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An Oceanographic Interpretation of Seabird Distributions in the Indian Ocean

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Abstract

When sightings of seabirds in the Indian Ocean are analyzed in conjunction with oceanographic data, the distributions of certain species and higher taxa show significant correlation with the temperature and salinity of the surface waters. Closely related species occur preferentially over different types of surface water. Characteristic associations of species were also found corresponding to surface water-types. Seabirds are not exempted by their mobility from the constraints of the marine environment.

Introduction

The purpose of this paper is to interpret pelagic distributions of seabirds in the Indian Ocean by relating them to the physical and chemical properties of the surface seawater. The large number of observations made during the International Indian Ocean Expedition (IIOE) plus other more recent data permit the analysis of seabird distributions in greater detail than was previously possible (Alexander, 1955; Bourne, 1963; Watson *et al.*, 1963).

Marine ornithologists (e.g. Murphy, 1936; Bourne, *in* Palmer, 1963; Ashmole, 1971; Shuntov, 1972; Watson, 1975) have used sea-surface temperature alone to define zones of surface water from which emerges a generally accepted division of seabirds into a pantropical fauna, a northern cool-water fauna, and a southern cool-water fauna (Serventy *et al.*, 1971). This simple treatment is inadequate in the Indian Ocean north of 40°S, where almost all the surface water for at least part of the year falls within their "Tropic(al) Zone". It should be more informative to follow oceanographic practice and consider surface water-types defined in terms of temperature and salinity combined, rather than by temperature alone, for by introducing salinity in conjunction with temperature, many more distinctive water-types are clearly definable (Scherbinin, 1967). This technique has been used to relate occurrence of sea organisms to the conditions under which they live (Bary, 1963; Fager and McGowan, 1963) and is here used to relate seabirds to the waters over which they are seen. It has to my knowledge been used only once before to interpret observations of seabirds: by Brown *et al.* (1975) in the Chilean fjords. Tropical seabirds should be good subjects for this analysis for they feed on prey at the surface of the ocean, deep-diving species being absent, and a clear distinction between pelagic and inshore species can generally be made (Diamond, 1978).

Sources of Data

Observations made during the IIOE by R. Pocklington, M. Palmieri, R.W. Risebrough, and P.R. Willis aboard R.V. "Atlantis II" and by others (listed in Table 1) were used in the analysis. In addition to the main body of IIOE data, observations of seabirds between Aden and Penang (Cheke, 1966), in the vicinity of the Chagos Archipelago (Bourne, 1971), the Gulf of Oman (Tuck, 1974), southeast of South Africa (van Zinderen Bakker, 1971) and off Western Australia (Aoyanagi, 1974) are included, as are seabirds of the Southern Ocean (Ozawa, 1967) when they fall within the designated area.

The nature and quality of environmental data given in conjunction with the seabird observations are uneven. Ocean-

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Table 1. Observations of seabirds during International Indian Ocean Expedition-IIOE (1961-1966). Latitudinal limits of observations are from 25°N west of, and 10°N east of 80°E to subtropical convergence at ca. 42°S (Orren, 1966). Longitudinal limits are from 20°E to 140°E north of, and 120°E south of, Australia. This is the Indian Ocean as conventionally defined, except that northern portion of Bay of Bengal and Andaman Sea is not included and Timor and Arafura Seas are

Vessel	Location[a]	Months	Data source	
			Ornithological	Oceanographic
"Discovery"	Arabian Sea	June-Aug. March, May	Bailey (1966)	Anonymous (1963)
	NW and SW	Aug.-Nov. Mar.-July	Bailey (1968) Bailey (1971)	Hamon (1967)
"Anton Bruun"	NW and SW	Jan.-Apr.	Gill (1967)	Anonymous (1965)
"Kampala"	Arabian Sea	May-June	Gill (1967)	Anonymous (1965)
"Umitaka Maru"	All quadrants	Dec.-Jan.	Ozawa *et al.* (1966)	Ozawa *et al.* (1966)
	Timor Sea, NE and SE	Nov.-Jan.	Ozawa and Nakamura (1966); Ozawa and Seno (1966)	Nasu and Shimano (1966)
"Atlantis II"	Red Sea, Gulf of Aden, NW and SW	Aug.-Nov.	Pocklington and Risebrough (1964); Pocklington (1965)	Present paper
	As above plus Gulf of Oman	Feb.-July	Bailey *et al.* (1968); Pocklington *et al.* (1972)	Present paper
	SE quadrant, Timor Sea	July-Aug.	Pocklington (1967)	Present paper
"Africana II"	SW quadrant	June-July June-July	Rand (1962) Rand (1963)	Orren (1963) Orren (1966)
"Akademic Berg" and "Seskar"	SE quadrant, Timor and Arafura Seas	Jan. May-July	Shuntov (1967) Shuntov (1972)	Rochford (1962) Rochford (1966)

[a] Limits of water bodies internal to Indian Ocean as defined by International Hydrographic Organization (Anonymous, 1976); quadrants refer to the equator and 80°E, the reference meridian of the IIOE (Wyrtki, 1971).

ographic data were recorded concurrently with seabird observations aboard "Atlantis II" and numerically coded for automatic data processing by methods akin to those of King *et al.* (1967), but this was the exception. The published records of Shuntov (1967, 1972), for example, are given in such a condensed form that only a general idea of the time and place of specific observations could be obtained. In such cases, sea surface temperature (T) and salinity (S) were interpolated for the appropriate location and time of year from the Oceanographic Atlas of the IIOE (Wyrtki, 1971). This procedure is less satisfactory than measurements made at the time, because of the smoothing introduced in data averaged monthly (T) or bimonthly (S) over one-degree squares, and some degree of refinement of interpretation is undoubtedly lost.

