, from about 85°E to 100°E , Arctic Terns were frequently met with by ROUTH (1949, p. 590) during the "Balaena" Expedition 1946-47. West of

Enderby Land the population is probably thinning out, but the sector between Enderby Land and Weddell Sea is very poorly known from an ornithological point of view. However, as far west as Coats Land, at the east coast of Weddell Sea, Arctic Terns were seen in thousands at 72° – 74° S, 22° W in early March 1904 by the Scotia Expedition (CLARKE 1913, p. 268). The German "Valdivia" Expedition 1898–99 observed (and captured) only a single bird in the pack-ice on $64^{\circ}14'S$, $53^{\circ}30'E$; it flew onboard the vessel in an exhausted state. Further west (until 8° E) no terns were observed in the pack-ice in late November, but another exhausted individual was found on board the ship on 2. December (VANHÖFFEN 1901, p. 312). It should be noted, however, that there may have been more birds, VANHÖFFEN'S observations not always being very accurate.

The Willem Barendsz Expedition when in rather heavy pack-ice on 63° – 64° S, 22° – 23° W, *i. e.* southeast of the South Sandwich Islands on 13.–24. March 1947 recorded almost daily flocks of several hundreds of individuals (BIERMAN and VOOS 1950, p. 114). As mentioned above (p. 12) there are reasons to believe that the majority of these birds were immature individuals.

The majority of birds wintering in the eastern Weddell Sea are undoubtedly of South American origin, having followed the South American or Falkland cyclone trajectories.

In the remaining part of the Antarctic zone, *i. e.* the region between the western Weddell Sea and westwards to Ross Sea the Arctic Tern is extremely scarce, and in most areas virtually absent. Most records are from the end of February or from March, *i. e.* during the latter part of the terns' residence in the Antarctic when they have regained their vigour after the wing moult.

In the western Weddell Sea an Arctic Tern was collected by the Scotia Expedition on 25. February 1904 at $64^{\circ}38'S$, $35^{\circ}13'W$. It was in winter plumage and "in the midst of quill moult" (MURPHY 1936, vol. 2., p. 1102), *i. e.* certainly a younger bird. Another specimen was obtained by the same expedition on 23. March 1904 at $68^{\circ}32'S$, $12^{\circ}49'W$, being in summer plumage and having finished the moult, probably being a fully adult bird. I do know of no other records from these parts of the Antarctic, and it is noteworthy that the many expeditions to Graham Land

and the island groups in the Scotia Sea have never met with the Arctic Tern.

In the Bellingshausen Sea there is a single record of a specimen collected by the Norwegian Antarctic Expedition at Peter I Island 5. February 1929, being a female "moulting into summer plumage" (HOLGERSEN 1945, p. 69), but apparently some other specimens were observed. In the Amundsen Sea the U.S. Antarctic Service Expedition collected a female in the pack-ice at $70^{\circ}30'S$, $106^{\circ}W$ on the 25. February 1940 (FRIEDMANN 1945, p. 312). The expedition did not obtain this species during its visit to Palmer Land, where altogether 13 specimens of the Antarctic Tern were collected.

In the westernmost part of the West Antarctic two specimens were collected by the Antarctic Expedition under JAMES CLARKE ROSS on 12. March 1841 at $66^{\circ}S$, $157^{\circ}W$ (SAUNDERS 1896, p. 66), and two individuals were observed on 16. February 1952 on about $70^{\circ}S$, $178^{\circ}W$ by v. OORDT and KRUIJT (1954, p. 278).

In addition to these very scattered records from the West Antarctic, careful notes on the occurrence of terns in this part of the south-polar regions have been made by HOLGERSEN (1957, p. 68–71) on the "Brategg" Expedition 1947–48. In the middle of February terns were seen daily at the ice-edge in the sector between $80^{\circ}W$ and $100^{\circ}W$, but never more than a few dozen a day. HOLGERSEN gives good reasons for the assumption that these birds were Arctic and not Antarctic Terns. Further west one individual was seen on 31. January at $68^{\circ}13'S$, $120^{\circ}16'W$, but this was the only record during the cruise from middle December to the end of January between $100^{\circ}W$ and $175^{\circ}W$, and "we should have seen them if there had been any as we spent days cruising along the ice edge" (HOLGERSEN, *loc. cit.*, p. 68).

We may conclude that the Arctic Tern is very scarce in the West Antarctic in February–March and apparently completely absent in October–January, going by the negative evidence that no specimens have been collected and no terns have been observed in this period.

The antarctic continent can be divided into three parts on the basis of tern distribution in summer: (1) The winter quarter of the Arctic Tern, from $150^{\circ}E$ westwards to $30^{\circ}W$. (2) The breeding area of the Antarctic Tern on the islands in the Scotia Sea and

Weddell Sea and on Palmer Peninsula, between 30°W and 80°W. (3) The remaining sector, between 80°W and 150°E, which is virtually devoid of terns. The two species of terns have completely separate ranges, the Arctic Tern keeping to the ice-edge, and the Antarctic Tern requiring icefree sea or areas with only a very slight coverage of ice near its breeding places on firm land. The only places on the continent where this condition is present are the northern coast and the west coast of Palmer Peninsula (Oceanographic Atlas 1957, fig. 32–33). Smaller parts of the coast of Wilkes Land and along the eastern coast of Ross Sea may temporarily be icefree, at least in March, and Antarctic Terns have been recorded from the latter area, although some doubt is attached to this record (FRIEDMANN 1945, p. 313).

After the arrival to the edge of the pack-ice belt the Arctic Terns are still under the influence of the wind conditions.

