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THE EFFECTS OF SEASONAL CHANGES ON THE SEABIRDS OF THE WESTERN INDIAN OCEAN*

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ABSTRACT

In this paper four aspects of seabird biology are reviewed for that part of the tropical Indian Ocean lying west of India : the breeding seasons, the composition of the avifauna, the density of seabirds at sea, and lastly seabird migration.

In species composition, there is little overlap between the seabird faunas of the Arabian Sea and the area south of the equator, where it is almost identical to that of the other tropical oceans. Breeding seasons south of the equator are mostly protracted if not continuous throughout the year, whereas annual breeding during the southwest monsoon is the rule around the periphery of the Arabian Sea. Exceptions are discussed.

Besides the high degree of endemicity in the Arabian Sea, the avifauna there contains, during the southwest monsoon, a high proportion of non-breeding migrants both from the southern hemisphere and the northern Pacific Ocean. In addition, several other species migrate within the Indian ocean concentrating off Arabia and in the Arabian Sea in the northern summer, at which time bird densities are many times higher than in the winter, or than in any area further south.

These regional differences can best be interpreted as the results of seasonal changes, acting through the food supply, which accompany the reversal of the monsoons, for these are most marked in the north. While it has not been possible to measure the seasonal changes in abundance of food organisms available to seabirds, the summer breeding and concentration of seabirds in the Arabian Sea occur at a time when the standing crop of zooplankton is highest. The unique Arabian Sea avifauna is presumably adapted to the seasonal changes.

INTRODUCTION

THE purpose of the present contribution is to trace the evolutionary and ecological effects on seabirds of the unique monsoonal changes that occur in the Indian Ocean. The area dealt with is that to the west of 80°E and north of the Tropic of Capricorn. Within this area climatic changes associated with the reversal of the monsoons are felt most strongly in the Arabian Sea, although south of the equator an intensification of the south-east trade-winds is noticeable during the northern summer also. Whilst the monsoons bring about immediate changes in the wind speed, rainfall, air temperature and humidity, it is the resultant oceanographic changes that have the greatest consequences on the intensity of organic production and thus on the marine communities. During the south-west monsoon between May and September, for instance, increased production due to upwelling leads to a substantial increase in

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organic production over a large part of the Arabian Sea (Wooster *et al.* 1967), but there is little evidence of a comparable enhancement either there or elsewhere during the opposite north-east monsoon. South of the Arabian Sea, the ocean is more characteristic of other tropical oceans, with a large anticyclonic gyre giving rise to the South Equatorial Current flowing westwards south of the equator throughout the year, though with some slight seasonal variation.

In this paper, four aspects of seabird biology are reviewed in the context of these broad seasonal oceanographic changes ; the marine avifauna, seabird breeding seasons, migration patterns and seasonal changes in the abundance of seabirds at sea. It is not proposed to deal fully with the sources of information on which this summary is based, but key papers are cited in the relevant places. The development of Indian Ocean marine ornithology is also reviewed by W. R. P. Bourne in another contribution to this symposium. Information on breeding seasons is taken from a paper, based on the published literature, in preparation.

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Species Composition

Oceanic Islands

The resident seabird species of the oceanic islands of the western Indian Ocean, i.e. those not on the continental shelf, are largely identical to those found in the tropical zone of the Atlantic and Pacific Oceans ; they are the species associated with warm oceanic areas throughout the world (Table 1). Within the western Indian Ocean, there is now little regional variation in the species that occur, though a number of extinctions may have changed the picture in the fairly recent past (Bourne, 1972). An example is the massive depletion of the seabird communities of the Mascarene Islands following colonisation by man (Bourne, 1968) and of a number of other islands due to exploitation of guano (Hutchinson, 1950), an important instance being the extinction of *Sula abbotti* on Assumption (Gibson-Hill, 1950 ; and Nelson, 1972.)

Excluding the islands in the Moçambique Channel, for which there is little information, the number of species apparently diminishes as one goes northeast until on the Maldives and Laccadives respectively only 11 and 5 species are known to breed (Betts, 1938 ; Mathew & Ambedkar, 1964; Phillips, 1963). This is the area most affected by the monsoons, though whether these are the reason for the small number is not altogether clear. The area, furthermore, is not well known and other species may have been overlooked.