Classification of Water-Types

Temperature and salinity corresponding to all the ornithological observations were plotted and the surface water-types defined (Fig. 1). The salinity scale chosen is the reverse of the conventional arrangement (Sverdrup *et al.*, 1942), so that the T-S figure approximates a chart of the Indian Ocean with very high-salinity surface water to the left (west), low-salinity surface water to the right (east), highest temperature at the top (north), lowest at the bottom (south). The 900 pairs of T and S used are a representative subset for the Indian Ocean, as can be seen by comparison with the surface T-S diagram in the IIOE Atlas (Wyrtki, 1971) which is based upon ten times as many observations.

The most obvious feature of this T-S diagram is the wide range in salinity of

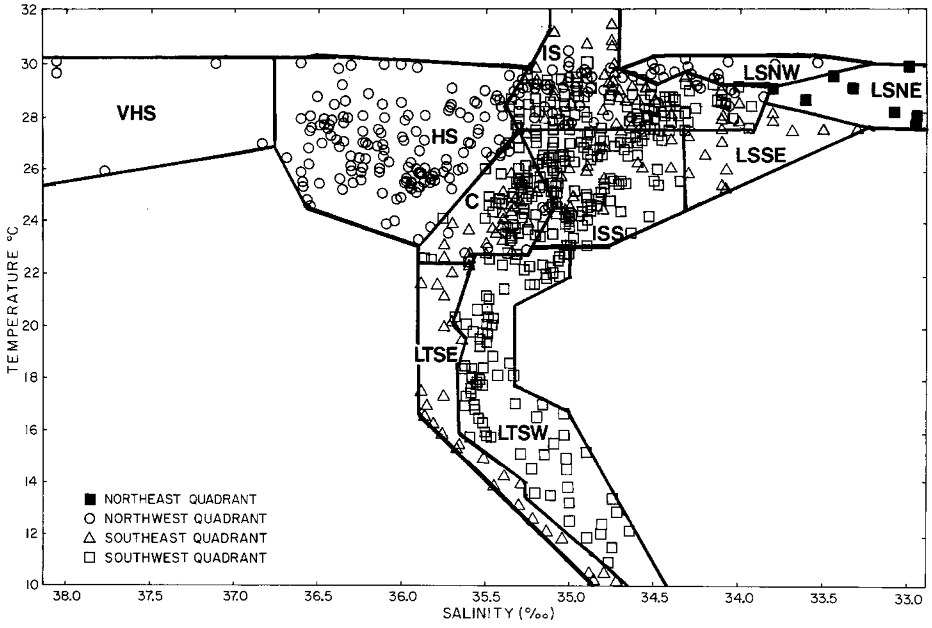

Fig. 1. Temperature and salinity of the surface waters of Indian Ocean. Envelopes enclose water-types described in the text

waters warmer than 23°C, and the narrow range of cooler waters, giving a rough "τ" shape to the figure. At the intersection of the two arms of the "τ", water from all quadrants except the northeast is represented. This is the "common denominator" of Indian Ocean surface waters and will be referred to as "common" (C) water. To the left is "high salinity" (HS) water, which occurs only in the northwest quadrant, and peripheral to this "very high salinity" (VHS) water, found only in the Red Sea and the Gulf of Oman (Laviolette and Frontenac, 1967). On the lower salinity side, "intermediate salinity" (IS) water is common to all quadrants, whereas "intermediate salinity south" (ISS) occurs only south of the equator. "Low salinity north west" (LSNW), "low salinity north east" (LSNE) and "low salinity south east" (LSSE) occur in their respective quadrants. The vertical leg of the "τ" comprises 2 low-temperature water-types, "low temperature south west" (LTSW) and "low temperature south east" (LTSE), found south of the equator in their respective quadrants. There is no year-round cool-water refuge north of the equator in the Indian Ocean (Serventy, 1953), but in July and August a water-type is found off the Somali coast (8°-12°N; 50°-54°E) with the same T and S characteristics as LTSW. Surface temperatures well below 23°C are encountered (to 13°C), while salinity remains within a narrow range (35.15 to 35.45‰). It is, however, a seasonal phenomenon of limited duration and extent, and the only water-type which appears and disappears although others wax and wane with the seasons. The use of geographically descriptive terms for the surface water-types as defined above (e.g. Arabian Sea water, southern subtropical water) was deliberately avoided. This is because there is marked seasonal change in the Indian Ocean (Gallagher, 1966) so that surface water-types, although they have continuity in time, are not necessarily found in the same location throughout the year (Fig. 2).

Relationship of Water-Types to Circulation

The surface water-types can be related to the circulation system of the Indian Ocean. The South Equatorial Current, which runs westward at all times of the year but with reduced intensity from October to November (Düing, 1970), corresponds largely to ISS in Fig. 2b, with low-salinity addition from LSSE east of 90°E. In southern summer (Fig. 2a) it is represented by the extension of LSSE west of 80°E and the body of IS to the west of this. The North Equatorial Current (0° to 8°N) also runs westward (IS north of equator in Fig. 2a), but fades out completely from May through November when its place is taken by the Southwest Monsoon Current which sets in the opposite direction. The Equatorial Counter-