Owing to the constant anticyclonic situation in the highlands of the eastern Antarctic continent, downslope (katabatic) winds blow regularly towards the marginal regions, where they turn eastwards owing to the earth's rotation. Out at sea these east winds are usually rather weak and do not penetrate further north than about 65°–66°S.

In October–December when the Arctic Terns arrive at their winter quarters the outer zone of the pack-ice is situated far out in the region with westerly winds (cf. fig. 7), and the terns wintering there are exposed to the full force of the storms. During heavy gales they may easily be carried passively away in an eastern direction, particularly when, during the wing moult, they have a reduced capability of flight. During the following months the pack-ice belt narrows and shrinks considerably, as seen in fig. 7, but parts of it are still within the reach of the westerly storms. Furthermore, the ice conditions differ widely from one year to the next. In summer the situation of the ice-edge at the entrance to Ross Sea has been found to vary as much as 400 miles. In 1913 the ice-edge at long. 123°E was situated at 54°S as late as 18. February, and several flocks of terns were observed there by HUNTER, while in 1929 the ice-edge at long. 79°E was situated as far south as 64°S as early as 11. December (FALLA 1937, p. 252).

The situation of the pack-ice in relation to the prevailing winds

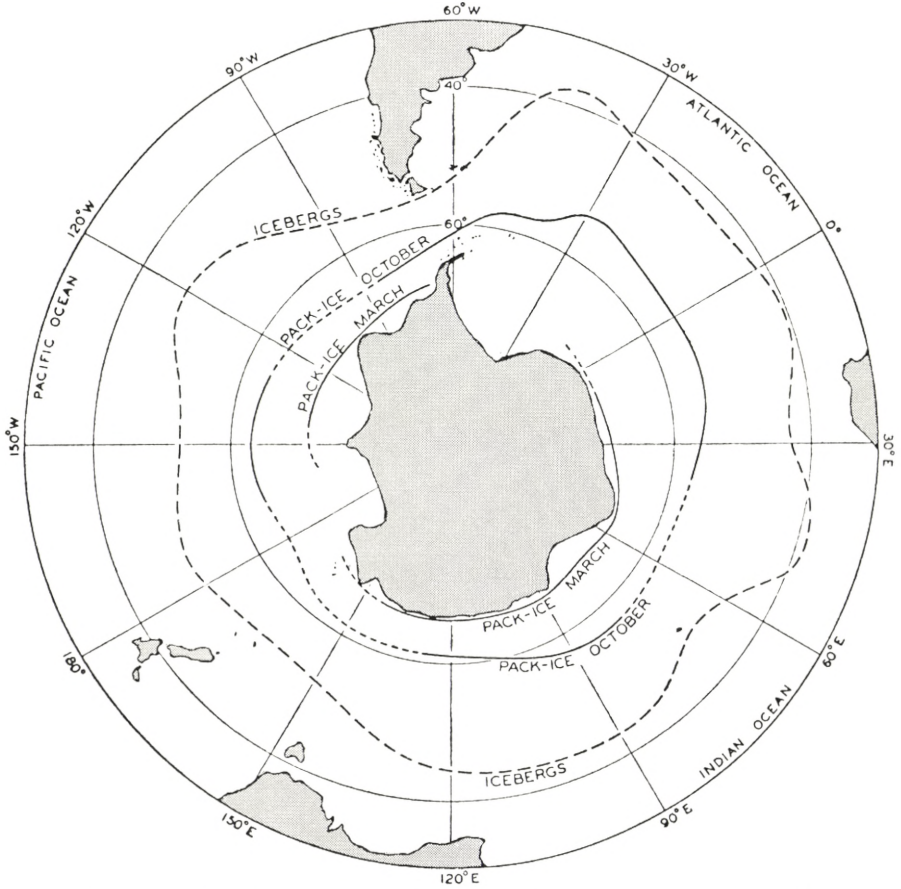


Fig. 7. Average northern limit of the Antarctic pack-ice belt in March and October, and average northern limit of icebergs. (After SVERDRUP, JOHNSON and FLEMING 1946).

makes it evident that the risk of the terns being drifted eastwards while staying in their winter quarters cannot be ruled out. The younger birds are more exposed to this danger than the adults. They roam about more, even out to sea, are unexperienced, and have not yet developed any fixed adherence to a definite wintering place. In addition, their wings are weaker, and the wing moult is prolonged well into March or even April. I am convinced that many—perhaps the majority—of the stray birds recorded in late summer (February–March) east of the Ross Sea and in the Amundsen and Bellingshausen Seas have been drifted to the

east from the ordinary wintering area in the East Antarctic, and that the greater part are young birds. It is possible that some of the birds observed by HOLGERSEN in Bellingshausen Sea in February have come directly from western Chilean waters, having crossed Drake Strait (cf. discussion above, p. 16). A few of these birds may during winter even penetrate westwards in the direction of Ross Sea, utilizing the east wind which blows at high latitudes. Such a movement must be exceptional, however, particularly since the east winds in this sector of the Antarctic are irregular and erratic, as will be shown below. It is very unlikely, at any rate, that the Arctic Terns occurring in West Antarctic originate from the Weddell Sea regions, *i. e.* that they should have forced their way against the very strong westerly winds in the Drake Strait. Some few individuals may possibly filter down the west coast of Palmer Peninsula, along which the wind is weaker and even may blow to the east, but these areas are within the premises of the Antarctic Terns, and the wintering Arctic Terns, therefore, would probably be inferior as competitors.

One more fact supports the assumption that the majority of the Arctic Terns occurring in the Amundsen and Bellingshausen Seas have a western origin. Birds which have entered the Ross Sea area are exposed primarily to westerly winds which blow right to the coast, because the cyclonic trajectories continue southwards far into the continent itself. As said above the anticyclone over the high plateau of East Antarctic is very staple and only rarely disrupted by disturbances. The lower plateau of West Antarctic, on the other hand, is frequently traversed by perturbations. Cyclonic systems moving into the eastern Ross Sea, along one of the major paths of entry, find relatively easy access across West Antarctic (SABBAGH 1962, p. 103). This phenomenon, which appears distinctly in fig. 3, makes it still more doubtful that Arctic Terns should move in an anticlockwise direction along West Antarctic.