The Mascarene Islands are richer in petrels (Procellarii) than elsewhere (Bourne, 1960), as might be expected from their proximity to the tropical convergence and the nearby subtropical surface water ; these include two endemic species. Besides the petrels, the only other species endemic to the oceanic islands of the Indian Ocean are Abbott's Booby *Sula abbotti*, now extinct in the area considered here, though still breeding on Christmas Island, and the Christmas Island Frigate-bird *Fregata andrewsi* not found in the western Indian Ocean ; an exceptionally well-marked race of tropic-bird *Phaethon lepturus fulvus* is also found there (Nelson, 1972). Of the remaining species, 13 also breed in both the Pacific and Atlantic Oceans, four in the Pacific only and one in the Atlantic only. There is

TABLE 1. *The breeding seabirds of the oceanic islands of the western Indian Ocean*

Species		Moçambique Channel	Aldabra Grp.	Mascarenes and Cargados Carajos Isles	Seychelles	Chagos	Maldives	Laccadives
Puffinus pacificus	P*	+		+	+	?	?	
Puffinus lherminieri	PA		+	+	+	+	+	?
Pterodroma aterrima	endemic			+				
Pterodroma arminjoniana	A			+				
Pterodroma baraui	endemic			+				
Phaethon rubricauda	P	+	+	+	+	?		
Phaethon lepturus	PA	+	+	+	+	+	+	
Sula abbotti	Indian Ocean endemic		+ (formerly)					
Sula dactylatra	PA		+	+	+			
Sula sula	PA	+	+	+	?	?		
Sula leucogaster	PA		+	?	+	?		
Fregata minor	PA		+	+		?		
Fregata ariel	PA		+	+			+	
Sterna dougalli	PA		+	+	+		?	
Sterna sumatrana	P		+		+	+	+	
Sterna anaethetus	PA		+		+		?	+
Sterna fuscata	PA	+	+	+	+	+	?	+
Thalasseus bergii	P	+	+		+	?	?	+
Anous stolidus	PA		+	+	+	+	+	+
Anous tenuirostris	PA			+	+	+	?	
Gygis alba	PA		+	+	+	+	+	
NUMBER OF SPECIES		6	16	16(+1?)	14(+1?)	7(+7?)	6(+6?)	4(+1?)

Notes.—* The first column refers to the species' extralimital distribution :

P, found in the Pacific Ocean ; A, found in the Atlantic Ocean. The seven areas are shown and named in Fig. 1

subfossil evidence, however, that *Puffinus pacificus* once bred on St. Helena in the Atlantic Ocean (Ashmole, 1963), and *Pterodroma arminjoniana*, *Pterodroma aterrima*, and *Pterodroma baraui* may be regarded as representatives (possibly even subspecies) of the Pacific species *Pterodroma heraldica*, *Pterodroma rostrata*, and *Pterodroma externa* respectively (Jouanin and Gill, 1967 ; Jouanin, 1970 ; W. R. P. Bourne, pers. comm.). Including these, over 80% of the breeding species have a worldwide distribution in tropical seas.

To summarise, the avifauna of the oceanic islands is essentially composed of tropical seabirds found in the other oceans. Bearing in mind the incompleteness of the information for most island groups, there appears to be a smaller number of species breeding north of the equator in the monsoon area.

The Continental Shelf

The species breeding in each major area, including the Red Sea and Persian Gulf, are listed in Table 2. Only eight of the 17 breed on the oceanic islands. Five of these are terns, one a petrel, and two are boobies. Thus, apart from the Sternidae, most species breeding on the oceanic islands do not breed on the shelf and are rare there even as non-breeding wanderers.

The other species breeding around the edge of the Arabian Sea are mainly distinctive Indian Ocean species, presumably evolved as a result of their isolation from similar areas elsewhere. *Phaethon aethereus* is unusual in that it breeds widely in the east Pacific and Atlantic Oceans, whereas it is confined to the north-western periphery of the Indian Ocean. *Thalasseus bengalensis* is confined to the Indian Ocean together with the Mediterranean and northern Australia.

Two of the Indian Ocean endemic species appear to be restricted to the upwelling areas and adjacent parts of the Arabian Sea. These are *Bulweria fallax*, a large recently described Indian Ocean representative of *Bulweria bulwerii* of the North Atlantic and Pacific (Jouanin, 1955), and *Phalacrocorax nigrogularis*. Others, such as *Larus hemprichi* and *Sterna repressa*, extend as breeding species south down the East African coast (Jackson, 1938).