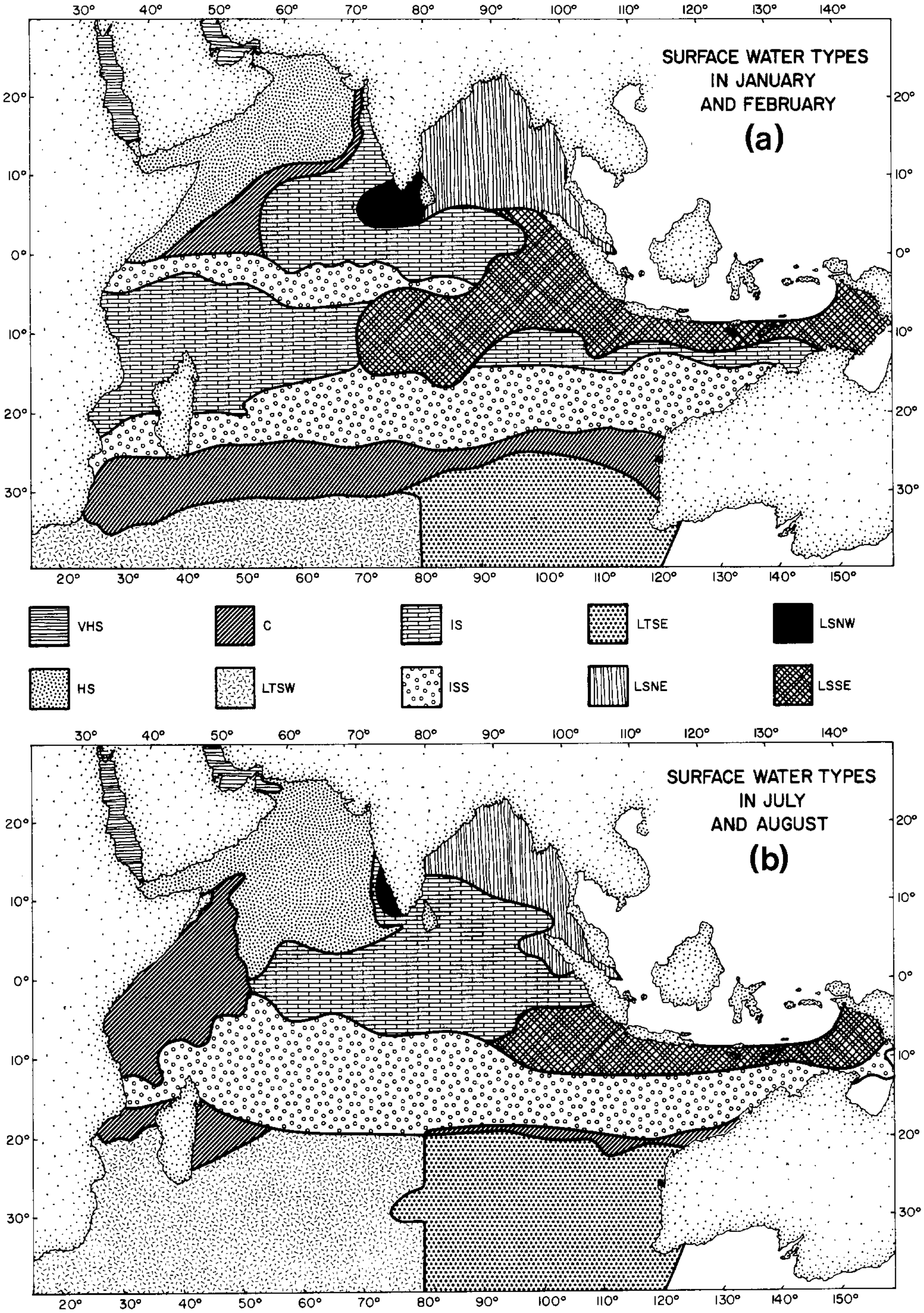

Fig. 2. Geographical distribution of surface water-types of Indian Ocean (a) Northeast Monsoon, and (b) Southwest Monsoon

current lies between these two, flowing east within a few degrees of the equator (ISS close to equator in Fig. 2a, IS at equator in Fig. 2b).

In addition to these analogues of the permanent currents of other oceans, there are the seasonal currents dependent upon the monsoon winds peculiar to the Indian Ocean. During the Northeast Monsoon (November-April), water moving strongly to the west, north of the equator and west of 75°E and flowing southwestward along the Somali coast, is known as the Northeast Monsoon Current (southwesterly extension of HS in Fig. 2a). During the Southwest Monsoon (May-September), a component of the South Equatorial Current crosses the equator off East Africa and flows northward supplying the northeast-setting Somali Current (northeasterly extension of C in Fig. 2b), then curves east over the central part of the Arabian Sea and southeast toward India (easterly extension of HS in Fig. 2b). The Southwest Monsoon drift extends across the whole ocean to Sumatra (extension of IS to east in Fig. 2b).

Table 2. Seabirds associated with low-temperature surface water-types (LTSE: low temperature south east; LTSW: low temperature south west). Number of sightings over each water-type is represented by following numerical classes: I = 1-3, II = 4-10, III = 11-30, IIII = 31-100; dash indicates species sought but not observed over water-type

Species	LTSW	LTSE
Diomedea exulans	IIII	III
Diomedea melanophris	III	II
Diomedea chlororhynchos	II	III
Diomedea chrysostoma	II	-
Diomedea cauta	III	-
Phoebetria fusca	III	II
Phoebetria palpebrata	II	I
Macronectes spp.	III	II
Daption capense	III	II
Pachyptila spp.	III	II
Halobaena caerulea	II	I
Pterodroma macroptera	III	II
Pterodroma lessoni	II	II
Pterodroma incerta	III	-
Pterodroma brevirostris	III	I
Pterodroma mollis	III	III
Procellaria aequinoctialis	III	III
Procellaria cinerea	II	-
Puffinus carneipes	I	I
Puffinus griseus	I	-
Puffinus gravis	I	-
Puffinus assimilis	I	I
Oceanites oceanicus	III	I
Fregetta spp.	I	I
Pelagodroma marina	-	I
Pelecanoides spp.	-	I
Moris capensis	II	-
Catharacta spp.	I	I
Stercorarius spp.	-	I
Larus dominicanus	I	-
Sterna vittata	I	-
Sterna fuscata	I	I

No. of unmatched pairs, u = 10 (12)
No. of matched pairs, n_{jk} = 11 (20)
Jaccard coefficient[a], S_j = 52 (63)

[a] Jaccard coefficient, $S_j = (n_{jk})/(n_{jk} + u)$, expressed as a percentage, indicates degree of similarity of avifaunas. The first value of S_j is based upon major occurrence over water-type (Class ≥ II), the second (in parentheses) after inclusion of minor occurrences (Class I). A value ≥ 63 is taken to imply identicality of faunas (Hagmeier and Stults, 1964).

