Studies on terns with particular reference to feeding ecology

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STUDIES ON TERNS WITH PARTICULAR REFERENCE TO FEEDING ECOLOGY

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ABSTRACT

Four species of sea terns in the genus Sterna were studied primarily to determine how they differed in strategies used to exploit available food, and to identify factors that influenced their success in obtaining it. Where the four species coexisted during the breeding season, interspecific differences were found in feeding dispersion, dive height, immersion time, use of 'contact-dipping' and size of prey taken. These variations should alleviate competition for food, and therefore facilitate coexistence.

The food-robbing behaviour exhibited by Roseate Terns on Coquet Island was examined. The intensity and success of attacks were correlated with the density of "host" terns. Fish size affected the likelihood of attack, and of robbing success.

Several variables were found to influence rates of fish capture at sea. Feeding rates contained both diurnal and tidal patterns, the latter corresponding with tidal variations in the rate of fish capture in the littoral zone. In Africa, first-winter Sandwich Terns were less successful than older birds at catching fish, suggesting that foraging skill is acquired gradually. An assessment of weather factors influencing fishing success and growth rates of chicks indicated that windspeed and/or sea surface disturbance increase to levels that optimise fishing ability of inshore-feeding terns, after which their effects become detrimental.

The inimical effects of paralytic shellfish poisoning on the breeding success of terns in 1968 are described.

Analysis of the composition of tern eggs demonstrated significant differences between the terminal egg and the prior egg(s) of any laying sequence.

The adaptedness of terns to a variable food supply is discussed with reference to other predator-prey systems. Hypotheses for the causation and function of deferred maturity in birds and other animals are assessed in relation to the slow acquisition of foraging skills by Sandwich Terns and some other seabirds.

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INTRODUCTION

BACKGROUND AND AIMS

When the basic trophic structure of biotic communities was first perceived, great interest centred on unravelling the ways in which the system functioned. In particular, biologists were interested in what regulates the numbers of animals, and predators were seen as an important cause of fluctuations in prey animals (e. g. Elton 1924, 1925). At the same time, the dynamics of predator-prey interactions attracted the attention of theoreticians like Lotka (1925), Volterra (1926) and Nicholson and Bailey (1935). As Elton (1935) pointed out, however, their mathematical models tended to outstrip contemporary knowledge of biological systems. Since then, the balance has been redressed by widespread field research in which predator-prey systems have increasingly been studied as components of community relationships, such as inter- and intra-specific competition, species diversity, and energy flow.

In all these studies, we are basically concerned with the adaptedness of the predator or its prey to the environment, and in terms of the predatory process, this means the efficiency of finding and capturing prey, or the efficiency with which prey animals evade capture. Since behaviour can be thought of as the "mechanism" by which adaptations to the environment are forged and maintained (Nelson 1970), an interpretation of the survival value of any predatory behaviour requires the following questions to be answered: What kinds of strategies does the predator employ and which factors determine the choice and effectiveness of these strategies in yielding prey? Answers have been sought through mathematical descriptions, field observations, and laboratory experiments and the results have been extensively reviewed in the literature (Andrewartha and Birch 1954, Carriker 1955, Varley and Edwards 1957, Holling 1961, Edwards 1963, Solomon 1964, Salt 1967, Royama 1971). This study is presented as a contribution to these fundamental questions concerning predator-prey systems, and has been based on field observation.

Many of the relevant studies have concerned landbirds in field situations, since avian predators are often conspicuous and their prey can be readily sampled. Various workers, notably Orians (1961), Verner (1965), Root (1967), Royama (1970) and Gill (1971) have demonstrated the intricate behaviours that tend to optimise the efficiency with which available prey resources are utilised. But while landbirds, and especially passerines, seem to offer immediate advantages as subjects for study, there are equally obvious disadvantages. The birds are often small and cryptic, making foraging behaviour difficult to observe in vegetated habitats. Furthermore, individuals are often widely dispersed and an inevitable temporal and spatial factor enters into inter-individual comparisons. Seabirds may at first seem to be unlikely contenders for a study of predatory behaviour, but they show certain characteristics that eliminate some of the difficulties cited above. Firstly, seabirds frequently breed in dense aggregations so that numerous individuals are susceptible to study, often in the same place and at the same time. Moreover, the birds are often large with conspicuous markings, and usually feed in exposed places which offer unobstructed views of foraging behaviour. The major item on the debit side is the difficulty of adequately quantifying the behaviour and availability of prey, but despite this impediment, a great deal can be inferred from observing the responses of the birds themselves.

For these, and other reasons, this study was concerned with four closely related species of terns, namely the Sandwich Tern Sterna sandvicensis Lath., Roseate Tern S. dougallii Mont., Common Tern S. hirundo L., and the Arctic Tern S. paradisaea Pont. These species differ in body size (the Sandwich Tern is the heaviest, being twice as heavy as the Arctic Tern which is the lightest) and some differences in feeding methods have been indicated (Marples and Marples 1934). They obtain the bulk of their food at sea, although they also forage in rivers and inland water bodies. Their main prey are fish which are caught by a skilful air-to-water plunge diving technique. While serious logistical problems attend the study of many seabirds at sea, these Sterna species often forage within sight of land and therefore present outstanding opportunities for observation. Although they are highly mobile predators, they usually quarter an area of sea rather slowly as they hunt, and so continuous surveillance of individuals is frequently possible. Since the conspicuous black cap on the head points downwards when the tern is hunting, and forwards when it is flying in transit, it is an easy matter to decide when a tern is definitely searching for prey. Lastly, since they swallow prey in the air after emerging from the water, the success of the attack, as well as the size and even the kind of prey taken, can usually be determined.

By any standards, plunge diving for fish at sea is a complicated way of obtaining food. Firstly, there is the problem of locating appropriate prey animals which may be patchily distributed and are partially hidden by the surface layers of the sea. A prey animal may be too deep for the tern to catch and even if it is not, a considerable degree of judgment and skill would seem to be necessary if the tern is to catch it. The specific demands of capturing submarine prey inevitably channel terns along a path of specialisation and it was of special interest to assess how this tendency in the Sterna species reconciled with the need to retain a measure of adaptability to a variable food supply.

Ashmole and Ashmole (1967) have described the attack style as "plunging to surface" which emphasises that these birds are dependent on the uppermost layer of the water column for food. Most fish are certainly captured within one metre of the surface. Despite the limited dimensions of the zone in which food is available to "impetus" divers like terns, several species have evolved methods of exploiting it. Ashmole and Ashmole (1967, 1968) and Ashmole (1968) have described the diversity of feeding behaviour within various species of tropical terns which enables them to share out the surface food supply without apparently incurring strong competition for it. Surprisingly, the feeding techniques of palearctic Sterna species have not previously been critically examined from this point of view. Even less is known about the factors that influence hunting success, although two recent studies have described certain effects of tidal changes (Boecker 1967) and the sizes and density of prey (Salt and Willard 1971).

The primary aim of this study was, therefore, to examine, by direct observation of foraging behaviour, the ways in which four tern species with an apparently similar diving technique, exploited a food supply that was potentially variable in both space and time. Secondly, some of the factors that influenced their hunting success were sought and investigated. Each species breeds to a varying extent in the palearctic and the location—Coquet Island, Northumberland—used for this study supported breeding populations of all four, allowing simultaneous comparison of foraging activities in the summer season. The project was partly stimulated, and greatly enhanced, by a comparative study of the breeding biology of the same four species at Coquet Island between 1965 and 1967 (Langham 1968). The results of this work, in turn, reinforced many of the findings of Pearson's (1964, 1968) investigation of the feeding ecology of various seabirds, including Sandwich, Common and Arctic Terns on the nearby Farne Islands. These two studies exemplify the insight that can be gained into the feeding relationship of seabirds by confining observations to the breeding colony. However, the causation of various phenomena observed at colonies, such as day to day variations in the growth rate of chicks, can only be surmised in the absence of first-hand knowledge of foraging behaviour, and the need for direct observations at sea has been emphasised by both Pearson's and Langham's work.

The four tern species migrate to various parts of the southern hemisphere during the north temperate winter and the study also included observations of Sandwich and Common Terns in tropical West Africa. As has been indicated, plunge-diving is a skilful technique and the principal objective of the fieldwork in West Africa was to compare the fishing ability of first-winter Sandwich Terns with that of older birds to determine how much foraging expertise the young birds had acquired in the 7-9 months since fledging. Ashmole (1963) considered that young birds are inefficient at obtaining food and are at a competitive disadvantage with experienced and more efficient adults. Ashmole and Lack (1954, 1966) have suggested that the presumed inexperience of young birds at obtaining food is largely responsible for retarding sexual maturity until such time as breeding can be attempted without undue risk to personal survival. The results of the study made in Sierra Leone have a bearing on these, and other hypotheses, concerning the significance of deferred maturity which is considered in the final discussion.

STUDY AREAS

The Northumberland coast is noted for the large numbers of seabirds it supports, notably on the Farne Islands and on Coquet Island. The major part of this study was made between 1968 and 1970 on the latter island which is situated at 55° 20'N, 1° 32'W (Nat. Grid Ref. NU 293045) but considerable use was also made of the adjoining coastline (Figure 1). The Farne Islands and Coquet Island are 32km (20 miles) apart and provide major breeding stations for terns summering on the eastern seaboard of England. Apart from a few Common Terns nesting at Teesmouth, the nearest major tern colonies to Coquet Island are in Norfolk (296km = 185 miles south) and the Firth of Forth in Scotland (112km = 70 miles north).

Coquet Island lies about 1.4km (¾ mile) offshore and about 2km (1½ miles) from the mouth of the River Coquet at Amble. The island consists of a level plateau which rises no more than 10m above sea level. It has an area of almost 7 ha (17 acres) most of which is covered by low-lying vegetation, mainly _Festuca ovina_ and _Rumex acetosa_ (Figure 2). The substratum is sandstone and a combination of sea erosion and early quarrying activities has led to the formation of extensive shelves of rock which, when exposed at low tide, represent an area about twice that of the vegetated plateau. The rocky perimeter extends in most places right up to the scarped edge of the plateau but is interrupted on the east side by several boulder beaches and, on the south side, by a sandy beach characteristically fringed with Marram Grass _Ammophila arenaria_.

On the south-west corner of the island are situated the lighthouse and its grounds which occupy about 0.3 ha. Immediately outside the grounds, about 1.2 ha (3 acres) are densely covered with Stinging Nettle _Urtica dioica_ which are avoided by nesting terns. _Urtica_ is steadily encroaching on ground formerly occupied by _Festuca_ and now covers about twice the area it did in 1965. The remaining parts of Coquet Island, comprising about 5.5 ha (13 acres), are available as potential nesting areas.