In sum, the monsoon areas of the western Indian Ocean have a rather peculiar breeding avifauna, consisting of a few of the oceanic species (some of them distinct subspecies), and several endemic species. As in the well-known upwelling areas of the eastern boundary currents in the Atlantic and Pacific Oceans, there appear to be distinctive elements associated with the Arabian coast upwelling, including *Bulweria fallax* and *Phalacrocorax nigrogularis*, while the representative Sulid is *Sula dactylatra*, a pantropical species.

Migrants

Although seabird migration patterns are the subject of a later section of this paper, it is relevant here to consider the part that migrants play in the avifauna of each area. Excluding the numerous vagrant species that have been recorded in the southern part of the area considered, mostly in the southern winter, most migrants visiting the western Indian Ocean outside their breeding seasons concentrate in the north where they often complete their moult. They can be divided into three groups ; those from the south ; those from the north ; and those from the east. The vagrants consist mainly of subtropical or subantarctic species, such as the albatrosses, petrels, and prions that wander north into the subtropics during the non-breeding

TABLE 2. *The breeding seabirds of the islands on the continental shelf in the western Indian Ocean*

Species		East Africa	Gulf of Aden	Red Sea	South-east Arabia	Persian Gulf	India, Pakistan & Ceylon
Puffinus lherminieri	IPA*				?	?	
Bulweria fallax	endemic		?		?		
Phaethon aethereus	PA		+	+	?	+	
Sula dactylatra	IPA	+	+	+	+		
Sula leucogaster	IPA		+	+	?		
Phalacrocorax nigrogularis	endemic		?		+	+	
Larus leucophthalmus	endemic		+	+			
Larus hemprichi	endemic	+	+	+	?	+	+
Hydroprogne tschegrava	IPA			+		+	+
Sterna dougalli	IPA	+					+
Sterna repressa	endemic	+	+	+	?	+	+
Sterna anaethetus	IPA	+	+	+	?	+	+
Sterna fuscata	IPA	+	+		+		?
Sterna albifrons	PA	+	+	+	+	+	+
Thalasseus bergii	IP	+	+	+	?	?	+
Thalasseus bengalensis	Indian Ocean & Mediterranean endemic		+	+	?	+	
Anous stolidus	IPA	+	+		?		
NUMBER OF SPECIES		9	12(+2?)	11	4(+10?)	8(+2?)	7(+1?)

Notes.—* The first column refers to the species' extralimital distribution :

I, found on oceanic islands in the Indian Ocean ; P, found in the Pacific Ocean ; A, found in the Atlantic Ocean.

The six areas are shown unnamed in Fig. 1.

season (Bourne, 1960). Some, like the prions *Pachyptila* spp. and the Great Skua *Catharacta skua* appear to become quite widespread north of the tropic of capricorn, but never abundant (Morzer Bruyns and Voous, 1965 ; Voous, 1966 ; Bailey, 1968).

The four southern species that migrate into the northern Indian Ocean in large numbers are the Pale-footed Shearwater *Puffinus carneipes* and the White-faced Storm-petrel *Pelagodroma marina* which nest around south western Australia, and the Black-bellied Storm-petrel *Fregetta tropica* and Wilson's Storm-petrel *Oceanites oceanicus* from the Antarctic (Bailey, 1966, 1968; Bourne, 1960 ; Gibson-Hill, 1948; Morzer Bruyns and Voous, 1964; Roberts, 1940). *Fregetta grallaria* also appears to migrate north but whether in comparable numbers to those of *Fregetta tropica* is not yet clear (Cheke 1966 ; Bourne, 1970). The first four at least migrate north of the equator to spend their non-breeding season in the Arabian Sea, concentrating to moult along the south-east coast of Arabia, particularly in and around the upwelling area (Bailey, 1966, 1968).

Migrants from the north are those transcontinental migrants that breed in northern Asia and winter in the tropics. They include the Red-necked Phalarope *Lobipes lobatus*, the Pomarine Skua *Stercorarius pomarinus*, several gulls and about three terns. Most of these are coastal forms dispersing around the Arabian Sea during the northern winter.

A fairly recent discovery is that three species of petrels breeding in the Northwest Pacific migrate westwards into the Indian Ocean. *Oceanodroma monorhis* disperses in the Arabian Sea, probably in rather small numbers, *Oceanodroma matsudairae* concentrates on the equator, while probably smaller numbers of *Bulweria bulwerii* disperse in equatorial seas (Bailey, Pocklington and Willis, 1968).