Results

Distributions of Individual Species

Some comments upon individual species are necessary before proceeding to discuss multispecies associations. Species sighted only once over a water-type are excluded from analysis unless they are rare, e.g. Abbott's booby, *Sula abbotti*. A "sighting" indicates observation of a species over a water-type and may represent from one to thousands of individuals. The relative sizes of the symbols in Figs. 3-6 give an indication of numbers at each sighting.

There is a clear distinction between petrels (Fig. 3; Tables 2, 3, 4 and 5) which were observed only over the LT (low temperature) water-types (e.g. *Halobaena caerulea*, *Pterodroma lessoni*) or with records only from the warmer water-types (e.g. *P. baraui*, *Bulweria fallax*, *B. bulwerii*) and those (e.g. *P. macroptera*, *P. incerta*, and *P. mollis*) which, although mainly seen over LT water-types, extended their range over C and ISS. *Pterodroma* spp. gadfly petrels are essentially absent from the warmer and more saline waters of the Indian Ocean (although this may be historically recent; Bourne, 1974) in notable contrast to the situation in the Pacific Ocean where a dozen species of the genus range over such waters (King, 1967). Jouanin's petrel (*B. fallax*) and Bulwer's petrel (*B. bulwerii*) provide one of the best illustrations (Fig. 3a) of the use of T-S diagrams to rationalize the pelagic distributions of closely-related forms. The generally less abundant *B. bulwerii* was observed only over IS. Although *B. fallax* was also seen over IS, it was only the more saline (>34.5‰ S) portion of it. The majority of the records of this abundant species were from HS, in particular the colder portions. The absence of both species of *Bulweria* from the LT water-types most favoured by *Pterodroma* spp. is most striking, the two genera of gadfly petrels being essentially mutually exclusive in the Indian Ocean.

Storm-petrels (Fig. 4; Tables 2, 3, 4 and 5) were so wide-spread that few clear patterns of environmental preference emerged. Both Swinhoe's storm-petrel (*Oceanodroma monorhis*) and Matsudaira's storm-petrel (*O. matsudairae*) were absent from the "peripheral" water-types (LTSW, LTSE, LSNE and VHS). Only *O. matsudairae* occurred over C, ISS and LSSE water-types, *O. monorhis* being confined to the warmer portions of IS, LSNW and HS. Temperature seems to be the major determinant of distribution, *O. matsudairae* preferring cooler (25° to 29°C) waters than

Table 3. Seabirds associated with intermediate-salinity (IS) surface water-types. (C: "common" water; ISS: intermediate salinity south)

Species	C	ISS	IS
Diomedea exulans	II	-	-
Diomedea melanophris	II	-	-
Diomedea chlororhynchos	II	I	-
Diomedea cauta	I	-	-
Phoebetria fusca	I	I	-
Macronectes spp.	-	I	-
Daption capense	I	I	-
Pachyptila spp.	-	I	-
Pterodroma macroptera	I	I	-
Pterodroma incerta	I	I	-
Pterodroma brevirostris	I	-	-
Pterodroma mollis	I	I	-
Pterodroma baraui	?	I	-
Procellaria aequinoctialis	I	I	-
Procellaria cinerea	I	-	-
Bulweria fallax	II	-	II
Bulweria bulwerii	-	-	III
Puffinus carneipes	II	I	III
Puffinus pacificus	III	III	IIII
Puffinus assimilis	I	I	-
Puffinus lherminieri	III	II	III
Calonectris leucomelas	-	-	II
Oceanites oceanicus	II	II	III
Oceanodroma monorhis	-	-	II
Oceanodroma matsudairae	I	I	II
Fregetta spp.	I	I	II
Pelagodroma marina	I	I	II
Phaethon aethereus	I	-	-
Phaethon rubricauda	-	II	III
Phaethon lepturus	II	III	IIII
Phaethon lepturus fulvus	-	I	II
Sula abbotti	-	I	I
Sula dactylatra	I	II	II
Sula sula	II	II	III
Sula leucogaster	-	II	II
Fregata andrewsi	-	-	I
Fregata minor	-	II	III
Fregata ariel	II	II	III
Catharacta spp.	-	I	I
Stercorarius spp.	I	-	II
Lobipes lobatus	-	-	I
Sterna fuscata	III	IIII	IIII
Anous stolidus	I	I	III
Gygis alba	-	II	II

No. of unmatched pairs,	u = 10 (18)	u = 11 (18)
No. of matched pairs,	n_{jk} = 7 (21)	n_{jk} = 12 (20)
Jaccard coefficient,	S_j = 41 (54)	S_j = 52 (53)

Table 4. Seabirds associated with low-salinity surface water-types (LSNW: low salinity north west; LSSE: low salinity south east; LSNE: low salinity north east)

Species	LSNW	LSSE	LSNE
Puffinus carneipes	III	-	-
Puffinus pacificus	-	II	II
Oceanites oceanicus	I	II	-
Oceanodroma monorhis	I	-	-
Oceanodroma matsudairae	-	I	-
Phaethon rubricauda	-	I	I
Phaethon lepturus	II	I	II
Phaethon lepturus fulvus	-	II	-
Sula abbotti	-	I	-
Sula dactylatra	-	I	-
Sula sula	-	II	II
Sula leucogaster	-	I	-
Fregata andrewsi	-	I	-
Fregata minor	-	I	I
Fregata ariel	-	I	-
Stercorarius spp.	I	I	-
Sterna fuscata	II	II	I
Anous stolidus	-	I	I