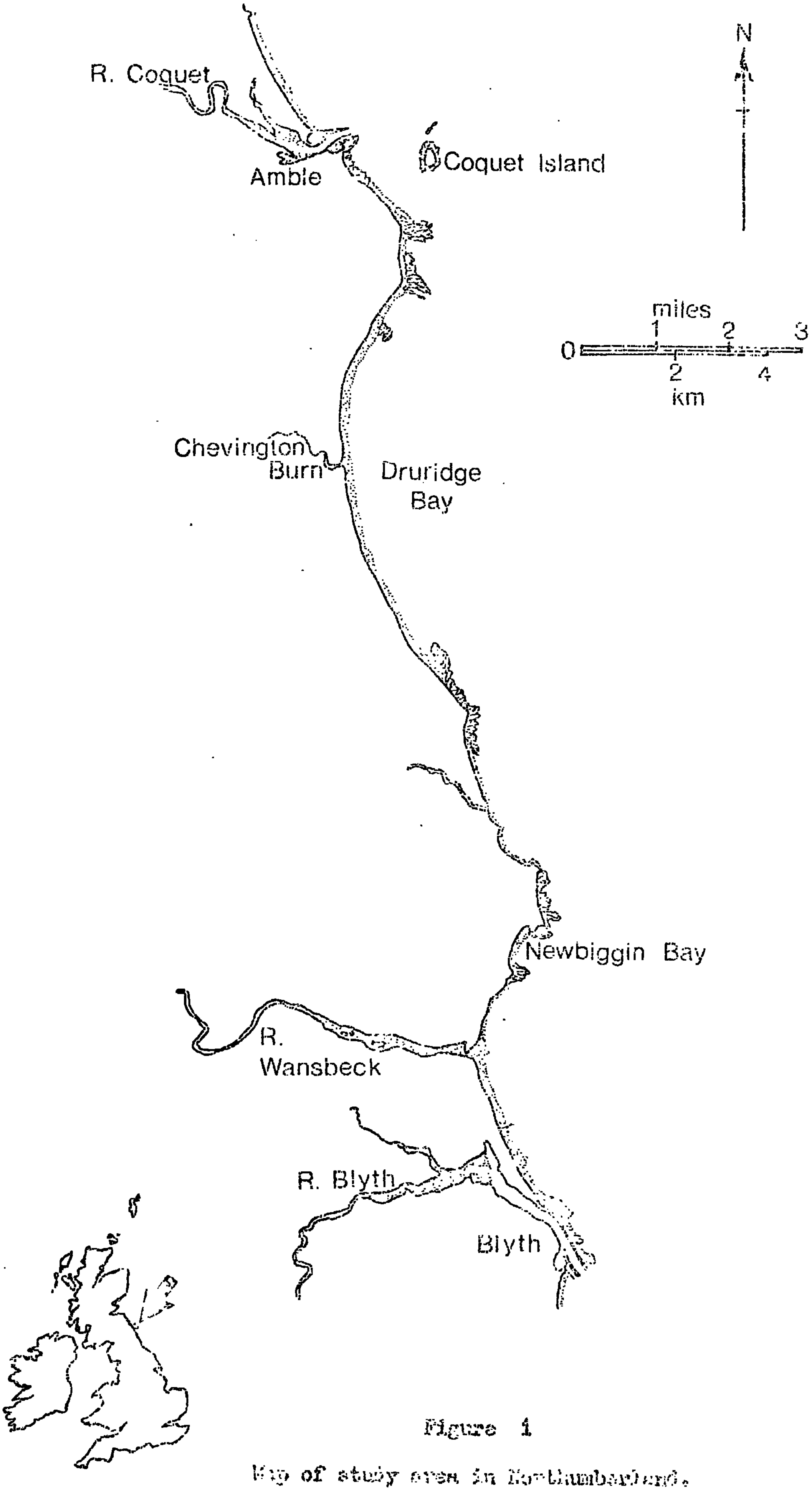

Figure 1

Map of study area in Northumberland.

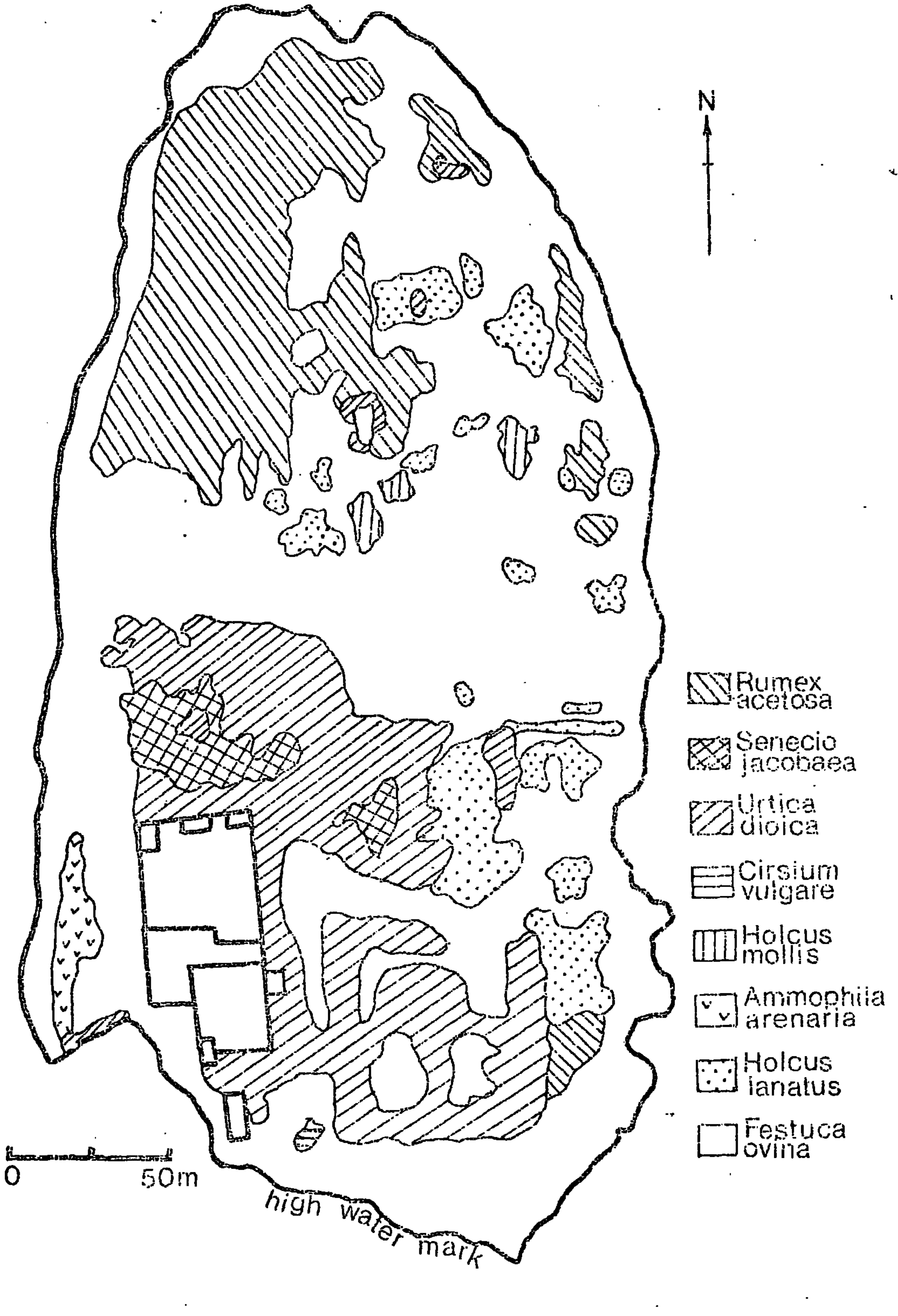

Figure 2

Map of Coquet Island, showing dominant vegetation types (modified from Langham 1968).

The study also embraced much of the coastline on the mainland west of the island. Here, the outstanding features are two large sandy bays, one (Alnmouth) to the north of Amble and the other (Druridge) to the south. In the headland between these two bays, the River Coquet emerges through a relatively short and narrow estuary. Druridge Bay extends south for about 8km (5 miles), after which there is a succession of rocky outcrops, the most prominent of which occurs at Newbiggin-by-the-sea (G. R. NU 3188). Between Newbiggin and Blyth, the shore is again mainly sandy and this is due partly to the delta of the River Wansbeck. Blyth is 23km (14½ miles) from Coquet Island and it represented the southerly limit of the study area (Figure 1). The known history and recent status of the various tern species is summarised in Appendix 1. In addition to the terns, Coquet Island also supports a small colony of Black-headed Gulls Larus ridibundus, about 250 pairs of Eider Ducks Somateria mollissima and an estimated 200 pairs of Puffins Fratercula arctica. Since 1967, 2-3 pairs of Herring Gulls Larus argentatus have usually attempted to breed but their nests and eggs have been systematically destroyed to prevent this species from becoming an established breeder. In 1970, two pairs of Fulmars Fulmarus glacialis laid clutches on the west side of the island but unfortunately the eggs disappeared before they could hatch. Nevertheless, this was apparently the first recorded breeding attempt by Fulmars on Coquet Island and certainly the first attempt since 1957 when regular checks on the breeding species were started. Other species nesting in small numbers include Oystercatchers Haematopus ostralegus (10-12 pairs), Ringed Plovers Charadrius hiaticula (3-4 pairs), Shelduck Tadorna tadorna (1-2 pairs), Skylarks Alauda arvensis (3-4 pairs), Rock Pipits Anthus spinoletta petrosus (10 pairs) and, in some years, the odd pair of Starlings Sturnus vulgaris, Blackbirds Turdus merula, and Swallows Hirundo rustica.

A study was also made between January and March 1970 at various places on the coast of Sierra Leone, West Africa, mainly in the Freetown Peninsula between 8° 10' - 8° 30'N and 13° 10' - 13° 18'W, and at Tissana on Sherbro Island (7° 34'N, 12° 56'W). This stretch of coastline, which consists of sandy beaches, rocky shores, and mudflats fringed by Mangroves *Avicennia nitida* and *Rhizophora harrisonii*, is part of the wintering area in West Africa of many of the Sandwich Terns (Muller 1959, Langham 1971) and Common Terns (Langham 1971) reared in western Europe. At the time of the study, the African Royal Tern *S. maxima albidorsalis* and Black Tern *Chlidonias niger* were also numerous along the coast of Sierra Leone while Caspian Terns *Hydroprogne caspia*, Gull-billed Terns *Gelochelidon nilotica* and Little Terns *S. albifrons* (probably the West African race '*guineae*') were present in small numbers. Grey-headed (= Grey-hooded) Gulls *L. cirrocephalus* and Lesser Black-backed Gulls *L. fuscus* and the occasional Pomarine Skua *Stercorarius pomarinus* also formed part of the wintering seabird community.

SECTION I

PATTERNS OF FOOD EXPLOITATION

This section deals with the ways by which the different tern species utilise available food resources. Part 1 describes the dispersion of terns within the feeding grounds, the methods they use to catch prey, and the sizes of prey they take. Part 2 presents a detailed account of the specialised food-robbing behaviour exhibited by Roseate Terns.