Direct evidence of the eastward movement of birds into the West Antarctic is practically lacking. I can refer, however, to the observation quoted above (p. 22) of a single bird flying southeast at 63°S , 166°E . Indirect evidence is furnished by the fact that young Arctic Terns in great number spend their first summer, when they are about one year old, in the off-shore zone of the

Humboldt Current. According to MURPHY (1936, vol. 2, p. 1100), BECK found Arctic Terns to be numerous in June 1913 off the coasts of central Peru, where they occurred up to 300 km out to sea. BECK observed them daily, passing singly, in groups of six or seven or even being "common", and he collected a number of specimens. It is out of the question that all these birds should have entered the Humboldt Current *via* Drake Strait, *i. e.* originating from the Weddell Sea, because this would imply a strenuous fight against the westerly storms over a long distance. Consequently, it must be assumed that the majority of the birds originated from further west, *i. e.* from the Bellingshausen and Amundsen Seas. Having already emphasized the improbability of a Weddell Sea or Chilean origin of any great number of the Arctic Terns wintering in the West Antarctic seas, it is fair to conclude that an essential part of the West Antarctic population must have derived from the East Antarctic, west of Ross Sea.

It is possible that hydrological factors may give rise to certain dislocations of the Arctic Terns wintering in the pack-ice, but these do not appear to be of any special importance. The pack-ice steadily drifts with the wind, but the direction of the drift deviates about 45° from the wind direction, *i. e.* it has a northern component, which, however, is much less pronounced than the eastern one. The reason for this deviation is the fact that the surface water layers are continuously transported to the north, owing to the upwelling of deep sea water along the coasts of the antarctic continent. When these northgoing water masses reach the Antarctic Convergence they sink abruptly down below the subantarctic water, which results in a sharp rise of temperature at the surface. When resting on the ice floes the terns are passively drifted in an easterly direction, but the speed is slight – from the view point of the birds – amounting to about one knot, only in Drake Strait reaching two knots; nevertheless, this may sum up.

The West Wind Drift is replaced by the East Wind Drift close to the coast, but this is of still less significance to the terns. The East Wind Drift is narrow, only about 2° wide, running approximately parallel to the shore line, and is of a weak order, because the east winds blowing over the coastal waters are weak, as said already. The northern limit of the East Wind Drift lies on about 66° S, along the so-called Antarctic Divergence, which separates the East and West Wind Drift and which is characterized by much upwelling (DEACON 1937, p. 10; SVERDRUP, JOHNSON and FLEMING 1946, p. 623; ASTAPENKO 1964, p. 15). The two drifts are circumpolar, but the East Wind Drift is interrupted at Graham Land and the adjoining South Shetland Islands. These landmasses force the current towards the north where it is directly

diverted into the West Wind Drift. On the west coast of Palmer Peninsula the East Wind Drift is narrow and very weak, but in the Bellingshausen Sea it soon regenerates.

This system of currents is extremely important for the organic productivity in the sea and for the life conditions of the marine fauna, but probably does not exert any appreciable influence on the localization of the Arctic Terns.

In early March, when the moult of the flight-feathers is completed and the wings have regained their vigour, at least in the adult birds, the spring migration in the Arctic Tern is initiated. It is very unlikely that the terns follow the same route as during the autumn migration from South Africa. All evidence tends to show that the terns move westwards from their winter quarter in the East Antarctic. The pack-ice is now (in March) reduced to its minimum size, and the ice edge is generally situated within the zone of eastern winds. The terns undoubtedly utilize these winds in their westward journey, but after the long period of rest on the wintering grounds the birds are vigorous enough to move against the westerly winds if necessary, at least for some distance and provided the wind is not too strong. The terns continue westwards to the Weddell Sea area, where they make a turn, moving northwards or northeastwards towards South Africa, in this way having the advantage of side-wind or even tail-wind. Cf. the routes given in fig. 8.

A number of observations support the view points set forth above. V. OORDT and KRUIJT (1954, p. 278) followed the first part of the migration in the East Antarctic in early March 1952. On 1. March they observed altogether 15 birds, all flying in a westward direction at $63^{\circ}31'S$, $106^{\circ}53'E$, moving against a strong westerly wind (force 8–9). Other individuals were observed flying westwards on 5. March at $64^{\circ}S$, $84^{\circ}E$ against a westerly wind of force 3–6. In the next days (6.–7. March), when the expedition had left the pack-ice belt, further individuals were noticed, all flying westwards against westerly winds of varying force, the last observation being made at $64^{\circ}09'S$, $74^{\circ}17'E$. No further terns were encountered until 11. March, when at $60^{\circ}S$, $39^{\circ}E$ five scattered birds were observed flying southwestwards, against a S.W.-wind with force 4–5. These latter birds must have been on their way to Weddell Sea. During the remaining voyage, which