No. of unmatched pairs,	u = 6 (7)	LS with ISS
No. of matched pairs,	n_{jk} = 7 (15)	
Jaccard coefficient,	S_j = 54 (68)	
No. of unmatched pairs,	u = 13 (9)	LS with IS
No. of matched pairs,	n_{jk} = 9 (18)	
Jaccard coefficient,	S_j = 41 (67)	

Table 5. Seabirds associated with high-salinity (HS) surface water-types (VHS: very high salinity)

Species	VHS	HS
Bulweria fallax	I	IIII
Puffinus carneipes	I	II
Puffinus pacificus	-	I
Puffinus lherminieri	II	III
Oceanites oceanicus	I	II
Pelagodroma marina	-	II
Fregetta spp.	-	II
Oceanodroma monorhis	-	I
Oceanodroma matsudairae	-	I
Phaethon aethereus	I	III
Phaethon lepturus	-	II
Sula dactylatra	I	III
Sula sula	-	I
Sula leucogaster	I	II
Phalacrocorax nigrigularis	II	II
Fregata ariel	-	I
Lobipes lobatus	II	III
Catharacta spp.	-	I
Stercorarius spp.	I	II
Sterna fuscata	-	III
Anous stolidus	I	I

No. of unmatched pairs,	u = 10 (10)
No. of matched pairs,	n_{jk} = 3 (11)
Jaccard coefficient,	S_j = 23 (52)

O. monorhis (27° to 30°C), which is probably a reflection of the fact that the latter is the warmest-water form of *O. leucorhoa*, whereas *O. matsudairae* belongs to a species group of generally cool-water forms (Austin and Kuroda, 1953; Kuroda, 1966).

The Phaethontidae were seen only over warmer waters (Fig. 5; Tables 3, 4 and 5). The red-billed tropic-bird *Phaethon aethereus* was predominantly the tropic-bird of HS and the only one over VHS. It did not occur over waters less saline than 35.2‰ S. It is quite clearly a species of high-temperature, high-salinity

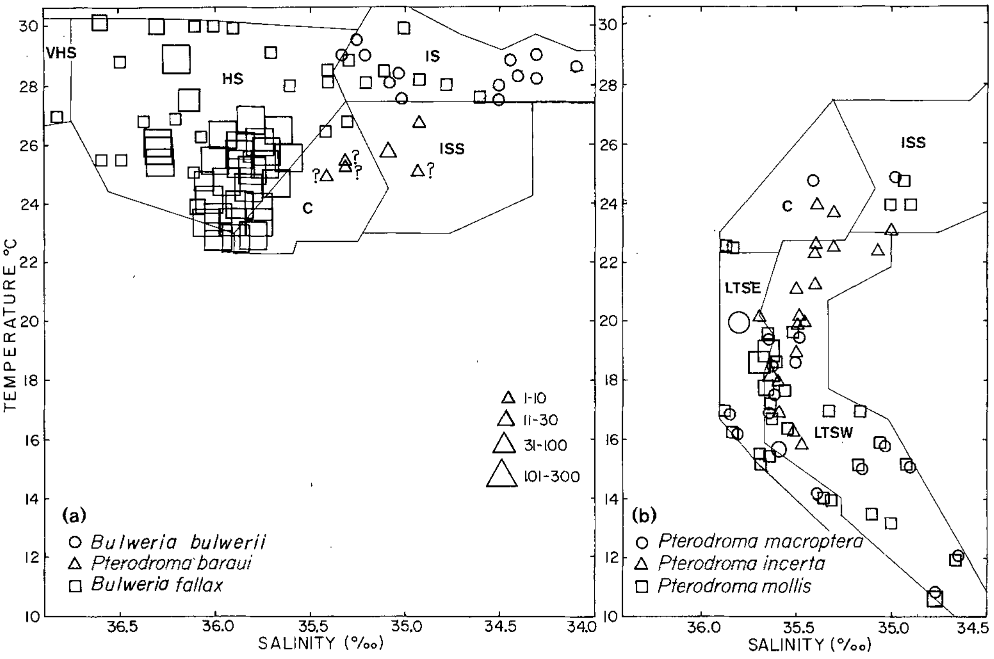

Fig. 3. Distribution of gadfly petrels in Indian Ocean. (a) Warm-water species; (b) cool-water species. Relative size of symbols in this and subsequent figures indicates approximate numbers seen over particular combinations of temperature and salinity

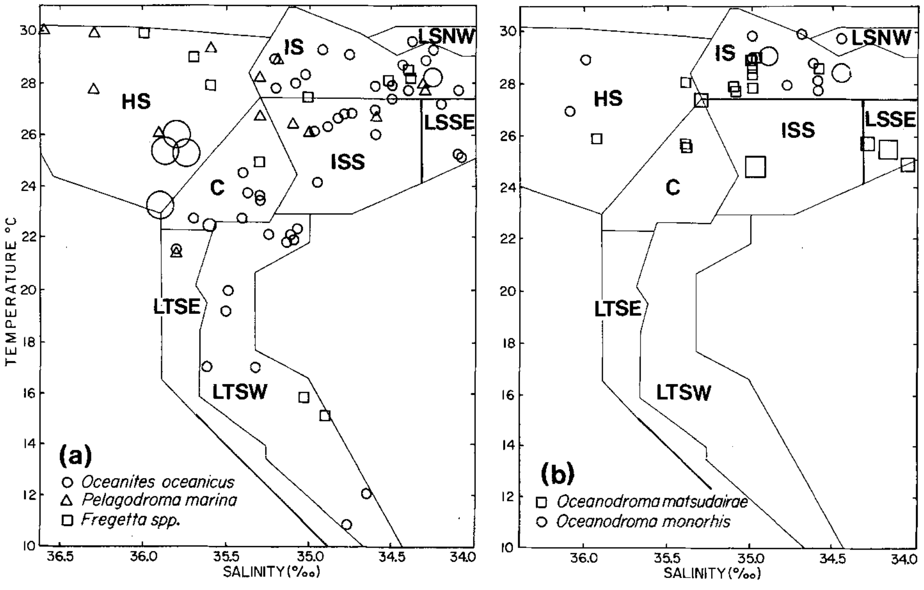

Fig. 4. Distribution of storm-petrels in Indian Ocean. (a) Wide-spread species; (b) warm-water species