PART 1. Interspecific variation

Introduction

There is now considerable evidence that closely related species can coexist by partitioning environmental resources so that competition for them is avoided or at least mitigated. In his recent review, Lack (1971) argued that this resource division is achieved through divergent ecology of the species involved and he cited differences in range, habitat and feeding as the principal mechanisms of segregation. The nature of interspecific variation in food selection has been described by Hinde (1959) who recognised that differences could occur in (i) feeding habitats (ii) location of feeding within a given habitat (e. g. vertical stratification of feeding zones in certain Paridae) (iii) size of food items taken (iv) kinds of food taken.

Two studies (Pearson 1968, Langham 1968) in Northumberland have already examined the possibility of competition between Sterna species during the breeding season and some of the factors that might prevent it occurring. On the Farne Islands, Pearson found considerable overlap in both the size and species of prey taken and in the distance of foraging trips; he concluded that food was superabundant in the breeding season and that competition for it was unlikely (cf. Lack 1946, Salomonsen 1955). On Coquet Island, Langham studied similar factors and his conclusion was the same as Pearson's. In particular, Langham found that Sandwich Terns and

Common Terns are mainly inshore feeders although further observations were considered necessary to clarify the status of the latter species. The Arctic Tern was found to feed largely offshore while the Roseate Tern's foraging area was "uncertain" but probably offshore also. The four tern species overlapped considerably in prey species (mainly Ammodytidae and Clupeidae); Clupeidae were predominant in the diet of all four tern species but the Arctic Tern differed by taking relatively more Ammodytidae than the other terns. Langham considered that these prey species provided an abundant food supply for the tern population during the breeding season and suggested that interspecific differences in diet represented nothing more than particular preferences.

Despite the apparent absence of interspecific competition, these two studies nevertheless indicate a considerable overlap in feeding ecology between similar, coexisting species and the need was therefore felt to examine the areas of overlap more closely. For reasons of access, the only area of overlap convenient for study was close inshore. "Inshore" in this context means literally 'along the shoreline', and does not extend to waters more than about one-half mile offshore. The following account describes the status and feeding habits of terns in this zone.

Methods

All the terns studied are aerial predators which capture prey in the surface layer of the sea. The attack style is described by Ashmole and Ashmole (1967, pp. 70-71) as "plunging to surface". Since the tern's head points forward when the bird is flying in transit but points downwards when hunting, there is never any doubt about when a bird is intent on capturing prey. When hunting, the tern flies slowly above the water and, on seeing a fish, drops (usually vertically) with the wings partly closed. Sometimes, the dive is preceded by a variable period of hovering. Depending on the height of the dive, the bird may, or may not, submerge completely below the surface. At the most, the tern emerges again from the water after two or three seconds (called here "immersion time") and if it has been successful, the prey is clearly seen held crosswise in the bill.

The locations near Coquet Island (Figure 1) were used to determine the species composition of terns actively foraging in the inshore zone. This was done by making counts of diving birds at half-hour intervals on several days. At the same time, the species composition of shore roosts in these areas was also recorded.

Details of dive height and immersion time were recorded for any dives made by terns of known species; when possible, however, single birds were observed for a short period. In 1968, this period was not less than 1 minute and not more than 10 minutes, but in 1969 and 1970 the minimum time was increased to 2 minutes. The height at the start of each dive was estimated to the nearest 5 feet (about 1.5m*). A stopwatch was used to measure, to the nearest 0.1sec, the time interval between the tern's entry into, and exit from, the water surface. This interval is so short that it requires practice to record accurately but it is considered that sufficiently consistent measurement was achieved to justify comparison between dives of different species. By mounting a pair of stopwatches on top of binoculars, one watch could be used to record the length of the hunting time observed and the other for recording immersion times.

If the dive was successful, the length of prey was estimated from the known length of the captor's bill, about 5cm for Sandwich Terns, 4cm for Common and Roseate Terns, and 3cm for Arctic Terns. Before commencing this study, I had several days' experience in assessing both fish lengths and dive heights in the field to reduce the possibility of progressive improvement or shift in estimation. Practice at estimating dive heights was gained at a narrow stretch of the River Coquet where the heights of terns above the water could be measured against trees of known height on the riverbank opposite the observer. Perspective effects and the lack of an accurate vertical scale impose limits on the

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* All heights are quoted in metres, converted from feet.

reliability of these estimates but, for the present purposes, consistency in scoring relative differences was more important than absolute accuracy.

Results

(i) Dispersion indicated by foraging terns

The counts done half-hourly on any given day were summed and the totals are presented in Table 1. A few birds must inevitably be recorded more than once in consecutive counts, so inflating these totals, but since terns usually hunt along a stretch of coastline in one direction, rather than remaining stationary, most individuals are probably counted only once. Even allowing for this possible bias, the pattern of species occurrence shown by the Table is so consistent from day to day that the status of each species is quite clear. The most striking feature is the negligible representation of Arctic and Roseate Terns. When 1969 and 1970 are considered together, Sandwich Terns were more numerous than Common Terns on 17 days out of 18, the only exception being 21 June, 1969.

However, the status of these four species in the inshore zone is only meaningful in relation to the numbers that could have been present. It can safely be assumed that in June and July, virtually all terns found along the coast south of Coquet Island originate from the Coquet colony. The next nearest source of other terns of the same species is the Farne Islands, 20 miles north of Coquet. These birds do not forage as far south as Coquet Island, according to Pearson (1968) who calculated a maximum range of 15 miles for Sandwich Terns from the Farnes and ranges smaller than this for the other tern species. Table 1 shows the percentages of different terns breeding on Coquet Island in 1969 and 1970. The Common Tern is easily the most numerous breeding species, followed by Arctic, Sandwich and Roseate Terns in that order. The daily totals for each species in Table 1 were then compared with the values expected if each species had been present in the inshore zone in proportion to its breeding numbers. On this basis, Sandwich Terns were seen more often than expected on all 18 days. Common Terns did not occur as often as expected

Table 1

Species composition of foraging terns in the inshore zone, represented by daily totals of half-hourly counts. Ratios of breeding numbers are shown for comparison.

Year	Date	Location	Number of counts	Sandwich Tern	Common Tern	Arctic Tern	Roseate Tern
1969	2 June	Druridge Bay	15	48	8	0	0
	17 June	" "	8	103	4	0	0
	19 June	" "	11	79	48	0	0
	21 June	" "	8	42	72	0	0
	7 July	" "	4	21	1	0	0
	8 July	" "	4	23	5	0	0
	9 July	Newbiggin Bay	7	38	8	0	0
	10 July	" "	2	13	4	0	0
	11 July	" "	9	49	17	1	0
	14 July	" "	4	83	24	0	9
	Total numbers		72	499	191	1	9
	Percentages of species foraging			71.3	27.3	0.1	1.3
	Percentages of species breeding[1]			8.2	53.5	28.8	9.5
1970	21 June	Druridge Bay	4	29	22	0	0
	22 June	" "	3	47	31	0	0
	19 July	" "	5	73	4	0	0
	20 July	" "	3	77	33	0	0
	21 July	" "	5	102	9	0	0
	22 July	" "	7	133	3	0	0
	23 July	" "	10	188	25	0	0
	26 July	" "	9	70	19	0	0
	Total numbers		46	719	146	0	0
	Percentages of species foraging			83.1	16.9	0.0	0.0
	Percentages of species breeding[1]			23.7	44.1	27.1	5.1

[1] Estimated total numbers of all tern species breeding on Coquet Island were 4,860 in 1969 and 5,900 in 1970.

on 17 days out of 18, while Arctic and Roseate Terns were grossly underrepresented on all 18 days. The species differences in foraging numbers are not, therefore, produced by differences in the numbers of each that are present in the breeding colony.

The results above refer only to "solitary" feeding terns. When flocks were seen feeding inshore (presumably attracted by dense shoals of fish) these usually contained all four species of terns. Such feeding aggregations did not occur very often but tern species were noted on a presence or absence basis in 5 flocks—4 in Druridge Bay and 1 in Newbiggin Bay. In 4 out of the 5 flocks, all 4 species of terns were represented and in the other flock only Arctic Terns were absent.

(ii) Dispersion indicated by terns in day roosts

A regular roosting site was located at Druridge Bay near the mouth of the Chevington Burn (G. R. NU275982). In 1969 roosts occasionally formed near the mouth of the River Wansbeck (G. R. NZ307856), outside the breakwater at Blyth Harbour, and also on the coast between these two positions. These were all day roosts which probably consisted largely of "off-duty" birds.

The species composition of any particular roost on any day was determined from the roost count which gave the greatest number of individuals on that day; this was usually the mid-day count. Counts for 20 days are presented in Table 2 and show that Sandwich Terns were most numerous on 10 days, Common Terns most numerous on 8 days and, on the remaining 2 days, equal numbers of both these species occurred. The data correspond closely with the counts of foraging birds as far as Arctic and Roseate Terns were concerned since these two species were rarely seen in roosts. Comparison with the numbers expected from breeding populations shows that Sandwich Terns were more numerous than expected on 18 days out of 20. Common Terns were more numerous than expected on 9 days and fewer than expected on the other 11 days. Arctic Terns were much rarer than expected on all days, as were Roseate Terns, with the single exception of the Blyth Harbour roost on 16 July where observed numbers of this

Table 2

Species composition of terns in shore roosts; each day's figures are derived from the count that gave the largest numbers of individuals (of any species) roosting during the day. Ratios of breeding numbers are shown for comparison.

			Numbers of different species			
Year	Date	Location	Sandwich Tern	Common Tern	Arctic Tern	Roseate Tern
1968	31 May	Druridge Bay	18	19	0	0
	29 June	" "	90	33	0	0
	Total numbers		108	52	0	0
Percentages of species roosting			67.5	32.5	0.0	0.0
Percentages of species breeding[1]			22.2	48.2	22.2	7.4
1969	2 June	Druridge Bay	25	2	0	2
	19 June	" "	15	11	0	0
	21 June	" "	11	8	0	0
	8 July	" "	4	36	0	0
	9 July	" "	15	15	0	0
	16 July	Mouth of River Wansbeck	18	0	0	1
	"	Between Wansbeck & Blyth Harbour	36	5	10	0
	"	Blyth Harbour	30	2	0	9
	Total numbers		154	79	10	12
Percentages of species roosting			60.4	31.0	3.9	4.7
Percentages of species breeding			8.2	53.5	28.8	9.5
1970	13 June	Druridge Bay	46	4	0	0
	18 June	" "	25	3	0	0
	21 June	" "	16	21	0	0
	22 June	" "	9	37	0	0
	19 July	" "	31	2	0	0
	20 July	" "	27	30	2	0
	21 July	" "	40	67	0	0
	22 July	" "	42	42	0	0
	23 July	" "	26	139	0	0
	26 July	" "	20	24	0	0
	Total numbers		282	369	2	0
Percentages of species roosting			43.2	56.5	0.3	0.0
Percentages of species breeding			23.7	44.1	27.1	5.1

[1] Estimated numbers of all tern species breeding on Coquet Island in 1968 were 5,400.

species were higher than predicted. Roost composition therefore reflects the numbers of Sandwich, Arctic and Roseate Terns foraging inshore, but not of Common Terns. The association between numbers of Sandwich Terns roosting and foraging inshore is shown in Figure 3, which relates numbers of roosting birds to mean counts of birds foraging per half hour on several days. These two parameters are directly correlated and the regression is significant ($t = 2.68$, 11 d. f., $p<0.05$). There was no correlation between the numbers of Common Terns roosting and foraging.