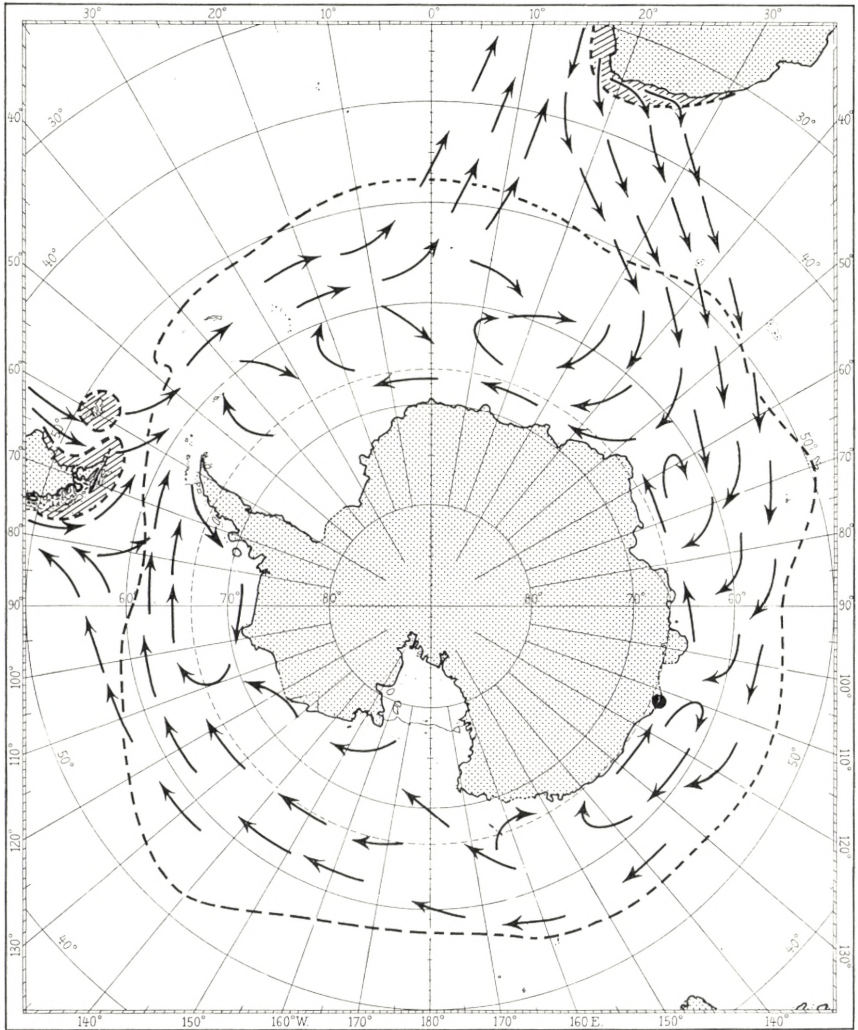


Fig. 8. Migratory system, indicated by arrows, of the Arctic Tern in the Antarctic Ocean, according to the view-points accepted in the present paper, somewhat schematical. The winter quarters off South America and South Africa are hatched, the position of the Antarctic recovery of a ringed Arctic Tern is shown by the solid circle, the Antarctic Convergence by the dashed line.

followed a straight northwestern direction to Cape Town (within the zone in which the autumn migration of the Arctic Terns took place), v. OORDT and KRUIJT did not see any terns at all. This tends to show that the Arctic Tern does not migrate towards the north in this area. After the arrival at Cape Town on 19. March

hundreds of terns were seen by the said observers in the sea west of Cape Peninsula and in Table Bay (but some of them might have been Common Terns).

Interesting observations were made also during the "Willem Barendsz Expedition". On 12.–15. April 1947 small flocks of Arctic Terns were observed steadily moving in northward direction in the area 55° – 47° S, 0° – 8° E (BIERMAN and VOOUS 1950, p. 114), *i. e.* in an area which was predicted above to be on the migration route when the terns had turned to the north from the Weddell Sea region.

This route, leading towards N.–N.E. from the Weddell Sea region, is undoubtedly the main path of the Arctic Tern on its way to the north. It is used not only by the main population wintering in East Antarctic, but also by the birds wintering in the Weddell Sea. It is even used by the majority of the terns wintering in the Bellingshausen Sea, which move with the westerly winds through Drake Strait and then join the other populations on their way northeastwards to South Africa. Part of the populations of the region further west, *i. e.* from the Amundsen Sea and westwards to about Ross Sea, probably go northeastwards to the waters off the Chilean west coast.

The northeastward route of the Weddell Sea winter birds is purely theoretical, but it is the only possible one. It is unrealistic to believe that the terns would move in a northwestern direction through the Drake Strait in order to reach Chilean waters. Such a crossing could be carried out during one of the rare periods of fairly calm weather, and some few individuals may probably succeed in making such a crossing, but generally the terns would run into one continuous succession of westerly storms, which would tax the strength of these light birds too heavily. An insistence by a population to follow this migratory route would challenge the selective forces beyond the limit of probability. This poses an interesting problem, however. It was argued above (p. 16) that the majority of birds wintering in the Weddell Sea originated from Chilean waters but now I advocate the view that these birds migrate north to South Africa and do not return to Chile. This discrepancy must imply that very few adult birds are involved in this migration, bearing in mind that adult terns generally return to their former breeding places. As a consequence

of this view it may be concluded that the migratory route along the west coast of the Americas must be used by a minority of birds only.

The recognition of this route is based mainly on the presence of large numbers of one year old birds observed and collected in the Humboldt Current in June–July in their second summer, and on the autumn migration recorded in the waters off western Chile in November–December. There are very few records of migrating Arctic Terns along the western coast of North America, Central America and northern South America, and the observations may in many cases refer to one-year old birds which have spent their first summer in the northern hemisphere and now are on their way south during their second autumn migration. It must be borne in mind that during their first summer the young Arctic Terns may wander as far north as the Arctic region. This has been proved by the recovery of ringed specimens, the northernmost record being a bird ringed as nestling in western Greenland 22. July 1947, captured in James Bay, Ontario, in arctic Canada, 4. July 1948. It was shot in a breeding colony of Arctic Terns, but was not itself in breeding condition (SALOMONSEN 1949, p.251 and 255). There are reasons to believe, therefore, that only very few adult birds participate in the migration along the western coasts of America.