affinities, maintaining a breeding population only in that part of the Indian Ocean with this combination of characteristics. In the Atlantic Ocean, this species also occurs only over waters of maximum salinity (Bialek, 1966; Cramp and Simmons, 1977). The red-tailed tropicbird *P. rubricauda* contrasts completely with *P. aethereus*, the distribution of the two nowhere overlapping, since *P. rubricauda* occurred only over lower salinity (<35.0‰) water-types. The white-tailed tropic bird *P. lepturus* was the most widespread tropic-bird, absent only from waters of highest salinity. The nominate race was most numerous over warmer (>27.5°C), less saline (<35.4‰ S) waters, the distinctive Christmas Island subspe-

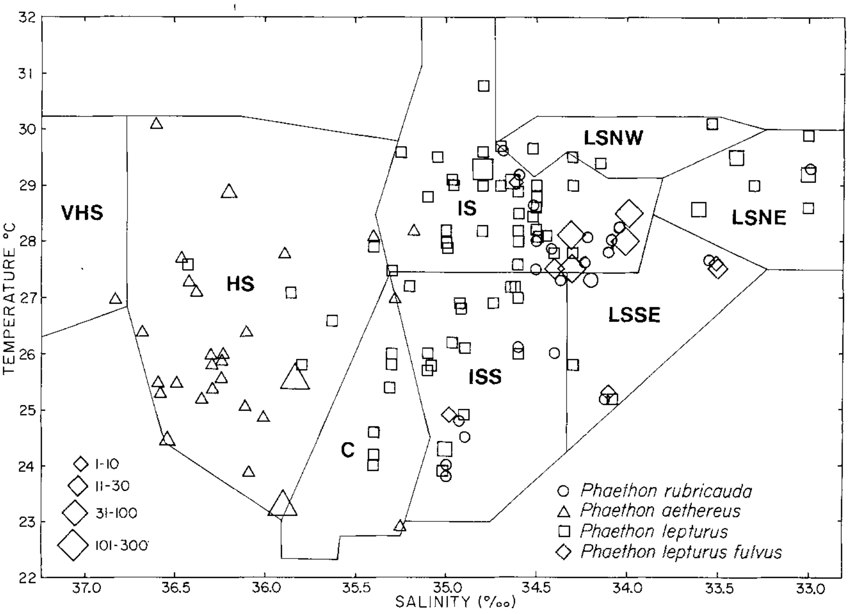

Fig. 5. Distribution of tropic-birds in Indian Ocean

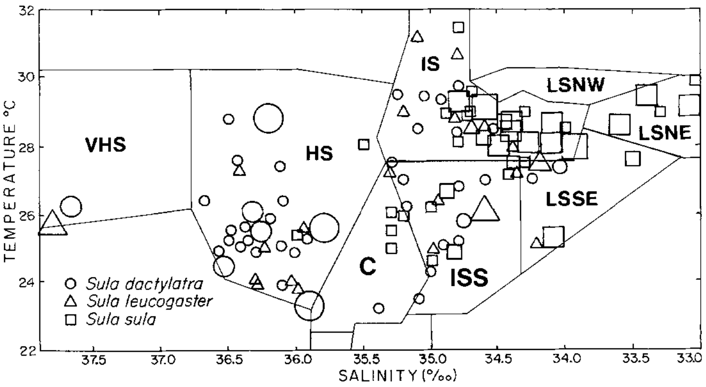

Fig. 6. Distribution of boobies in Indian Ocean

cies *P. lepturus fulvus* occurring over ISS, IS and LSSE. The most striking feature of the records of this eastern Indian Ocean race is that its T S preferences were identical with those of *P. rubricauda* in the western Indian Ocean.

The Cape gannet *Moris capensis* was the only representative of the Sulidae (Fig. 6; Tables 2, 3, 4 and 5) to occur over a low-temperature water-type (LTSW); the boobies were absent from such water-types, also from low-salinity water in the northwest quadrant (LSNW), most probably because this is relatively fresh and turbid water and hence unsuitable for their mode of fishing (Murphy, 1936). The brown booby *Sula leucogaster* was the most widespread species of booby, probably because it is the least pelagic (Cramp and Simmons, 1977). The blue-faced booby *S. dactylatra* was predominantly a species of HS; the sightings over that water-type are most likely assignable to the western Indian Ocean breeding population. The remainder of sightings over less saline water probably represent the eastern Indian Ocean population, which is doubtfully distinct from that of the western and central Pacific Ocean (Palmer, 1962). The red-footed booby *S. sula* was most numerous over the warmer, less saline waters which extend to the western and central Pacific where birds of the same subspecies breed (Alexander, 1955). Our records of Abbott's booby, *S. abbotti*, were from IS, LSSE and the warmer, less-saline portions of ISS (>27.5°C, <35.5‰ S). Water of these types extends in a band across the central Indian Ocean from the present breeding station at Christmas Island (Nelson, 1974) to the former breeding stations in the western Indian Ocean (Bourne, 1976) and surrounds the Chagos Archipelago where pairs of Abbott's booby were recently seen (Hirons *et al.*, 1976). There appears to be no restraint in the marine environment upon the distribution of this rare sulid.