With the possible exception of *Oceanodroma matsudairae*, and some migrants from the north whose winter distribution is not well-known, all the common non-breeding migrants to the western Indian Ocean spend their time north of the equator in the Arabian Sea. In this area, therefore, non-breeding migrants form a significant part of the avifauna, both in species and numbers of birds.

Breeding Seasons

Despite the fragmentary nature of the information on breeding seasons in the Indian Ocean, it is possible to draw some tentative conclusions about the variation of breeding seasons within the area considered here. A paper documenting the evidence available is in preparation. Below is a summary of the main conclusions.

In Figure 1 the predominant breeding regimes are shown for each main area in the western Indian Ocean. The evidence on which the pie diagrams are based is in many cases unsatisfactory and the proportions given indicate the most reasonable interpretation of the information at present available. The two categories of annual breeders include those species which appear to stop laying for a significant period at the same time each year. The third category includes species for which there is evidence of some laying at most times of year, and those which have been recorded laying at widely different times in different years. For some species in a few areas, it has been necessary to include in this category species that have been recorded at a number of stages of the breeding cycle (i.e., eggs together with fairly well-developed

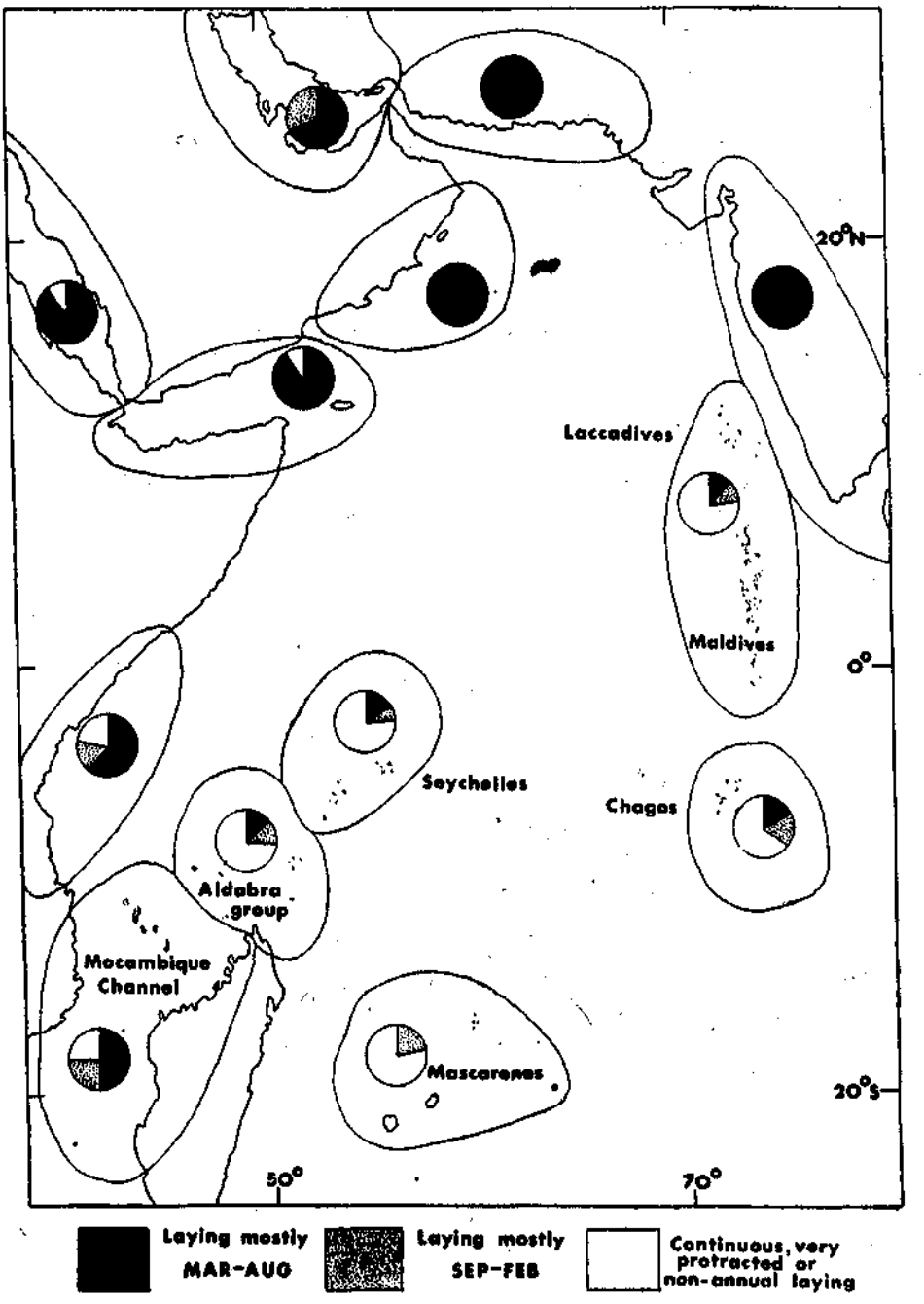

Fig. 1. Seabird breeding seasons in the Western Indian Ocean. The circles show the proportion of species attributable to each of three breeding regimes.

young) on a single visit to an island. This is clearly inadequate in itself, but in species like frigates and boobies with long incubation and fledging periods, it is indicative of a very protracted laying season. In a few instances recent visits to the islands concerned [notably Aldabra (Diamond, 1971), and Round Island, Mauritius (Gill, Jouanin and Storer, 1970)] have confirmed the existence of continuous laying throughout the year. As Snow (1965) has pointed out, laying throughout the year is likely to be found in birds with non-annual breeding cycles. It is clear that annual laying is commonest on islands along the continental shelf from the Moçambique Channel to Ceylon. There are, incidentally, few mainland colonies in this area. On the oceanic islands birds with a clearly-defined laying season at the same time each year form, in most areas, roughly a quarter of the species. The other species either lay over a very protracted season, or throughout the year, individuals possibly laying at non-annual intervals.