The birds passing the Chilean waters on their way south can be divided into four groups, according to age, origin and destination:

Individuals originating from the breeding area, including juvenile birds and adult ones, migrating

A-1: southwards to the Bellingshausen Sea.

A-2: southeastwards to the Weddell Sea.

One-year old individuals (occasionally two-year old birds) summering in the Humboldt Current, more rarely further north off the west coast of the Americas, migrating

B-1: southwards to the Bellingshausen Sea.

B-2: southwards to the Weddell Sea.

Groups A-1 and B-1 comprise only a small number of birds, as has been demonstrated already in this paper. A few of these birds may move westwards as far as Ross Sea, but during their

spring migration return to the east and go northeastwards to Chilean waters. The adult birds as well as those which are now in their third summer continue northwards along the Pacific coast of America towards the breeding places. The juvenile birds, now in their second summer, remain generally in Chilean waters until they go south during the subsequent autumn migration.

Group A-2 comprises only very few adult birds, because these run a grave risk of being wiped out by selection, as shown above. The juvenile birds may probably move northeastwards to South Africa during spring-migration and survive.

In my opinion group B-2 comprises the main bulk of the birds migrating from Chilean waters to the Antarctic. The majority are of Atlantic, not of Pacific, origin, and comprise individuals which during their first winter have drifted eastwards from the East Antarctic. In this way they finally reach the Amundsen and the Bellingshausen Seas and during their spring migration continue northeastwards to the Humboldt Current. During their second winter the majority of these birds migrate southeastwards to Weddell Sea, and next spring northeastwards to South Africa, from where they started for the Antarctic about one and a half years previously. They have in this way performed a circumnavigation of the Antarctic Continent. It is very probable that some individuals carry out this circumnavigation in one season, continuing the migration directly to South Africa *via* Drake Strait during their first spring.

The regular drifting of a number of young birds from East Antarctic in a clockwise direction towards the Amundsen and Bellingshausen Seas must be viewed in the light of the special situation of the young birds, not least their moulting condition. When the adult birds in early March gradually start the spring migration westwards towards Weddell Sea the greater number of young birds are not in a very good condition to follow, owing to the belated moult of the flight feathers. At the same time, their urge of migration is much weaker and their sense of direction less acute than in the adult birds. Moreover, owing to their lack of experience they sometimes roam far out to sea. They are, therefore, much more liable than the adult birds to be caught by the wind. Evidently, the birds have been adapted to this situation and utilize the wind power to their own advantage. The

circumnavigation, therefore, must undoubtedly be of a considerable survival value to the birds.

Some young birds, being victims of a misleading sense of direction, will attempt to move northwards in too eastern longitudes, to the effect that they sooner or later drift further eastwards. Under these circumstances they may eventually reach Australia. Two such cases are known, and, strangely enough, both individuals had been ringed. The first one was caught alive off Fremantle in Western Australia on 16. May 1956, having been ringed as nestling near Murmansk at the White Sea 5. July 1955 (HINDWOOD 1958, p. 261). The second bird was found dead near Perth in Western Australia on 10. June 1963, having been ringed as nestling near Stockholm in Sweden on 27. June 1962 (SERVENTY 1963, p. 22). The occurrence at Macquarie Island on 20. April 1950 of two Arctic Terns, which were collected there by N. J. FAVALORO (DOWNES 1952, p. 309) is another instance of this eastward drift during spring migration. Naturally, also adult individuals may participate in this eastward drifting, but the majority must definitely be younger birds.

The circumnavigation of the Antarctic Continent by a varying number of young Arctic Terns is not so peculiar as it may seem at first glance. Recent ringing of the Giant Petrel (*Macronectes giganteus* (Gmelin)) on the breeding places on Palmer Peninsula, South Orkney Islands and Heard and Macquarie Island¹ (STONEHOUSE 1958, p. 204; HITCHCOCK & CARRICK 1958, p. 54) has demonstrated that the juvenile individuals of this species perform enormous migrations which follow the westerly winds in the subantarctic zone, while the adult birds are more or less stationary. Recoveries of juvenile birds have shown that a circumnavigation can be easily carried out in less than two months. Evidently, many other species of petrels as well as albatrosses perform such clockwise movements around the Antarctic continent (cf. DORST 1962, p. 196), but this has not yet been proved by ringing.

STONEHOUSE (*loc. cit.*, p. 206) emphasizes the importance of the westerly winds in aiding the Giant Petrels in their movement from west to east, but impeding their flight to an extraordinary

¹ The specimens ringed on Macquarie Island may belong to the related species *Macronectes halli* Mathews (BOURNE and WARHAM 1966, p. 45).

degree if they attempt to fly against it. These birds "fly easily with the wind, but only with the greatest difficulty against it". This, of course, holds good to a still greater degree for the Arctic Tern. Being a much smaller and lighter bird, it is much less apt to resist strong winds. Transportability by wind (*i. e.* possibility for drifting) increases geometrically with decrease in weight, and "the Arctic Tern is so light that in a breeze it cannot keep a straight course" (WYNNE-EDWARDS 1935, p. 326). On the other side, by means of its highly developed manoeuvrability and flight control the Arctic Tern is extremely well suited to utilize the wind power to its advantage.

On the map fig. 8 I have attempted to illustrate the complete migratory system of the Arctic Tern within the Antarctic zone, in its close dependence on the winds. The representation is somewhat schematical, it is true, and it has not been possible to separate all details in the complicated pattern. Needless to say, many particulars have not been proved, but I hope that the map may be of some use as a basis for future studies.