Fregatidae (Tables 3, 4 and 5) were much more restricted in T-S preference than either the Phaethontidae or the Sulidae, there being no sightings over water <24.5°C or >35.5‰, i.e., all three Indian Ocean species show high-temperature, low-salinity preference. The Christmas Island frigate-bird *Fregata andrewsi* was confined to warmer (>28.5°C) waters of IS and LSSE. It was the most limited in T-S preference, as it is in breeding range. The lesser frigate-bird *F. ariel* was the only frigate-bird from HS and common water; the greater frigate-bird *F. minor* was the only representative of the family over LSNE. Other than this, separation of the two more abundant species on the basis of T-S is slight: some preference of *F. ariel* for more, and of *F. minor* for less, saline water is apparent, but more often than not the two species were seen together. They appear therefore to be sympatric in their pelagic distributions in the Indian Ocean as they are at many of their breeding stations, in contrast to the tropicbirds and boobies which appear largely allopatric in their at-sea distributions, even though they do share breeding stations.

This analysis of several families of seabirds shows that individual species can be related to the surface water-types through the medium of the T-S figure.

Distribution of Species Associations

The pelagic distributions of individual seabird species are rationalized by the hypothesis that they occur preferentially over particular surface water-types. Species can be grouped according to occurrence over the same surface water-types; first, the low-temperature assemblage of LTSW and LTSE (Table 2).

Seabirds associated primarily with the low-temperature assemblage are: the albatrosses, fulmarine petrels, prions, the blue petrel *Halobaena caerulea*, *Pterodroma* spp. gadfly petrels, *Procellaria* spp. shearwaters, three *Puffinus* spp. shearwaters (*P. griseus*, *P. gravis*, *P. assimilis*), the diving petrels, a gannet, southern skuas, a gull (*Larus dominicanus*) and a tern (*Sterna vittata*). The majority of these species breed south of the subtropical convergence (Watson, 1975), and were encountered at the northern limits of their range (Ozawa, 1967). The rest breed at the western margin (*Moris capensis*) or outside the Indian Ocean (*Diomedea cauta*, *Pterodroma incerta*, *Puffinus griseus*, *P. gravis*). The breeding seabirds of the Antarctic and sub-Antarctic have been recently reviewed by Watson (1975), who interprets marine distributions in terms of sea-surface temperature alone. He recognizes salinity differences between surface water-types (e.g. his "Australasian sub-Antarctic water"), but does not use this in analysis. Our observations shed light upon environmental preferences during the large portion of the seabirds' life-span when they are absent from their breeding grounds and foraging continuously at sea. Although capable of long-distance vagrancy (Gibson-Hill, 1953; Bourne, 1967), they are largely constrained within the LT water-types in the Indian Ocean.

The degree of association of multi-species groups with surface water-types can be quantified by calculation of Jaccard coefficients, S_J (Sokal and Sneath, 1963). This coefficient gives equal weight to matched and unmatched pairs but omits consideration of negative matches. Seabird species associated with the two low-temperature water-types are significantly different from those associated with the warmer water-types (C/LTSW/LTSE, S_J = 16%). Although the major occurrences over LTSW and LTSE deny identicality (S_J = 52%), the marine avifauna associated with LTSW is not significantly different from that associated with LTSE when all occurrences are included (S_J = 63%). The more-saline waters of the southeast quadrant share many but not all of the species of the less-saline southwest quadrant. This is largely because species breeding to the west (*Diomedea cauta*, *Pterodroma incerta*, *Puffinus gravis*, *Moris capensis*) and to the far south (*Diomedea chrysostoma*, *Phoebetria palpebrata*) are better represented over LTSW than LTSE. The major determinant is geographic. There simply are no islands north of the Antarctic continent and south of the subtropical convergence between 80° and 120°E. The predominant direction of surface currents and winds north of the subtropical convergence is not west-east as it is to the south of the convergence but east-west. This tends to keep species within the southwest quadrant. What tertiary production data there are for the area (Cushing, 1973) indicate little difference between LTSW and LTSE throughout the year, although in the centre of the southern subtropical anticyclone there is generally low primary production (Krey and Babenerd, 1976).

The other species from the LT water-types either have their centres of distribution over warmer surface water-types (*Puffinus carneipes* and *Sterna fuscata*) and were encountered at the southern edge of their range, or move regularly between the LT water-types and warmer water-types (storm-petrels and jaegers). The southern skuas (*Catharacta maccormicki* and *C. lonnbergi*) are occasional visitors to warmer surface water-types.

The intermediate-salinity assemblage of surface water-types consists of C, ISS, and IS (Table 3). Certain species appear to be confined to intermediate-salinity waters. The recently described Barau's petrel, *Pterodroma baraui*, represented by a few records over ISS from the vicinity of its only known breeding station at Reunion, is so imperfectly known that interpretation of its at-sea distribution is probably premature (Jouanin and Gill, 1967). Bulwers' petrel, *Bulweria bulwerii*, an Indo-Pacific breeding species, was recorded only from IS, as was the streaked shearwater *Calonectris leucomelas* from the western Pacific.

As indicated by the Jaccard coefficient, the species associations of ISS and IS are more similar (S_j = 52%) than those of C with ISS (S_j = 41%). There is a more abrupt change of marine avifauna on passing from C to IS (S_j = 35%). The intermediate-salinity assemblage has the highest total number of species (44) because its component surface water-types are interfaces between warmer and colder, and more and less saline waters. A greater variety of pelagic species can find a living for at least part of the year over waters of intermediate character. The areal extent of these water-types is also the greatest.