As Moreau (1950) pointed out, the northern summer is the main laying season along the whole east coast of Africa north of the Zambesi. Further east in the Persian Gulf and along the coast of India and Pakistan, laying tends to take place a little earlier. On the mid-oceanic island groups it is less easy to generalise, for the few annual breeders appear not to lay at the same season. Laying in the south of the area, on the Mascarene Islands, seems to reach a peak in the southern spring, although there are certainly some that lay at least over a very long period each year, if not continuously. Elsewhere within the tropics, there is remarkably little evidence of the expected switch from spring and summer laying in the north to (northern) autumn and winter laying in the south.

It is more illuminating to consider the variation of breeding seasons within particular species. Those restricted to the northern part of the Indian Ocean tend to lay in the spring and summer at all their known stations, examples being *Larus leucophthalmus* and *hemprichi*, *Sterna repressa* and *albifrons*, and *Thalasseus bengalensis*. Species also breeding in other areas, such as *Sterna anaethetus*, *Sterna fuscata*, *Thalasseus bergii* and *Anous stolidus* lay in the northern summer around the Arabian Sea, but often throughout the year on the oceanic island groups: while many of the pan-tropical species on the oceanic islands (e.g. *Puffinus lherminieri*, *Sula sula*, *Sterna fuscata*, *Anous tenuirostris*, and *Gygis alba*) tend to have protracted laying, indicating non-annual cycles at most of their oceanic stations, as in other areas [e.g. on Ascension Island in the Atlantic ('Ibis' 103b, 1962-1963)].

Some of the exceptions to these rules are interesting even if at present inexplicable. *Puffinus pacificus*, for instance, lays solely in the northern autumn at all its stations, which range in latitude from the Mascarene Islands (20°S) to the Seychelles (5°S). On the other hand *Sterna fuscata* has very protracted laying, possibly resulting from a non-annual cycle, at a number of the mid-oceanic stations and on Latham Island, East Africa (M. Gillham, pers. comm.), and may even breed twice a year on the Chagos Islands (Lalanne, 1962). On the Seychelles, however, it lays without exception in the northern summer, apparently timing its arrival at the breeding islands to coincide with the onset of the south-east monsoon, i.e. when the south-east trade-winds reach the latitude of the islands (Ridley and Percy, 1958). As mentioned above this species also breeds during the south-west monsoon in the Gulf of Aden (North, 1946) and possibly along the west coast of India (Abdulali, 1942), although not apparently on the Laccadive Islands, where laying has been recorded at completely different times of year in two different years (Betts, 1939; Mathew and Ambedkar, 1964). *Sula dactylatra* also appears to have an annual season along the Arabian coast, but laying there starts much earlier (in the spring) than in other

species. Furthermore, on islands off Socotra, laying seems to be very protracted (Ripley and Bond, 1966), as it is on many of the oceanic islands further south, so this species seems to be one of the few exceptions to the rule of strict summer breeding in the Arabian Sea. Lastly, *Sterna dougalli* lays predominantly in the northern summer and autumn at all its stations from the equator south to the Cargados Carajos Islands.