(iii) Differences in foraging techniques

Table 3 gives a qualitative description of the various foraging methods used by each tern species on Coquet Island and the relative contribution each method makes to the overall hunting repertoire.

Table 3

Methods of obtaining food used by terns on Coquet Island and inter-specific differences in the frequency of use.

Method of obtaining food	Sandwich Tern	Common Tern	Arctic Tern	Roseate Tern
Plunge dive	mostly	mostly	mostly	mostly
Contact dip	rarely	occasionally	occasionally	occasionally
Steal food from other terns	never	occasionally	occasionally	habitually*
Hawk for insects	never	rarely	rarely	never

*It is argued later that habitual robbing is confined to a few specialist individuals.

This section deals with those methods that are used to some extent by all 4 species, i. e. plunge diving and contact dipping.

(a) Plunge diving

Since this foraging method is the main source of food for terns on Coquet Island, a detailed investigation was made of the interspecific variation in certain aspects of the technique.

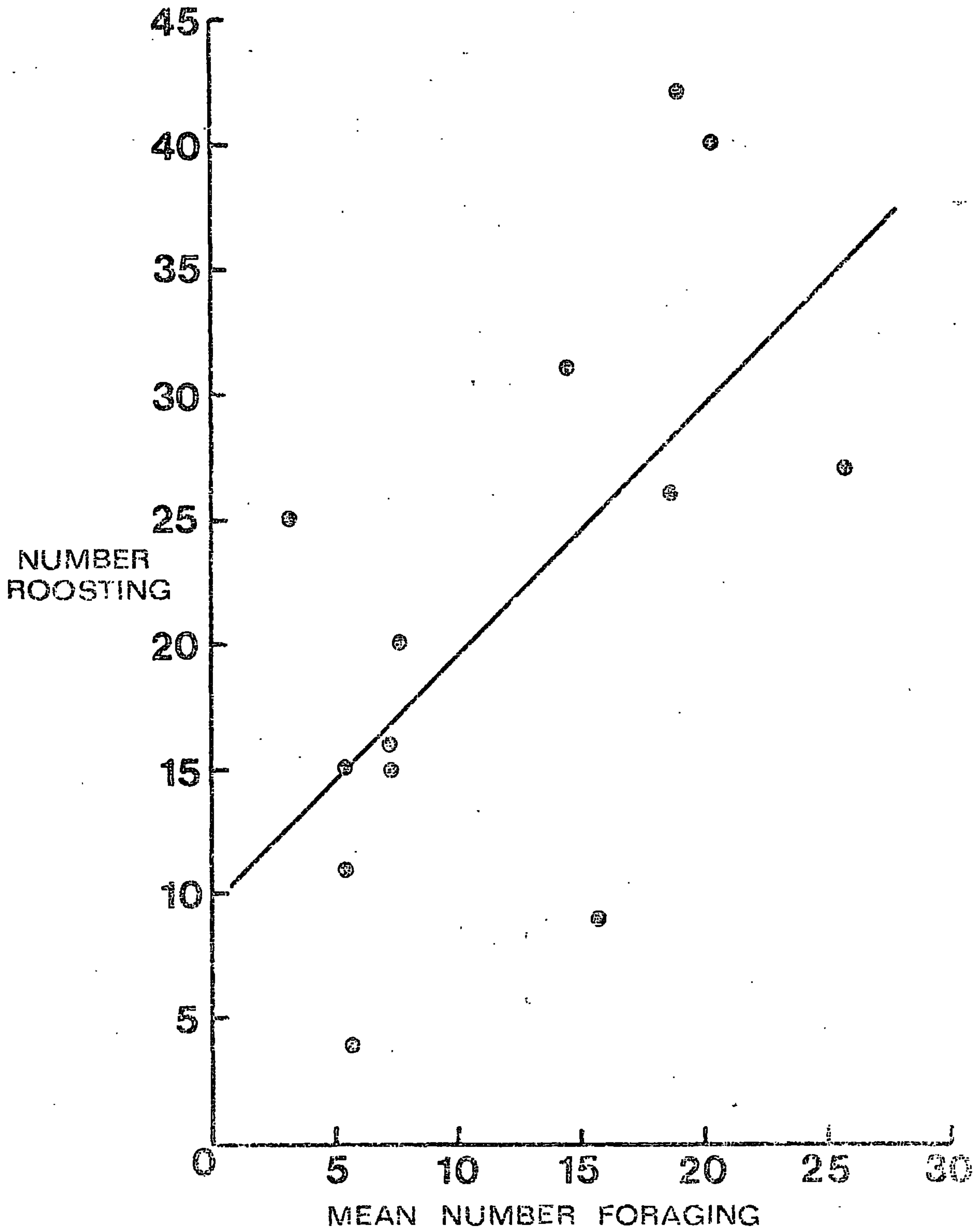


Figure 3

Relationship between numbers of Sandwich Terns roosting and numbers foraging inshore. The calculated regression line ($y = 0.99\ x + 9.67$) is shown.

Dive height

It was desirable to compare the dive height of the four species under identical conditions. Simultaneous observations of all four while foraging alongside one another would have provided the ideal comparison but in practice this situation was seldom found since Arctic Terns, in particular, were rarely seen feeding inshore.

All species shared a minimum dive height of about 1m. Common, Arctic and Roseate Terns shared a maximum dive height of 6m (20 feet). Sandwich Terns, however, exceeded the maximum dive height of the other three terns; they occasionally dived from a height estimated at 9m (30 feet) and on rare occasions from even higher than this.

Mean dive heights were derived from observations made over several days. The results of the 1968 and 1969 analyses are shown in Table 4. Species rankings in the two years agree well and show that Sandwich Terns were the highest divers, followed by Roseate Terns, while Common and Arctic Terns tied for third place. Apart from Common and Arctic Terns which were statistically inseparable as regards dive height, all other interspecific differences were highly significant ($p<0.001$).

Such differences are characteristic of solitary feeding, i.e. when each individual was widely separated from its nearest neighbour. However, whenever a dense, mixed-species flock formed over a shoal of fish, there was no interspecific difference in dive height.

Substantial differences exist between Sandwich, Common and Roseate Terns in the frequency distribution of dive height (Figure 4). The Sandwich Tern shows a positively skewed distribution, suggesting that it has a preferred dive height (5-6m) near the upper limit for the species. Dive height is much more evenly distributed in the Roseate Tern; although 3m was the most commonly recorded height, 4.5m and 6m were not appreciably less frequent. However, the Common Tern, like the Sandwich Tern, displays a clear preference and dives more frequently from 3m than from any other height. The Arctic Tern probably resembles the Common Tern in this respect (see Table 4).

Table 4

Comparison of mean dive height (± 1 standard error) in metres of different tern species in 1968 and 1969. Each column of the Table represents a comparison involving simultaneous observations of the species that appear in the column. e. g. the first column shows dive heights of Sandwich and Common Terns when they were the only two species foraging together.

	1968						1969			
Species	Height	N[1]	Height	N	Height	N	Height	N	Height	N
Sandwich Tern	5.6±0.05	346	4.9±0.16	30	5.7±0.07	131	5.2±0.08	270	5.4±0.08	179
Common Tern	3.1±0.05	281	n.s. { 3.0±0.02	64	3.5±0.15	37	2.5±0.05	250	2.9±0.05	169
Arctic Tern			3.0±0.06	25						
Roseate Tern					4.2±0.13	41			4.2±0.10	190

---

[1] Number of dives.

[2] Since dive height deviated from a normal distribution (see Figure 4) the Kolmogorov-Smirnov two-sample test (2-tailed) was used to compare pairs of species where each value of N = 40 (Siegel 1956). Where samples were smaller than 40, however, this test is inappropriate and, since Student's t-test is still valid when a population only approximates to a normal distribution, the latter test was used in these few cases. The resulting significance levels are so extreme that differences are real; apart from the single pair comparison that was not significant (n.s.) all other differences between values within columns were highly significant (i. e. $p<0.001$).

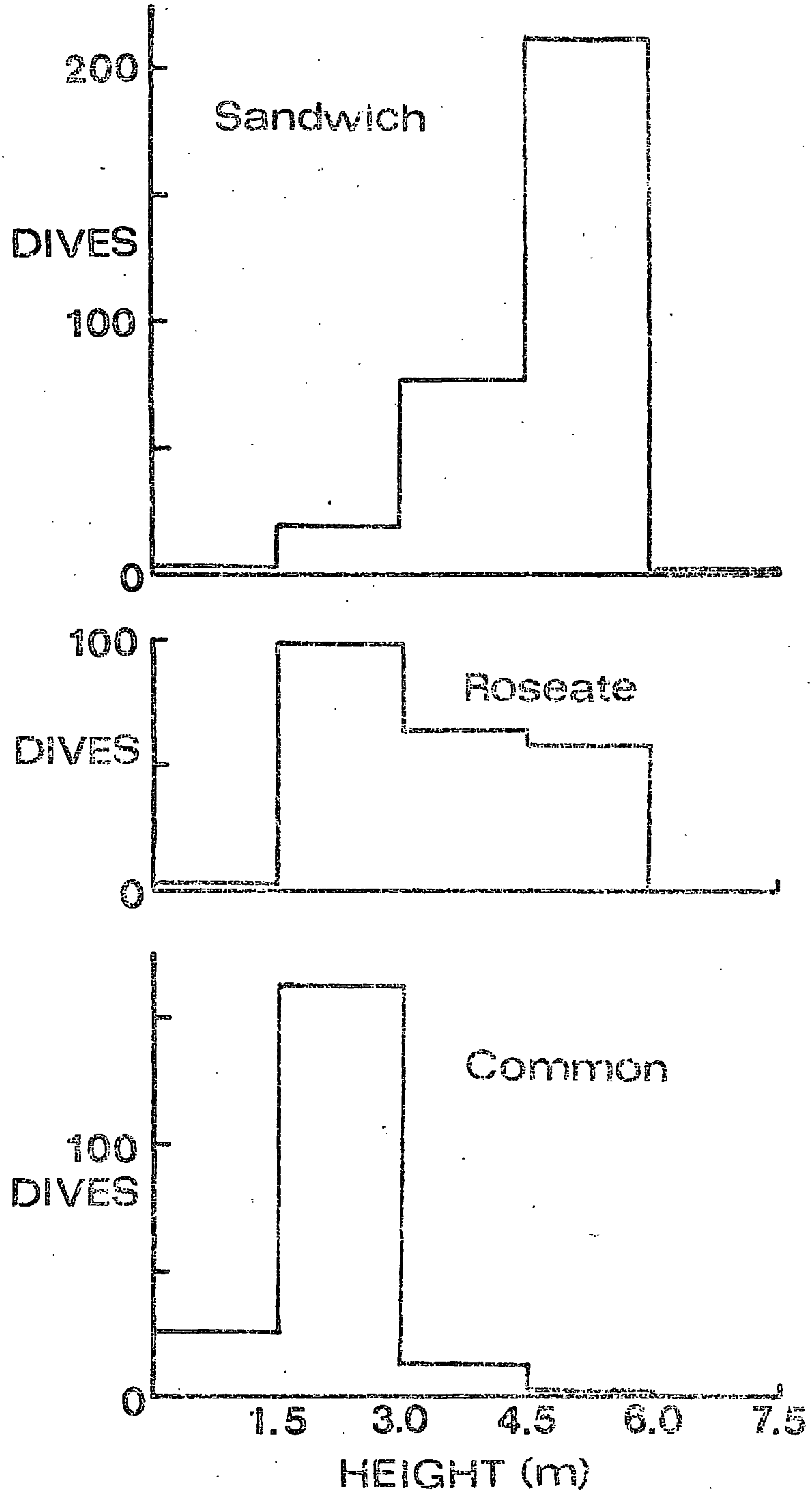


Figure 4

Frequency distributions of dive height (m) of Sandwich, Roseate and Common Terns in 1968 and 1969 from simultaneous observations on all three species.