The low-salinity assemblage (Table 4) is the one for which records are poorest. To give a larger set for comparison, sightings over three surface water-types (LSNW, LSSE and LSNE) were combined as "low salinity" (LS) surface water-type. The extent of similarity between LS and ISS as measured by the Jaccard coefficient (S_j = 54%), exceeds that between LS and IS (41%). No species was encountered exclusively over this water-type assemblage for even Abbott's booby *Sula abbotti*, the Christmas Island tropic-bird *Phaethon lepturus fulvus* and the Christmas Island frigate-bird *Fregata andrewsi*, although breeding exclusively on an island within LSSE water-type, were observed over other surface water-types southeast and west of Christmas Island. Typically associated with low-salinity water-types are *Puffinus pacificus*, *Phaethon rubricauda*, *Sula sula*, *Fregata minor* and *Sterna fuscata*.

The high-salinity assemblage (Table 5) contains a high proportion of endemics, e.g. *Bulweria fallax*, *Puffinus lherminieri persicus*, *Phaethon aethereus*, *Phalacrocorax nigrigularis*, and visitors, e.g. *Lobipes lobatus Catharacta* spp., *Stercorarius* spp., as has been noted by Bailey (1974). The species assemblages of VHS and HS are not as similar (S_j = 23%) as IS and HS (S_j = 42%) or C and HS (S_j = 35%), indicating the relative ease of connection with less-saline over that with more-saline waters. The high-salinity assemblage has a strong "Mediterranean" or even "North Atlantic" aspect (Watson, 1966) in contrast to the Pacific affinities of the low-salinity assemblage (King, 1967).

Discussion and Conclusions

The highest total number of species (31) was seen over the ISS surface water-type, which corresponds largely to the South Equatorial Current of the conventional surface current systems. The maximum abundance of herbivorous copepods (Cushing, 1973), the greatest diversity of epipelagic euphausiids (Mauchline and Fisher, 1969), abundance of albacore (Suda, 1973) and yellow-fin tuna (Uda and Nakamura, 1973), and number of flying fish (Plomley, 1968; Shuntov, 1968) occur in this water-type. The South Equatorial Current extends across the Indian Ocean over a wide latitudinal range and is the most consistent current in the Indian Ocean north of 40°S, because it is located south of the region of monsoonal influence (Düing, 1970). A lower total number of species (27) was seen over IS. This surface water-type, warmer than ISS, occurs both north and south of the equator. It is not so readily identified with one particular current system, but contains elements of the Equatorial Countercurrent and the North Equatorial Current and Southwest Monsoon Current. The distinctive HS surface water-type ranks lower in total number of species encountered (21). It corresponds more or less with the area of the Indian Ocean of highest primary productivity (Krey and Babenerd, 1976), and may be the water-type over which the greatest concentrations of seabirds occur (Bourne, 1961; Bailey, 1966). The greatest diversity of seabird species, however, is clearly associated not with this most productive, but with the most persistent, surface water-types. This is in accord with the general ecological principle that regions with high species diversity also tend to have high environmental predictability and low variability (Slobodkin and Sanders, 1969).

No significant correlation could be found between numbers of any species, including the widespread and numerous sooty terns (*Sterna fuscata*), and the nutrient concentrations in the surface sea water. High nutrient concentrations indicate waters potentially productive, but high organic production is found in these waters only after they have been displaced in space and time from the area and the events of their formation (Blackburn, 1965). It is perhaps relevant that the coastal area of Somalia and southeast Arabia, where upwelling is located in the second and third quarter of the year, is characterized by poor long-line catches of tuna (Suda, 1973). The connection between upwelling and concentrations of birds is through their food, and is indirect because of time lags between peaks of production at different trophic levels.

That seabirds have a zonal pattern to their distribution related to latitude has been known for some time, and is generally attributed to progressive decrease in annual mean air and sea surface temperature between the equator and the poles. Variety of terrestrial habitat is readily discernible, and environmental constraints within the larger context of "tropical, temperate, boreal" are recognized. The ocean also has detailed structure and offers variety of habitat just as the land. Surface water-types, as defined by temperature and salinity, are a simple indicator of different "habitat" in the oceans.

The T-S relationships are used here only as a convenience; the important thing is the associated marine community which provides the birds with their food and of which the birds are part. Different potential prey species are known to be associated with the different water-types. Two examples illustrate the point. In the genus *Euphausia*, the "*distinguenda*" group are crustaceans of C and HS, and "*diomediae*" of IS as well; *breviso* appears to be confined to ISS, *paragibba* ISS, and *recurva* to LTSW (Brinton and Gopalakrishnan, 1973). At a higher level in the food web, the yellowfin tuna *Thunnus albacares* are caught mainly in C, ISS and IS, the albacore *T. alalunga* in LTSW and ISS, and the southern bluefin *T. thynnus* in LTSW, ISS and IS (Suda, 1973). These, in driving their prey to the surface, make it available to pelagic seabirds. What little is known of the comparative feeding ecology of tropical seabirds (Ashmole and Ashmole, 1967) confirms these associations.

The T-S diagram is a more sophisticated approach to understanding the at-sea distributions of seabirds than temperature (latitude) alone. The use of salinity in addition to temperature as an environmental variable makes possible interpretation of pelagic distributions of seabirds along the same lines as other marine organisms. Although seabirds are more difficult to correlate with water-types than are plankton, because they are more mobile and may not be actively feeding when observed, they are well-known taxonomically and are visually observed more readily than the smaller fauna of the ocean. I hope someone will test the validity of associations of seabirds with surface water-types in oceans other than the Indian. Echoing Bourne (1963), Brown (1976), and others, bird observers aboard oceanographic vessels are urged to record environmental data at the same time as their seabird observations. To demonstrate relationships between seabird species and water-types concurrent oceanographic and ornithological observations are required.

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