MIGRATION

The four main species of migrants from the southern hemisphere arrive in the Arabian Sea during May and leave between September and November (Bourne, 1960; Bailey, 1966). Thus, they are in the area for the duration of the south-west monsoon. There is some debate about the exact route that the migrants take, a clockwise migration having been postulated for *Puffinus carneipes* (Gibson-Hill, 1953). Recent observations, however, have indicated that at least part of the population of both this species and *Pelagodroma marina* take a fairly direct great circle route from Australia, passing the Laccadive and Maldive Islands, and no doubt giving rise to some of the reports of dark shearwaters offshore around the Maldive Islands (Phillips, 1963). Reports of *Oceanites oceanicus* in the northern spring suggest that these migrate north on a broad front (Bailey, 1968). In the autumn there are reports of large concentrations off Cape Comorin in southern India in early November (Phillips, 1954, 1955).

The ultimate destination of the four southern migrants is the northern parts of the Indian Ocean, particularly the Arabian Sea (Bailey, 1966). *Puffinus carneipes* appears to concentrate in and around the upwelling area off south-east Arabia, with smaller numbers scattered over the Arabian Sea. *Oceanites oceanicus* also concentrates along that coast, but it is not tied to the upwelling area and extends into the Gulf of Aden and the Red Sea, though only stragglers reach the Persian Gulf. Off Arabia it tends to keep fairly close to land, and further offshore there appears to be a zonation of the other two species of storm-petrels, with *Pelagodroma marina* occupying the area between 50-100 miles offshore and *Fregetta tropica* more scattered over most of the central Arabian Sea (Bailey, 1966, 1968).

In the northern autumn, even as early as August, phalaropes (almost entirely *Lobipes lobatus*) arrive in the Arabian Sea (Bailey, 1966) after a long overland migration from the northern Palaearctic Zone, during which an unknown percentage may halt on the Caspian Sea (Feeny *et al.*, 1968). They appear to arrive in the upwelling area off Arabia, but during the winter they concentrate in other areas, especially the Gulfs of Aden and Oman (Bourne, 1961). Large numbers of other northern gulls, terns and skuas also appear in this area at the same time, some of them probably migrating straight through the area to winter further south off southern Africa or India. *Stercorarius pomarinus* appears to remain in the northern Indian Ocean throughout the winter, whereas *S. parasiticus* probably passes through to winter off South Africa (Bailey, 1966).

There are also migrations of seabirds within the Indian Ocean area. Many of the species of terns breeding in the Red Sea and Gulf of Aden in the northern summer appear to leave for unknown destinations in the winter, examples being *Sterna repressa, S. anaethetus,* and *Thalasseus bengalensis.* Some may winter along the east coast of Africa or the west coast of India. Similarly, *Sterna fuscata* leaves

the Seychelles Islands after breeding but whether they migrate or simply disperse at sea is not known (Ridley and Percy, 1958).

Those species that concentrate in the Arabian coast upwelling area in the summer mainly leave in the winter. *Puffinus lherminieri* and *Phalacrocorax nigrogularis* apparently concentrate at this time at the mouth of the Persian Gulf [the latter breeding in the Gulf in the winter and early spring (Löppenthin, 1951)], and along the northern coast of Somalia (Bourne, 1961) where there appears to be upwelling during the north-east monsoon (Bailey, 1971). *Bulweria fallax* may disperse at sea at this time (Bailey, 1968; Gill, 1967) for flocks have been seen at the mouth of the Gulf of Aden and individuals in the southern Arabian Sea, while one was also collected in Kenya (Jouanin, 1957). It is likely that the winter records of dark petrels in the southern Red Sea (Smith, 1953, 1957) also belong to this species.