Summary

The stupendous flight of the Arctic Tern (*Sterna paradisaea* Pontoppidan) from the breeding places in the polar region to the winter quarters in the antarctic zone has been described a number of times, but the migratory routes are not known in detail, and virtually nothing has been published on the migratory movements in the huge area south of Africa and South America. Two migratory routes are recognized generally, as shown in fig. 2. It is shown in the present paper that the Pacific flyway is of little importance. A comparatively small number of Arctic Terns spend the winter in the coastal waters of South Africa and southern South America, but by far the majority continue the autumn migration further south, crossing the Antarctic Ocean and wintering in the border zone of the pack-ice belt.

The crossing of the Antarctic Ocean, a flight of more than 3000 km, forms the most dangerous and difficult part of the long migration. When leaving South African waters for the south, the terns have exhausted their resources during the extensive

journey already carried out, and their efficiency of flight is considerably reduced owing to the weak condition of their wing-feathers, which are almost one year old, having not been renewed (in adult birds) since the previous stay in the winter quarters. During the oversea voyage across the Antarctic Ocean the terns are exposed to incessant westerly storms (cf. fig. 1), against which they cannot possibly fight, owing to their present debility. It is unavoidable, therefore, that they are drifted more or less to the east by the wind.

The renewal of the flight feathers in the Arctic Tern does not take place until the crossing of the Antarctic Ocean has been accomplished and the winter quarters have been reached. In all other palearctic species of terns the wing-moult takes place without interruption during the entire non-breeding period, *i. e.* about 300 days. The Arctic Tern is the only species which continues the migration from South Africa across the Antarctic Ocean. The aberrant moulting condition in the Arctic Tern must be explained, therefore, as an adaptation to the extremely strenuous and demanding flight across the stormy seas from South Africa to the Antarctic, which can be carried out successfully only under special conditions, *i. e.* the moult must be restricted to the comparatively short resting period in the winter quarters. Consequently, the moult must be considerably speeded up when comparing with conditions in all other species of terns.

The wing-moult of the young Arctic Terns in their first winter is delayed up to two months in comparison with that in the adult birds. It never starts until the end of January and is probably not over until April, but moulting specimens have been recorded from as late as June.

The shortest distance from South Africa to the pack-ice belt is found in a due south direction, but when leaving South Africa on the migration across the southern ocean the Arctic Terns are drifted eastwards by the westerly storms and gales, and the resulting flight direction will be E.S.E. or S.E. This direction, which undoubtedly is genetically fixed, exactly corresponds with the course of the meridional cyclone trajectories leading across the sea to the Antarctic Continent (cf. fig. 3). All evidence tends to show that the migration of the terns is intimately connected with these air movements.

When leaving South Africa the majority of Arctic Terns assumably reach the area of the Kerguelen trajectory (cf. fig. 3), while smaller numbers will follow the South African or the West Australian trajectory. The Arctic Terns leaving South America will follow the South American and the Falkland trajectories. According to these migration routes the Arctic Terns will reach the pack-ice in the area from about 150°E westwards to the eastern Weddell Sea. Observations during recent expeditions have demonstrated that the winter range of the Arctic Terns covers the area delimited above on the basis of the theoretical migratory routes. Even the few observations of terns during the actual ocean crossing support the theoretical considerations. Special emphasis has been laid on the careful observations by DOWNES on Heard Island; cf. fig. 4 for this and other geographical localities.

It is probable that some individuals migrating southwards well off the Chilean coast use the trajectory leading almost due south, west of Cape Horn (cf. fig. 3). It cannot possibly be a much frequented route, because the westerly winds in northern Drake Strait are extremely strong and will usually drift the birds farther east, through the strait.

A minority of individuals leaving South African waters are carried away by strong westerly gales and drift across the southern Indian Ocean in due eastern direction in the subtropical zone between 30°S and 40°S , in extreme cases reaching western and southern Australia and even New Zealand. The prevalence of western winds is as pronounced at these latitudes as further south, as shown in fig. 5. The long eastward drift of the terns is probably due to strong zonal cyclones along the polar front. All known cases of this drift migration have been enumerated on p. 19–20, and the probable migration route has been outlined on the map fig. 6.

The geographical distribution of the Arctic Tern in the south-polar zone extends from about 150°E westwards to eastern Weddell Sea (about 30°), as outlined above on the basis of observations and collections made on various expeditions. In the remaining part of the antarctic zone, roughly the area from Weddell Sea westwards to Ross Sea, the Arctic Tern is extremely scarce, and in most localities completely absent.

During the first part of their sojourn in the outer zone of the

pack-ice belt the terns are still subject to the influence of the westerly winds and may easily, during heavy gales, be carried away in an eastern direction, particularly when during wing-moult they have a reduced capability of flight. Later in the season the pack-ice belt narrows considerably (cf. fig. 7), and the ice-edge gradually moves within the reach of the continental eastern winds. It is evident, however, that the risk of the terns being drifted eastwards during their stay in the winter quarters cannot be ruled out. The young birds are more exposed to this danger than the adults. It is most probable to assume that the majority of the stray birds recorded in late summer (February–March) east of the Ross Sea area and in the Amundsen and Bellingshausen Seas have been drifted to the east from the ordinary wintering area in the East Antarctic, and that the greater part are young birds.

The return journey to the breeding places in March and early April leads from the East Antarctic in a westerly direction towards the Weddell Sea region, and during this flight the terns undoubtedly utilize the continental east winds. Off the Weddell Sea the migratory birds turn to the north or to northeast towards South Africa, in this way having the advantage of side-wind or even tail-wind; cf. the routes given in fig. 8. A number of observations support these view-points.