Immersion times

Table 5 shows the mean period for which each species is submerged in the water after a dive, measured from moment of entry to moment of exit. The ranking of species by this parameter follows the same sequence as for dive heights. Sandwich Terns remain submerged for the longest periods. Roseate Terns did not differ significantly from Sandwich Terns in 1968 when very few dives by the former species were timed, but in 1969 a highly significant difference emerged between these two terns. Again in 1969 when more dives were timed, it was found that Common Terns submerge for significantly shorter periods than Roseate Terns in the same foraging situation. In 1968, Arctic Terns showed the briefest immersion times of all, but the difference was not significant from that of Common Terns. It was not possible to investigate the Arctic Tern further but it seems probable that its immersion time differs little from that of the Common Tern. Figure 5 shows that in Sandwich, Roseate and Common Terns, immersion times are distributed symmetrically on either side of the mean value.

Just as there were no detectable differences in dive height when these various species assembled together over a shoal of fish, so there were no differences in immersion times under these conditions.

To examine the relationship between immersion time and dive height, successful and unsuccessful dives were first considered separately. In 1968, successful dives by Sandwich Terns were associated with significantly longer immersion times than were unsuccessful dives at the following dive heights: 4.6m (15 feet), 6.1m (20 feet) and 7.6m (25 feet). However, the individual regressions of immersion time on dive height for successful and unsuccessful dives respectively were not significantly different in slope or elevation. Similarly, the regressions for successful dives and for unsuccessful dives did not differ significantly for Sandwich Terns in 1969 or 1970, nor did they differ for the other two species in 1968 and 1969 (no information was obtained for these two species in 1970). For this reason, immersion time was regressed

Table 5

Comparison of mean immersion times (± 1 standard error) in seconds of different tern species in 1968 and 1969. Each column of the Table represents a comparison involving simultaneous observations of the species that appear in the column.

	1968						1969			
Species	Time	N[1]	Time	N	Time	N	Time	N	Time	N
Sandwich Tern	* * * 1.32±0.03	241	1.19±0.04	22	* 1.25±0.02	176	* * * 1.23±0.02	250	* * * 1.30±0.02	147 * * *
Common Tern	1.13±0.02	164	1.15±0.03	37	1.17±0.03	58	0.99±0.14	198	* * * 1.02±0.02	96
Arctic Tern			1.10±0.05	14						
Roseate Tern					1.22±0.04	21			1.16±0.03	100

[1] Number of dives

* = $p<0.05$

* * * = $p<0.001$

All other differences between values within columns are not significant.

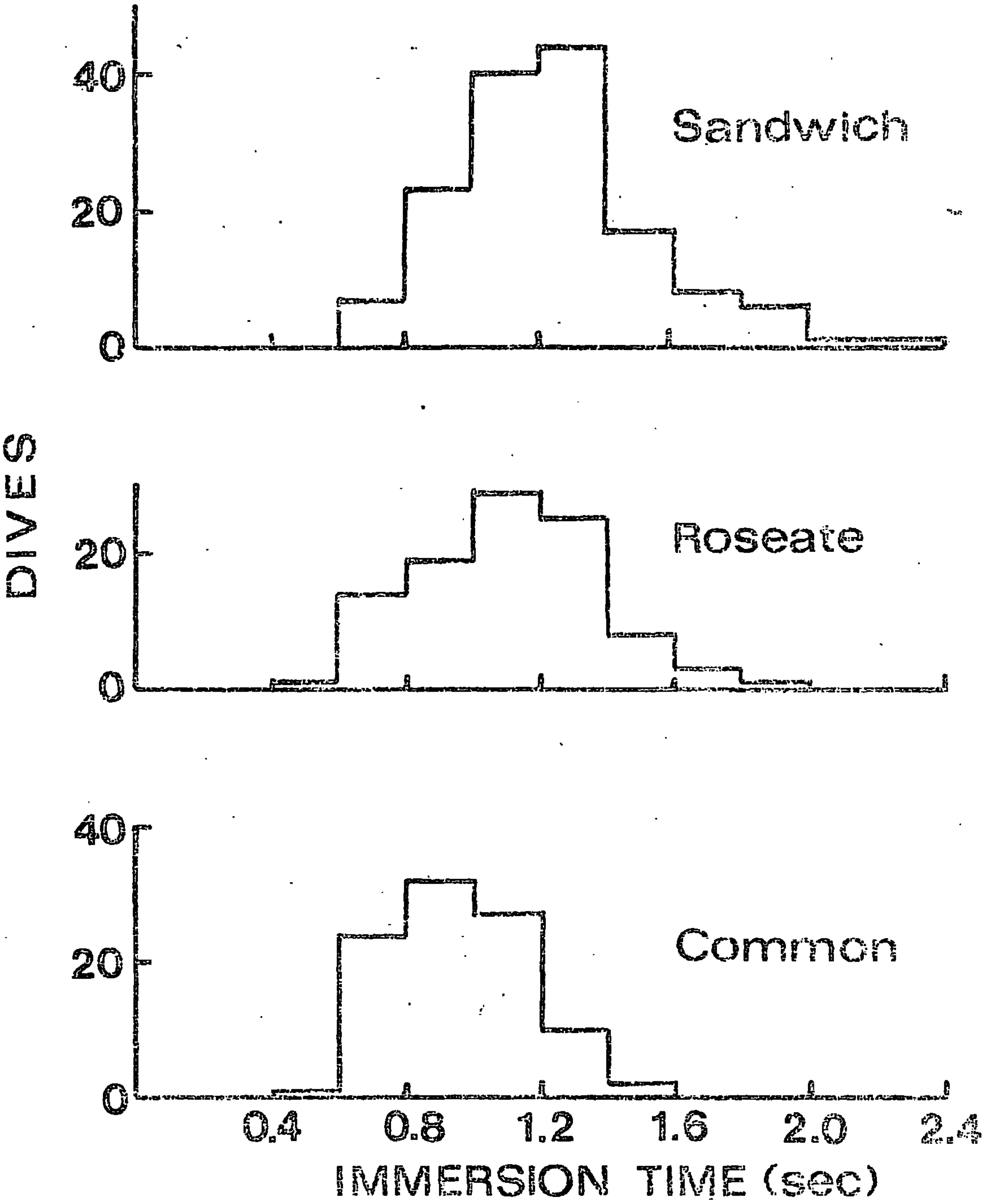


Figure 5

Frequency distributions of immersion times (sec) of Sandwich, Roseate and Common Terns in 1969 from simultaneous observations on all three species.

on dive heights for all dives, successful or not, as shown in Figure 6. Immersion time is seen to be directly related to dive height in all cases and the correlations are highly significant ($p<0.001$ in each case). The slope of the regression for Sandwich Terns in 1968 was significantly greater than that for Common Terns in the same year ($t = 2.36$, 861 d. f., $p<0.02$) and also exceeded the slope for Sandwich Terns in 1969 ($t = 4.00$, 1,343 d. f., $p<0.001$) and in 1970 ($t = 2.44$, 1,015 d. f., $p<0.02$). These differences may have arisen from sampling error since there were no other significant differences in regression coefficients either between species in any year or within species between years. This reinforces the idea that the behaviour of these three species underwater (e.g. lack of active pursuit of prey) is similar.

The tendency for successful dives by Sandwich Terns in 1968 to be accompanied by longer immersion times than for unsuccessful dives requires explanation. There are two questions to be answered: (i) why should a successful dive increase immersion time? (ii) why was such an increase only apparent in 1968 and then only in Sandwich Terns? To sieze and manipulate a fish underwater presumably adds "handling time" to the immersion time and adequately accounts for (i). It is likely that (ii) is answered by a combination of fish size and the methodology adopted in the study. In 1968, the mean length of fish caught by Sandwich Terns at Druridge Bay was 6.55cm whereas in 1969 at Newbiggin it was only 4.98cm. If handling time is longer for larger prey, then fish may have been big enough to produce a measurable difference between successful and unsuccessful dives in 1968 but not in other years. This suggestion is supported by Table 6 which presents data for Sandwich Terns in three years. The Table shows (a) the mean length of fish captured by Sandwich Terns in five different foraging situations (based on several days' observations at each site) and (b) the mean difference in immersion time between successful and unsuccessful dives made from the two dive heights (4.6m and 6.1m) common to all five situations.