During the northern summer there is some evidence of a northward dispersal of some of the pantropical oceanic species into the Arabian Sea. Indeed a definite migration has been suggested for *Puffinus pacificus*, but the extent of this is not known because of the confusion caused by the still relatively recent discovery of *Bulweria fallax* (Jouanin, 1955, 1957), a species that is difficult to distinguish from *Puffinus pacificus* at sea. The few records of birds collected or captured suggest that *Puffinus pacificus* disperses northwards during the south-west monsoon, but not that it migrates to the Arabian coast upwelling area, where there are still no positive records (Bailey, 1966). Other species, such as *Sula sula* and *Fregata* sp., also appear to be commoner north of the equator at this season (Bailey, 1968).

Of the Pacific migrants there are still too few records to describe the migration of *Oceanodroma monorhis*. *Oceanodroma matsudairae* appears to be commonest in the equatorial zone with concentrations right on the equator during the south-west monsoon (Bailey, Pocklington and Willis, 1968), though Gill (1967) has records at other seasons which suggest that it occurs in the western Indian Ocean throughout the year.

From the above, it is clear that many species congregate in the north-western Indian Ocean during the south-west monsoon. Most leave during the north-east monsoon, while some concentrate in more localised areas such as off the northern coast of Somalia (Bourne, 1961; Bailey, 1971), in the entrance to the Persian Gulf (Bourne, 1961) and in the southern Red Sea (Smith, 1951, 1953). This pattern of migration is amply attested by the numerous reports of transects indicating a wealth of birds in the Arabian Sea in the south-west monsoon and a dearth in the north-east monsoon, except in those few areas mentioned above (e.g. Alexander, 1929; Norris, 1952; Phillips, 1947, 1950, 1954; and numerous unpublished observations in the files of the Royal Naval Bird-watching Society summarised in their annual reports published in '*Sea Swallow*').

Seabird Distribution and Abundance

From the preceding sections it is clear that the monsoon areas of the western Indian Ocean support a unique seabird fauna, rich in endemic species and migrant forms, many of which leave with the onset of the north-east monsoon (Bourne, 1963; Bailey, 1966). In this final section, it is proposed to consider the factors which cause these changes in the bird communities associated with the monsoons.

South of the equator the relatively seasonless environment is likely to provide similar conditions throughout the year, except perhaps locally at the boundaries of opposing surface currents, or where there is a surface current of fluctuating force impinging on an island, producing variations in the extent and intensity of local upwelling. Overall, however, there will probably be a constant and limited supply of food throughout the year, so that breeding is as likely to be successful at one time as at any other. In this area, continuous laying throughout the year or laying over a very protracted season appears to be the commonest type of breeding regime. The other consequence of stable conditions is that there is never likely to be a surplus of food available to support migrants such as those that reach the Arabian Sea during the south-west monsoon (cf. Moreau 1966 : 269).

While seasonless breeding occurs in a number of species in the Indian Ocean, especially those that feed mainly within about 50 miles of oceanic islands, *Puffinus pacificus* lays in the northern autumn at all its stations, while *Sterna fuscata* lays in the northern summer on the Seychelles and Amirante Islands and possibly other islands in mid-ocean. Both these species are pelagic, i.e. range over the whole ocean to feed, probably even while they are breeding (Ashmole and Ashmole, 1967). One may tentatively infer from this that the species which are most affected by seasonal changes are those that are most dependent on gross oceanic changes, as opposed to local, possibly unpredictable, changes around islands. From this it might be expected that *Sterna fuscata* would breed annually in all areas affected by the monsoons, yet the present evidence suggests that it may lay at non-annual intervals on the Laccadive Islands (Hume, 1876 ; Betts, 1939).

During the south-west monsoon, seabirds concentrate in the Arabian Sea and especially along the south-east coast of Arabia (Bourne, 1963 ; Bailey, 1966). It has been argued elsewhere (Bailey, 1966) that they are attracted by the increase in organic production resulting from wind-induced upwelling that occurs only at that season. Cushing (1971) lists this upwelling area as one of moderate importance in terms of the productivity of the ocean, partly because it is seasonal, unlike the great upwelling areas off Peru and south-west Africa. Upwelling also occurs at this season off the east coast of Somalia north of about 8°N, yet seabirds seem not to be as abundant there as they are off Arabia (Bailey, 1971). The reason for this is not entirely clear, though the upwelled water may sink or flow offshore before organisms suitable as food for seabirds, such as fish and squid, can develop or concentrate.