The route leading N.–N.E. from the Weddell Sea region is undoubtedly the main path of the Arctic Tern on its way to the north. It is used not only by the main population wintering in East Antarctic, but also by the birds wintering in the Weddell Sea. It is even used by many of the birds wintering in the Bellingshausen Sea, which move with the westerly winds through Drake Strait and then join the other populations on their way to South Africa. The birds originating from Bellingshausen Sea (or from further west in the West Antarctic) have been drifted to these regions from the East Antarctic, as described above. They are mostly young birds, and in returning to South Africa in spring they have performed a complete circumnavigation of the Antarctic Continent during their first winter. Not all young birds of the West Antarctic population take this route, but many, perhaps the majority, continue from the Amundsen and Bellingshausen Seas to the N.E. to the Humboldt Current, where they

spend their first summer. The subsequent autumn they move southeastwards to Weddell Sea, following the South American cyclone trajectory, and the following spring go northeastwards to South Africa. In this way the antarctic circumnavigation takes two years.

The regular drifting of a number of young birds around the Antarctic Continent in a clockwise direction must be viewed in the light of the special situation of the young birds, *i. e.* their moulting conditions, their lack of adherence to a certain circumscribed winter quarter, their lack of experience and their less acute sense of direction. They are, therefore, much more liable than the adult birds to be caught by the wind. Evidently, the birds have been adapted to this situation and utilize the wind power to their own advantage.

The antarctic circumnavigation of the young Arctic Terns has a parallel in similar movements in the subantarctic zone performed by the immature Giant Petrels (*Macronectes giganteus* (Gmelin)), and undoubtedly also by many other sea birds.

In fig. 8 an attempt is made in a schematical way to illustrate the complete migratory system of the Arctic Tern within the antarctic zone.

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References

- ASTAPENKO, P. D. 1964: Atmospheric Processes in the High Latitudes of the Southern Hemisphere. – Jerusalem (286 pp.).
- BIERMAN, W. H. and K. H. VOOUS 1950: Birds Observed and Collected during the Whaling Expeditions of the "Willem Barendsz" in the Antarctic, 1946–1947 and 1947–1948. – *Ardea*, vol. 37, extra-number (123 pp.).
- BOURNE, W. R. P. and JOHN WARHAM 1966: Geographical Variation in the Giant Petrels of the Genus *Macronectes*. – *Ardea*, vol. 54, p. 45–67.
- CARRICK, R. 1958, see W. B. HITCHCOCK.
- CLANCEY, P. A. 1965: A Catalogue of Birds of the South African Sub-Region. Part II: Families Glareolidae–Pittidae. – *Durban Mus. Novitates*, vol. 7, p. 305–388.
- CLARKE, W. E. 1913: Ornithology of the Scottish National Antarctic Expedition. Section 7: On the Birds of the Weddell and Adjacent Seas, Antarctic Ocean. – *Sci. Res. Scottish Natl. Antarctic Expedition*, vol. 4, p. 255–270.
- DEACON, G. E. R. 1937: The Hydrology of the Southern Ocean. – *Discovery Rep.*, vol. 15, p. 1–123, plates I–XLIV.
- DORST, JEAN 1962: The Migrations of Birds. – London (476 pp.).
- DOWNES, M. C. 1952: Arctic Terns in the Subantarctic. – *The Emu*, vol. 52, p. 306–310.
- FALLA, R. A. 1930: Birds Observed between Melbourne and Durban. – *The Emu*, vol. 29, p. 175–180.
- 1937: Birds. – *B. A. N. Z. Antarctic Research Expedition 1929–1931, Reports*, ser. B, vol. 2, p. 1–304, plates I–IV.
- FISHER, JAMES and R. M. LOCKLEY 1954: Sea-Birds. An Introduction to the Natural History of the Sea-Birds of the North Atlantic. – London (320 pp., 40 plates).
- FLEMING, C. A. (Convener) 1953: Checklist of New Zealand Birds. – Wellington (80 pp.).
- FLEMING, R. H. 1946, see H. U. SVERDRUP.
- LA FOND, E. C. 1966: Upwelling. *In*: FAIRBRIDGE, R. W. (Editor): *The Encyclopedia of Oceanography*, p. 957–959. – New York (1021 pp.).
- FRIEDMANN, HERBERT 1945: Birds of the United States Antarctic Service Expedition 1939–1941. – *Proc. American. Philosoph. Soc.*, vol. 89, no. 1, p. 305–313.
- HERDMAN, H. F. P. 1940, see N. A. MACKINTOSH.
- HINDWOOD, K. A. 1958: The Arctic Tern in Australia. – *The Emu*, vol. 58, p. 259–263.