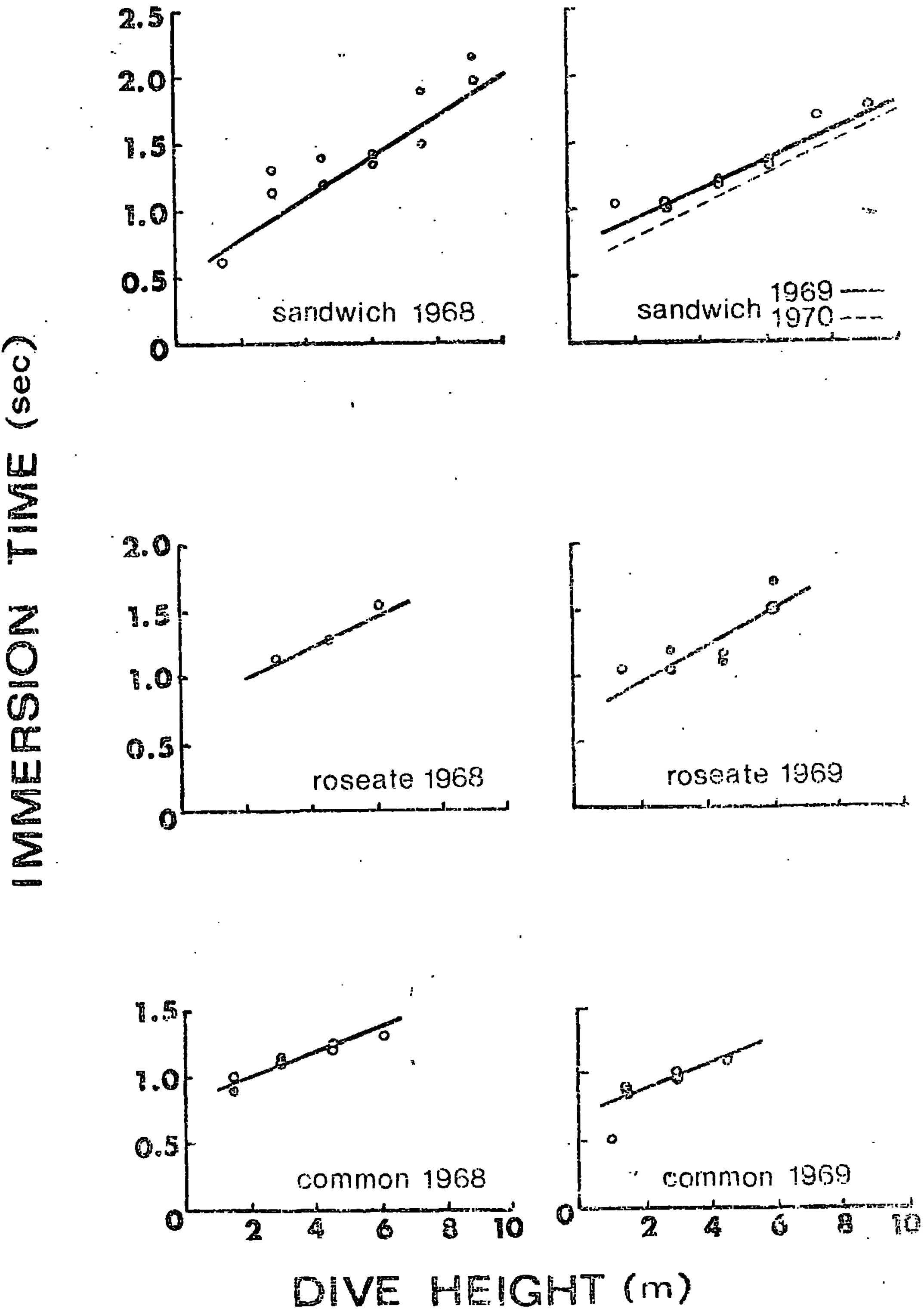


Figure 6

Relationship between dive height and immersion time in Sandwich, Roseate and Common Terns in 1968 and 1969. Each point is the mean for several dives; points based on unsuccessful dives are represented by open circles (o) and those based on successful dives by closed circles (●). Regression lines are shown, and in the case of Sandwich Terns in 1970, points are omitted.

Table 6

Relationship between fish length (± 1 standard error) and difference in immersion time for successful (T_s) and unsuccessful (T_u) dives of Sandwich Terns. Values are shown ranked by descending order of fish length.

Year	Location	Number[1] of fish	Mean length[2] of fish (cm)	$T_s - T_u$ (sec)	Number of dives
1968	R. Coquet	150	7-10	0.36	458
1969	R. Coquet	211	7.58 ± 0.04	0.18	345
1968	Druridge	200	6.55 ± 0.11	0.13	535
1970	Druridge	208	5.63 ± 0.10	0.10	245
1969	Newbiggin	365	4.98 ± 0.06	0.00	494

[1] The number seen to be caught.

[2] No systematic estimates of fish length in 1968 but field notes state that average length was 3-4 inches (= 7.5-10.0cm).

The greatest difference in immersion time was recorded at the River Coquet site where fish were the largest. At the other extreme, no difference in (T) was demonstrated at Newbiggin in 1969 where the smallest fish size was recorded. A more rigorous test of this relationship is shown in Table 7 which compares the mean immersion time for Sandwich Terns diving from an estimated 6.1m (= 20 feet, the commonest dive height of this species) in three different years. The immersion time of a successful dive (i.e. T_s) is directly proportional to the length of fish captured and the correlation is highly significant ($r = 0.31$, 208 d. f., $p<0.001$): the relationship is described by the regression equation, $y = 0.08x + 0.91$, where y is T_s. Thus, for every 2.5cm (≃1 inch) increase in fish length, a Sandwich Tern's immersion time is prolonged by 0.2 sec.

Table 7

Relationship between fish length and immersion time (T_s) ± 1 standard error for successful dives by Sandwich Terns.

Year	Location	T_s (sec) for different fish lengths (cm) 2.5	N^1	5.0	N	7.5	N
1968	Druridge	-	0	1.28 ± 0.04	34	1.58 ± 0.08	30
1969	Newbiggin	1.13 ± 0.11	6	1.35 ± 0.03	81	1.44 ± 0.10	7
1970	Druridge	0.88 ± 0.13	4	1.23 ± 0.05	35	1.28 ± 0.08	13
	Mean	1.03 ± 0.09	10	1.31 ± 0.02	150	1.48 ± 0.06	50

[1] The number seen to be caught.

It is now clear why the 1968 graph of immersion time against dive height for Sandwich Terns is the only case in Figure 6 that shows an appreciable increase in immersion time when dives are successful. Roseate Terns and Common Terns generally capture smaller fish than do Sandwich Terns (see below) and, like Sandwich Terns in 1969 and 1970, the difference in immersion time caused by fish capture was probably too small to be detected by the methods used.

(b) Contact dipping

This term is used by Ashmole and Ashmole (1967) to describe the feeding method used by many terns to catch prey which is on, or very near, the water's surface. The method involves making a controlled, shallow swoop to the surface and maintaining continuous forward momentum so that only the bird's bill makes brief contact with the water. It is a much more rapid manoeuvre than the plunge dive and the tern can potentially execute several dips in the space of a minute.

Contact dipping was not a feeding technique often seen around Coquet Island, but under certain conditions it substituted for plunge diving over extended periods. Thus, in June 1969, terns seemed to be experiencing considerable difficulty in capturing fish by plunge diving. The mean daily fishing success (proportion of plunge dives that yielded a fish) of Sandwich Terns in Druridge Bay was exceptionally low at 2.2% ± 0.7 (S.E.) but the species persisted with plunge diving. Most Common Terns, however, abandoned plunge diving and resorted instead to contact dipping. Arctic Terns were also seen dipping but no observations were made of Roseate Terns at this time. Records for 14 individual Common Terns gave a mean dipping rate of 8 ± 1 (S.E.) dips/bird/min. It was usually impossible to score the success of these contact dips because the items picked up (if at all) were not visible at a distance. Only one of these prey types was identified, namely the common shrimp Crangon vulgaris. Some of these were recovered uneaten from Coquet Island.

By early July, Druridge Bay had been virtually abandoned as a feeding area. On 7 July, only 17 dives (all by Sandwich Terns) were seen during three hours continuous observation. On 8 July, only two dives were seen in three hours and on 9 July, no dives in an hour. The terns were flying past Druridge Bay and were evidently foraging much further south. About this time, contact dipping ceased and Crangon were no longer found in the colony. These changes coincided with the discovery of terns feeding very successfully on fish about 12-14 miles south of Coquet Island. Although this new feeding ground involved more flying time than Druridge Bay, the fishing success it offered seemed to be more than adequate compensation. For the remainder of July, Sandwich Terns achieved an average fishing success of 46.6% ± S.E. 4.9 and Common Terns a success of 30.3% ± S.E. 4.4 and these are relatively high success levels for both species. To summarise, contact dipping was only a prominent feeding technique when food seemed to be in short supply and then it was used by Common and Arctic Terns, but not by Sandwich Terns.

In Sierra Leone, Common and Sandwich Terns occasionally feed alongside each other on small fish, often Sardines Sardinella eba and Anchovies Engraulis guineensis about 5cm long, which escape to the water surface from seine nets being hauled ashore. Almost all the fish were caught by dips involving the merest contact with the surface such that only a forward and upward flick of the head was required to secure the prey. Table 8 shows that the fishing success of Sandwich Terns and Common Terns did not differ appreciably in this situation.

Table 8

Fishing success of Sandwich Terns and Common Terns in Sierra Leone, 1970, using the contact dipping method of feeding.

Date	Duration of observation (min)	Sandwich Tern Dips	 No. S[1]	 % S	Common Tern Dips	 No. S	 % S
7 Feb	90	70	46	65.7	28	25	89.3
12 Feb	97	83	73	88.0	40	38	95.0
14 Feb	113	62	39	62.9	108	66	61.6
Totals	300	176	129		215	158	
Means				73.3			73.5

[1] S=successful.

(iv) Length of prey captured

Comparisons were made of the length of fish that were seen being caught by different species of terns under apparently identical conditions, i. e. approximately in the same place at the same time. Table 9 shows that in 1968, the mean length of fish caught by Sandwich Terns was 1.50cm greater than the length caught by Common Terns and the difference was significant ($t = 6.59$, 144 d. f., $p<0.001$). In 1969, the corresponding difference (0.81cm) was smaller than in 1968 but was still highly significant ($t = 4.21$, 209 d. f., $p<0.001$).

Table 9

Length of fish (cm) caught by Sandwich and Common Terns during 10 days in 1968 and 8 days in 1969.

	SANDWICH TERN			COMMON TERN		
Year	Mean length	S. E.	N	Mean length	S. E.	N
1968	6.65	0.18	76	5.15	0.14	70
1969	4.81	0.13	112	4.00	0.14	99

In 1969 sufficient numbers of the captured fish were identified to enable a separate comparison of the lengths of sand-eels (Ammodytidae) and sprats (Clupeidae) taken by Sandwich Terns and Common Terns (Table 10). The Ammodytidae caught by Sandwich Terns were, on average, significantly longer (by 1.12cm) than those caught by Common Terns ($t = 2.03$, 58 d. f., $p<0.05$) but there was no difference for Clupeidae.

Table 10

Length (cm) of Ammodytidae and Clupeidae caught by Sandwich and Common Terns in 1969.

	SANDWICH TERN			COMMON TERN		
Fish type	Mean length	S. E.	N	Mean length	S. E.	N
Ammodytidae	7.62	0.66	10	6.50	0.21	50
Clupeidae	5.40	0.46	16	5.14	0.06	41

Roseate Terns were found feeding alongside Sandwich Terns and Common Terns on a few days in 1969. The lengths of prey caught by the three species on these occasions are shown in Table 11.

Table 11

Length of fish (cm) caught by Sandwich, Common and Roseate Terns during three days in 1969.

	Sandwich Tern	Roseate Tern	Common Tern
Mean length	4.72	4.48	3.97
S. E.	0.22	0.22	0.22
N	49	34	39

The mean length of fish caught by Sandwich Terns was significantly greater (by 0.75cm) than that of fish caught by Common Terns ($t = 2.33$, 86 d. f., $p<0.05$) but did not differ significantly from the value obtained for Roseate Terns. There was no significant difference in the length of fish caught by Common and Roseate Terns.