Cushing (1971) has reviewed the evidence that the biological effects of upwelling in the form of enhanced standing stocks of zooplankton can be detected much farther offshore (perhaps 2-300 km) than the physical limits of the upwelling areas. Thus, enhancement of organic production in the surface layers over much of the western Arabian Sea (as indicated by Ryther *et al.* 1966 and Wooster *et al.* 1967) may explain the general increase in the number of birds found in the Arabian Sea (as opposed to the upwelling areas *sensu strictu*) during the south-west monsoon.

Less is known about upwelling in other parts of the western Indian Ocean, though upwelling areas listed as of minor importance by Cushing (1971) are those off the Malabar coast of India during the south-west monsoon, a wedge north-west of Madagascar where the south equatorial current diverges to give the Somali and Agulhas currents, along the Baluchistan coast beginning in April, and off south-west India in September and October. As in other oceans there is also likely to be upwelling along the equator and in the equatorial current system. All the important upwelling known at present, however, occurs during the south-west monsoon.

Ornithological information for these areas is fragmentary and in some cases almost non-existent, but what little there is may be worth summarising. There is little information for the coasts of Pakistan and India, though the Persian Shearwater *Puffinus lherminieri persicus*, which is strongly associated with the upwelling area off Arabia, occurs along the northern coast of the Gulf of Oman (Bourne, 1961). As mentioned above *Oceanites oceanicus* has been recorded in large numbers off the southernmost tip of India in early November (Phillips, 1954, 1955) and this may be associated with the upwelling that occurs there at this time. There are a number of important seabird colonies on islands to the north of Madagascar including Aldabra, Cosmoledo, Farquhar and, before guano was exploited, Assumption (Hutchinson, 1950), one of the two original stations of the Indian Ocean endemic species *Sula abbotti*. The other station is Christmas Island lying close to an upwelling area off Java and Sumbawa (Wyrtki, 1962, Cushing, 1971, Nelson, 1972).

Upwelling north-west of Madagascar may also explain the occurrences of subantarctic seabirds (*Pachyptila* spp., *Diomedea melanophris*, *Phoebetria* sp. and *Macronectes giganteus*) in this area and along the East African coast (Bailey, 1968; Bednall, 1956; Moreau, 1942; Voous, 1966). Upwelling along the equator, for which there was some evidence on the 'Discovery' cruises (Royal Society 1965, quoted by Bailey, 1968), may also explain the concentration of *Oceanodroma matsudairae* there, though the concentration of *Puffinus pacificus* and *Gygis alba* at the northern boundary of the counter current in March 1964 (Bailey, 1968) is more likely to have been associated with a convergence which appears to concentrate food organisms (Ashmole and Ashmole, 1967).

There are a number of other areas where seabirds concentrate, namely the north coast of Somalia in the Gulf of Aden (Bourne, 1961; Bailey, 1971), the mouth of the Persian Gulf (Bourne, 1961) and the southern part of the Red Sea (Smith, 1951, 1953) during the north-east monsoon. Incidental observations of sea-surface temperature indicate that upwelling occurs at least in the first of these areas (evidence summarised by Bailey, 1971). Since in other parts of the Indian Ocean seabirds appear to be good indicators of the enhanced productivity associated with upwelling, it seems likely that these areas may re-pay further oceanographic investigation.

From the above it can be seen that upwelling with its concomitant high rate of organic production occurs in the northwestern Indian Ocean to the greatest extent during the south-west monsoon (Cushing, 1971). Since a number of species of birds are clearly tied to the upwelling areas (Bailey, 1966), it seems likely that it is this feature that controls the distribution and migration patterns, and the breeding seasons of many species of seabirds. Clearly many details still require to be elucidated, such as why breeding of some species is not seasonal in the Laccadive Islands. In the case of *Sula dactylatra*, which has a protracted breeding season even in the northern Arabian Sea, it is possible that it is some feature not dependent on upwelling, such as flying fish abundance (Bailey, 1966), that might release the populations from a rigid breeding season during the south-west monsoon. While the upwelling occurring during the north-east monsoon is on present evidence far less extensive, it may nevertheless be important in providing refuges with sufficient food to maintain those bird populations that remain in the Arabian Sea during the winter, notably *Puffinus lherminieri persicus*, *Bulweria fallax*, and *Phalacrocorax nigrogularis*.

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