- HITCHCOCK, W. B. and R. CARRICK 1958: First Report of Banded Birds Migrating between Australia and Other Parts of the World. – Commonwealth Scientific and Industrial Research Organization, Wildlife Research, vol. 3, p. 54–70.
- HOLGERSEN, HOLGER 1945: Antarctic and Sub-Antarctic Birds. – Scientific Results of the Norwegian Antarctic Expeditions 1927–1928 et sqq., Instituted and Financed by Consul Lars Christensen, no. 23 (100 pp.).
- 1957: Ornithology of the “Brategg” Expedition. – Scientific Results of the “Brategg” Expedition 1947–1948, no. 4 (80 pp.).
- JOHANSEN, HANS 1959: To interessante ringfund. – Dansk Ornith. Foren. Tidsskr., vol. 53, p. 40–41.
- JOHNSON, M. W. 1946, see H. U. SVERDRUP.
- KETCHUM, B. H. 1963, see A. C. REDFIELD.
- KRUIJT, J. P. 1954, see G. J. VAN OORDT.
- KULLENBERG, BERTIL 1946: Über Verbreitung und Wanderungen von vier Sterna-Arten. – Ark. Zool., vol. 38A, no. 17 (80 pp.).
- LOCKLEY, R. M. 1954, see JAMES FISCHER.
- MACKINTOSH, N. A. and H. F. P. HERDMAN 1940: Distribution of the Pack-Ice in the Southern Ocean. – Discovery Rep., vol. 19, p. 287–296, plates LXIX–XCV.
- MARSHALL, A. J. and D. L. SERVENTY 1956: Moults Adaptation in Relation to Long-distance Migration in Petrels. – Nature, vol. 177, p. 943.
- MÖRZER BRUYN, W. F. J. and K. H. VOOUS 1964: Arctic Tern (*Sterna paradisaea*) in Southern Indian Ocean. – Ardea, vol. 52, p. 117–118.
- MURPHY, ROBERT CUSHMAN 1936: Oceanic Birds of South America. – New York (2 vols., 1245 pp.).
- 1938: On Pan-Antarctic Terns. Birds Collected during the Whitney South Sea Expedition, XXXVII. – American Mus. Novitates, no. 977 (17 pp.).
- Oceanographic Atlas of the Polar Seas. Part I: Antarctic. 1957. – U. S. Navy Hydrographic Office, Washington.
- VAN OORDT, G. J. and J. P. KRUIJT 1954: Birds, Observed on a Voyage in the South Atlantic and Southern Oceans in 1951/1952. – Ardea, vol. 42, p. 245–280.
- PAULIAN, P. 1953: Pinnipèdes, Cétacés, Oiseaux des Iles Kerguelen et Amsterdam. Mission Kerguelen 1951. – Mém. Inst. Sci. Madagascar, ser. A, vol. 8, p. 111–234, plates I–XXX.
- 1954: Migrateurs continentaux dans les Iles Nouvelle-Amsterdam et Kerguelen. – L'Oiseau, vol. 24, p. 136–142.
- RADFORD, M. C. 1961: A Study of the British ringing records of the Common Tern and Arctic Tern and comparison with some foreign records. – Bird Study, vol. 8, p. 174–184.
- REDFIELD, A. C., B. H. KETCHUM and F. A. RICHARDS 1963: The Influence of Organisms on the Composition of Sea-Water. In: HILL, M. N. (Editor): The Sea. Ideas and Observations on Progress in the Study of the Seas, vol. 2, p. 26–77. – New York (554 pp.).

- REID, J. L. 1963, see W. S. WOOSTER.
- RICHARDS, F. A. 1963, see A. C. REDFIELD.
- ROUTH, MARTIN 1949: Ornithological Observations in the Antarctic Seas 1946-47. – *The Ibis*, vol. 91, p. 577-606.
- RØEN, ULRIK 1965: Et besøg ved verdens nordligste sø. – *Grønland*, p. 121-130.
- SABBAGH, MICHAEL E. 1962: A Preliminary Regional Dynamic Climatology of the Antarctic Continent. – *Erdkunde*, vol. 16, p. 94-111.
- SALOMONSEN, FINN 1949: Tredie foreløbige liste over genfundne grønlandske ringfugle. (With a Summary in English: Third Preliminary List of Recoveries of Birds Ringed in Greenland). – *Dansk Ornith. Foren. Tidsskr.*, vol. 43, p. 251-255.
- 1951: *The Birds of Greenland*. – Copenhagen (603 pp.).
- 1967: *Fugletrækket og dets gåder*. (Second, enlarged edition). – Copenhagen (332 pp.).
- SAUNDERS, HOWARD 1896: *Gaviæ (Terns, Gulls, and Skuas)*. – *Catalogue of the Birds in the British Museum*, vol. 25, p. 1-339.
- SCLATER, W. L. 1906: *The Birds of South Africa*. Vol. 4: *Game-Birds, Shore-Birds and Sea-Birds*. – London (545 pp.).
- SERVENTY, D. L. 1963: Second Record of a Ringed Arctic Tern in South-Western Australia. – *Western Australian Naturalist*, vol. 9, p. 22-23.
- 1956, see A. J. MARSHALL.
- STONEHOUSE, BERNHARD 1958: Notes on the Ringing and the Breeding Distribution of the Giant Petrel *Macronectes giganteus*. – *The Ibis*, vol. 100, p. 204-208.
- STORR, G. M. 1958: Migration Routes of the Arctic Tern. – *The Emu*, vol. 58, p. 59-62.
- STRESEMANN, ERWIN and VESTA STRESEMANN 1966: *Die Mauser der Vögel*. – *Journ. Ornith.*, vol. 107, Sonderheft (VIII + 448 pp.).
- SVERDRUP, H. U., M. W. JOHNSON and R. H. FLEMING 1946: *The Oceans, their Physics, Chemistry, and General Biology*. – New York (1087 pp.).
- VANHÖFFEN, E. 1901: Bericht über die bei der deutschen Tiefseeexpedition beobachteten Vögel. – *Journ. Ornith.*, vol. 49, p. 304-322.
- 1905: Bericht über die bei der deutschen Südpolarexpedition beobachteten Vögel. – *Journ. Ornith.*, vol. 53, p. 500-515.
- VOOUS, K. H. 1950, see W. H. BIERMAN.
- 1964, see W. F. J. MÖRZER BRUYN.
- WARHAM, JOHN 1966, see W. R. P. BOURNE.
- WOOSTER, W. S. and J. L. REID 1963: Eastern Boundary Currents. *In*: HILL, M. N. (Editor): *The Sea. Ideas and Observations on Progress in the Study of the Seas*, vol. 2, p. 253-280. – New York (554 pp.).
- WYNNE-EDWARDS, V. C. 1935: On the Habits and Distribution of Birds on the North Atlantic. – *Proc. Boston Soc. Nat. Hist.*, vol. 40, no. 4, p. 233-346, plates 3-5.

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