Discussion

(ii) Foraging areas

The results show that, for the inshore localities that were observed, Sandwich Terns were more numerous than Common Terns while Arctic and Roseate Terns were almost totally absent. The latter two species must inevitably be foraging offshore, as Langham's (1968) study also indicated. However, the distribution of Sandwich and Common Terns is harder to assess on the available evidence. The situation in 1969 is particularly interesting because only 200 pairs of Sandwich Terns bred on Coquet Island compared with about 1300 pairs of Common Terns and yet the Sandwich Tern was consistently the more numerous of the two species feeding inshore. The same reversal of breeding and feeding ratios occurred in 1970. Two possibilities may account for the relatively small numbers of Common Terns seen inshore compared with Sandwich Terns: (a) Within the inshore zone, Sandwich Terns were more concentrated than Common Terns in Druridge Bay where most of the observations were made. (b) Common Terns were widely distributed (i. e. occupied both inshore and offshore areas) while

Sandwich Terns preferred to feed inshore.

Langham (op. cit.) concluded that Sandwich Terns preferred sandy to rocky shores for feeding whereas Common Terns showed no particular preference. In 1969, Sandwich Terns were more numerous than Common Terns not only along the sandy shores of Druridge Bay but also along the rocky shores flanking Newbiggin Bay (Table 1). Thus the generality of a marked substrate preference in feeding areas is not substantiated. It seems much more likely that the terns' choice of feeding place within the littoral zone would be subject to considerable flexibility depending on several fluctuating factors such as distribution of fish and depth of water. If Sandwich Terns had foraged more successfully than Common Terns in Druridge Bay, then there might be some grounds for expecting a higher concentration of them there. But, as will be shown later, Common Terns achieved a higher fishing success than Sandwich Terns in Druridge Bay throughout summer 1968 and in a variety of tidal and weather conditions. In short, it is improbable that local aggregations of terns exist on a sufficient scale to explain the observed ratios of feeding species. Instead it is suggested that large numbers of Common Terns remained undetected because they were offshore. It is possible that these birds made a variable and unknown contribution to the numbers of Common Terns in shore roosts and so accounted for the lack of correlation between numbers of individuals foraging inshore and roosting in this species. To summarise, the evidence favours possibility 'b' above, namely that relatively more Sandwich Terns than Common Terns must be feeding close inshore.

The constraints on species to occupy discrete foraging areas seemed to be relaxed whenever a dense shoal of fish was available. When this occurred, a mixed flock, usually containing all four tern species, rapidly formed over the shoal. Such assemblages are widespread among seabirds (Rand 1954) and in other groups which experience temporary gluts of particular food items. Lack (1946) maintained that this phenomenon was a significant corollary to ecological isolation by pointing out that when a food supply is temporarily superabundant, so that it is not significantly reduced by the species preying on it, several species can exploit it without effectively competing.

(ii) Foraging technique and prey size

Figure 6 shows that the greater the height from which a dive is started, the longer is the subsequent immersion time. This suggests that the higher the dive, the deeper is the penetration below the surface and the longer the immersion time as a result. The interspecific differences in heights and immersion times may, therefore, indicate that there is some vertical stratification of feeding levels below the sea surface for these tern species. Segregation of this kind has previously been noted between closely related species that actively pursue their prey underwater (e. g., between the Cormorant Phalacrocorax carbo and Shag P. aristotelis, Lack 1945) but the possibility does not seem to have been considered for those plunge diving species that must depend mainly on their impetus at immersion for determining what depths they can reach. Little is known about the relationships between morphology and feeding technique in such birds although Nelson (1966a, 1970) has pointed out that the male Blue-footed Booby Sula nebouxii is about 520g lighter than the female (1800g) and that this difference is probably related to their separate feeding niches; both sexes feed close inshore but the male seems to specialise in diving into much shallower water (less than 2 feet deep) than the female.

Considering the body weights and dive heights of the terns involved (Table 12) it seems possible that, on average, Sandwich Terns dive the deepest, followed by Roseate Terns, Common Terns and Arctic Terns in that order.

Table 12

Adult weights (source Langham 1968), dive heights and immersion times of terns.

Species	Mean weight (g)	Mean dive ht (m) in 1969	Mean immersion time (sec) in 1969
Sandwich Tern	229	5.4	1.30
Roseate Tern	124	4.2	1.16
Common Tern	126	2.9	1.02
Arctic Tern	109	c3.0	-

Since the potential energy (p) at the start of a dive is converted into work done against water resistance or drag, it can be shown that $p = mgh = sd$ where:

m = mass of bird
g = acceleration due to gravity
h = height of dive
s = depth of penetration
d = drag

Thus 's' can be calculated from $\frac{mgh}{d}$. The absolute values for drag coefficients in water are not known and are likely to vary in a very complex manner. Nevertheless, it is possible to estimate the magnitude of differences in depth penetrated by the different species. The cross-sectional area of a Sandwich Tern is 1.3 - 1.4 times greater than values for the other three terns which differ little in this respect. Assuming that this difference is reflected in the size of 'd', and substituting values for 'm' and 'h' from Table 12, we find that Sandwich Terns should dive about twice as deep as Roseate Terns and three times as deep as Common and Arctic Terns.

Unfortunately, no direct observations of terns underwater are available to support these proposals, but estimates of maximum depths penetrated by the terns have been made by a few authors. Salt and Willard (1971) state that Forster's Tern Sterna forsteri does not catch fish at depths exceeding 0.5m and I would suggest a similar maximum for the Common Tern which resembles Forster's Tern in general body proportions and repertoire of dive heights. From the ratios of 's' for Common and Sandwich Terns, the latter species would then be expected to penetrate to about 1.5m. This approaches Borodulina's (1960) estimate of 2m for this species although his figure is probably overestimated. Borodulina considered that the Sandwich Tern was the deepest diver of all the north temperate tern species with the possible exception of the Caspian Tern Hydroprogne caspia. Sophisticated field techniques are evidently required to measure these depths and the actual differences may turn out to be small. However, if even a slight separation of feeding levels is achieved, the potential number of prey items available to each of the species could differ.

When food was superabundant, the different tern species showed convergence in their feeding methods, notably in the heights from which they dived. Similarly, Orians and Horn (1969) found that a massive emergence of damselflies (Odonata) elicited convergent foraging behaviour from three species of blackbird. When food was in more limited supply, however, the blackbirds demonstrated a greater degree of divergence and this phenomenon was also a feature of the terns' foraging habits. Thus, at a time when fish were evidently scarce, many Common and Arctic Terns stopped plunge diving and started contact dipping for very small prey. Although Sandwich Terns persisted with plunge diving, the observations in Africa show that this species is capable of contact dipping for fish as successfully as Common Terns, at least for short periods. Considering that the prey items available in the surface waters around Coquet Island seemed to be very small and that a buoyant flight may have been necessary to exploit them efficiently, it might have been more profitable for Sandwich Terns to continue hunting for larger prey even though these may have been deeper or more sparsely distributed. This segregation of feeding strategies is consistent with the hypothesis which states that, as a food supply dwindles, the exploitation patterns contract, with each species concentrating on those situations for which it is best adapted (MacArthur and Levins 1964, Root 1967, Ashmole and Ashmole 1967).

It is clear that Sandwich Terns do take larger prey than the other species (Pearson 1968, Langham 1968). Although this difference was more likely to reflect a genuine selective process rather than a difference in available size distribution of prey associated with different feeding areas, this could not be ascertained by these earlier studies in which length determinations were made only at the colony itself. By eliminating feeding area and time as variables, the present results confirm the likelihood of real selection by Sandwich Terns of prey larger than those taken by Common and

Roseate Terns. There is also some evidence (Appendix 2) that the size difference in prey is maintained in the winter quarters, at least between Sandwich and Common Terns.

To conclude, the populations of different tern species on Coquet Island do not usually distribute themselves at random over the surrounding foraging area. Arctic and Roseate Terns seem to feed almost exclusively offshore and Sandwich Terns mainly inshore. Common Terns are probably the most ubiquitous and utilise both inshore and offshore areas to some extent. Even where species do overlap inshore, Sandwich Terns select larger prey and it is speculated that a degree of vertical stratification of feeding layers may also exist. When fish are scarce a further polarisation of feeding techniques occurs. The only occasions when all these spatial and behavioural differences disappear are when food is superabundant in one locality but this is only a temporary phenomenon. For the rest of the time, there would appear to be adequate mechanisms operating to alleviate competition for food between these species, especially among those that frequent the inshore zone. However, it is important to point out that my main purpose has been to identify the sorts of differences in feeding ecology that might influence competition between these terns. The results do not <u>prove</u> that competition is avoided or greatly mitigated by these differences. As Colwell and Futuyma (1971) have recently remarked, a lack of demonstrable overlap in resource use by two species can be evidence either for or against the existence of competition between them. Equally, using different arguments, it is possible to show that overlap in resource utilisation can be marshalled to support a case for, or against, competition. Colwell and Futuyma maintained that the critical test requires careful measurement of the niche dimensions of each species, both in the presence and absence of its suspected competitors. Such tests were beyond the scope of the present study.

PART 2. Robbing behaviour of Roseate Terns

Introduction

In addition to plunge diving for prey at sea, Roseate Terns obtain food at Coquet Island by swooping on other terns in order to steal their fish. This kind of cleptoparasitism was first noted by Watt (1951) on the nearby Farne Islands but the regularity of the behaviour was not confirmed until 1962 when Bannerman presented an account based on observations accumulated by Dr. J. M. Cullen over three years. A notable feature of these early reports was that the parasitic terns always operated singly, rather like foraging raptors and Langham (1968) observed that Roseate Terns on Coquet Island behave in the same way. From the increasing number of accounts in recent years, it has become apparent that this habit of stealing food from other birds is a fairly widespread phenomenon among the Laridae (Nørrevang 1960, Hatch 1970, Hays 1970). Where Laridae or Stercorariidae (Meinhertzhagen 1959, Belopol'skii 1961, Grant 1971) are the antagonists, they often band together into chasing groups of varying size and the interactions are complex (Hatch, op. cit.). The solitary behaviour of parasitic Roseate Terns seemed, by comparison, to be particularly suitable for a study of the relationships between the parasites and their hosts. The following account describes the behaviour and considers several responses of the Roseate Terns to changes in the abundance and nature of the food supply in the form of fish brought by the host population of terns to the island. In 1969, when the major part of this work was undertaken, Coquet Island supported about 1300 pairs of Common Terns, 700 pairs of Arctic Terns, 250 pairs of Roseate Terns, 200 pairs of Sandwich Terns and, in addition, 105 pairs of Black-headed Gulls.

Methods

Between May and July 1968, the airspace above the island was observed periodically to determine which tern species were being robbed and in what manner. In July 1969 a hide was situated facing area A (Figure 7) which was

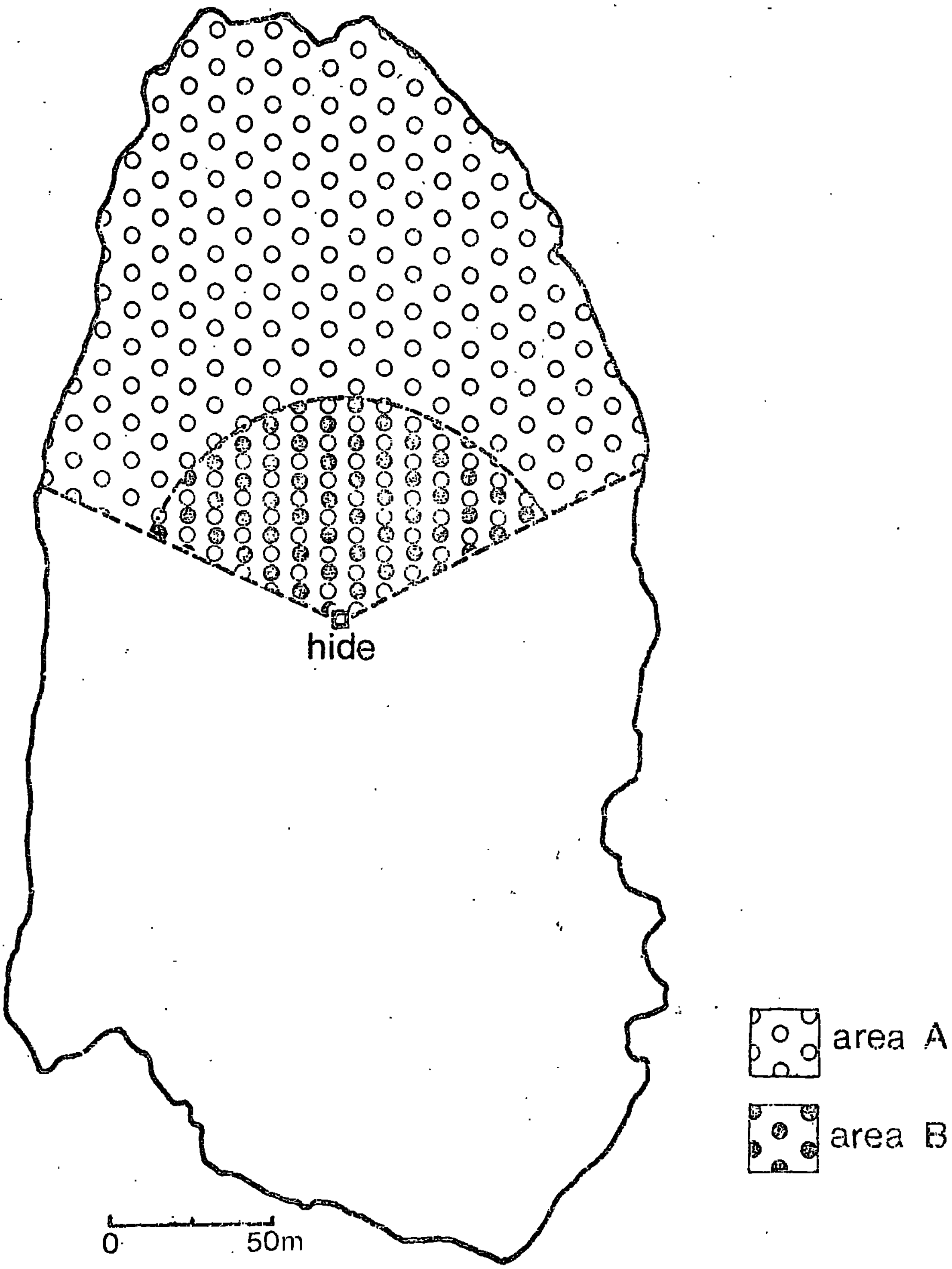


Figure 7

Coquet Island showing the study areas used in 1969.

See text for details.

colonised mainly by Common Terns. Daily observations of robbing behaviour were subdivided into fifteen minute watches. During each watch, the total number of Roseate Terns actively parasitising above area A were counted. Roseate Terns did not pursue other terns with fish but attacked them mainly by making brief, rapid swoops; all such flight manoeuvres directed at terns carrying fish were scored as attacks, irrespective of whether or not there was any physical contact between the terns. Attacks which resulted in the host bird being dispossessed of its meal were "successful" and all others were "failed". Very occasionally, a host dropped its fish when it was attacked. If the fish was not retrieved by the parasitic tern, the attack was scored as a failure. All four tern species carry fish crosswise in the bill. Most birds (98%) carried only one fish but a few (2%) carried more than one and sometimes as many as five (based on 3,011 sightings). For each interaction seen in area A, the species of host tern involved, the species and length of fish (to the nearest inch, i. e. 2.5cm) and the success or failure of the robbing attempt were recorded; when necessary, 10 x 50 binoculars were used to verify these details. Two main fish species were brought back to the colony by the terns. Almost all (99%) were either sand-eels Ammodytes marinus or sprats Clupea sprattus. The remaining food items usually belonged to the Gadidae or Crustacea and comprised a negligible proportion of the terns' diet.

The length of fish carried was estimated by comparing it with the length of the tern's bill, as described in Part 1. All these observations were made by the author, so ensuring consistent estimation throughout. Previous practice in estimating fish lengths reduced the possibility of progressive change or improvement in assigning fish to particular size categories.

The "intensity" of robbing at any time was assessed both by the number of terns robbing and by the frequency of their attacks. The rapid, free-ranging flight of parasitic terns frequently took them out of sight behind the hide, so precluding any record of "attack rate" based on the detailed performance of particular individuals. The attack rate during any particular watch was therefore derived by dividing all the attacks seen in the period by the number of parasites most frequently recorded in area A during the watch (usually only one or two parasites were active at any one time (Figure 9)). "Robbing success" was calculated as the percentage of attacks which was successful.

Within area A (about 25,000 sq.m), a smaller representative area (area B, covering about 5,000 sq.m) shown in Figure 7 was selected and its boundary marked out with conspicuously coloured stakes. This area was of such size that all host terns entering the "volume" of airspace above it could be easily seen. The species of all host birds, and the length and species of their fish, were recorded to provide an index of the relative numbers (density) and species of fish potentially available to Roseate Terns in area A. The number of fish considered to be available during each 15-minute watch was the average count in area B made from three rapid spot counts at 5-minute intervals.

Results

(i) The behaviour

A Roseate Tern intent on robbing easily distinguishes itself from other Roseate Terns by flying high (about 10-20m) above the colony where it can observe other terns returning with fish. The most common subsequent behaviour pattern closely resembles the fishing method used by Roseate Terns at sea: the parasitic tern suddenly dives—but without a preliminary hover—and attempts to seize the fish from the other (host) tern's bill.

Three distinct variations in the parasite's strategy were seen. In most encounters, the host tern was attacked from vertically above, usually in mid-air (Figure 8a) but sometimes on the ground (Figure 8c). Considerable skill was evidently required in the latter method in order to strike a fine balance between the rapid, unchecked stoop needed to surprise the host and the sudden arrest of downward movement necessary to prevent collision with the ground. Occasionally the Roseate Tern approached the host from behind

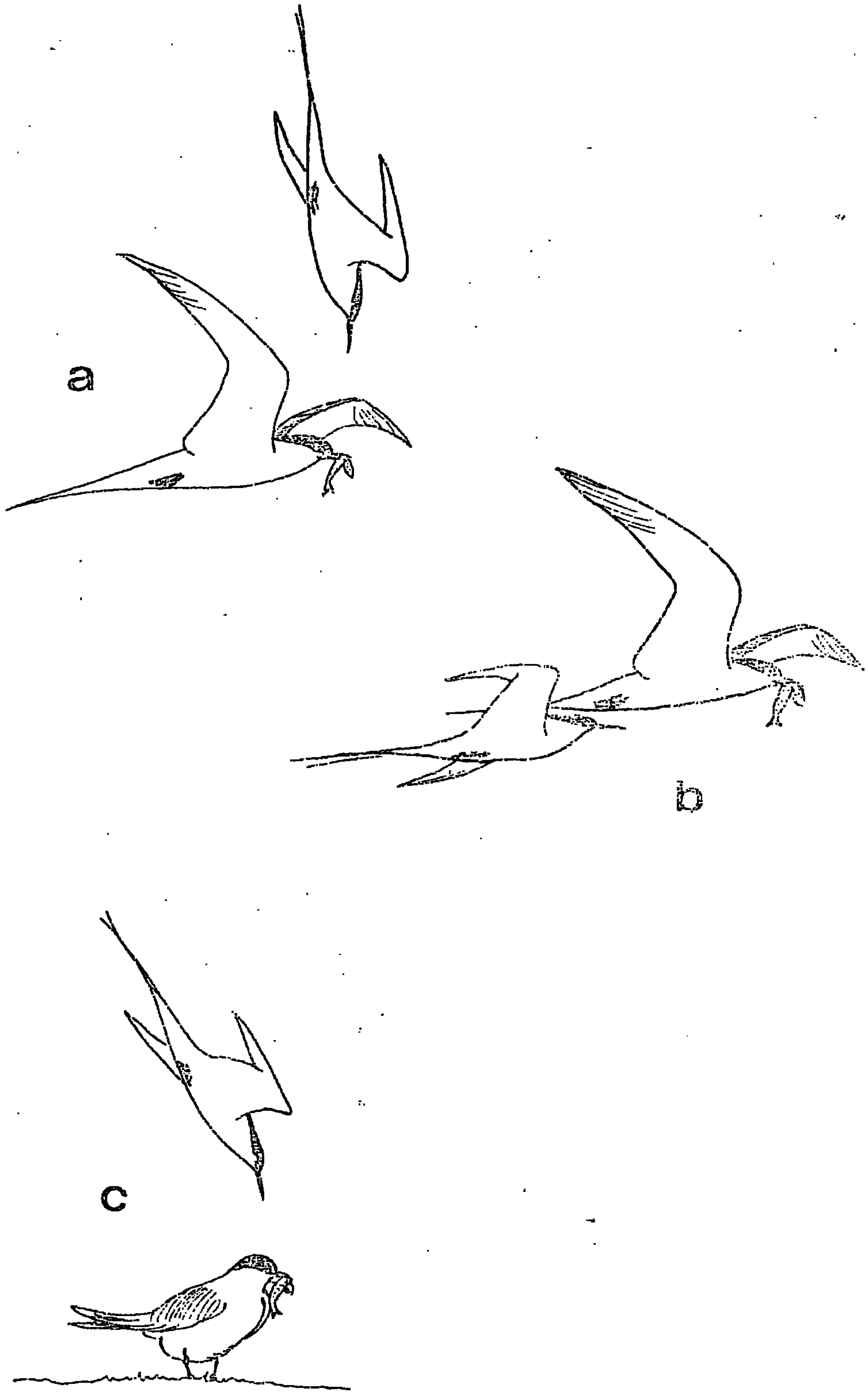


Figure 8

The three robbing strategies used by Roseate Terns.

In each case, the "host" tern is the one carrying the fish.

and dipped below the apparently unsuspecting tern to snatch the dangling fish from the underside of the bill (Figure 8b). This method was not seen till the summer of 1969 and then in only 15 out of 2,114 attacks.

Just as in a plunge dive into the sea, the success of these strategies was largely dependent on the element of surprise and consequently there was no pursuit or prolonged harassment. Occasionally there was a brief tussle over the fish when the host bird kept a firm grip but usually the robbing attack was an instantaneous, all-or-nothing attempt. Frequently, instead of following through an attacking dive, the Roseate Tern would terminate its descent prematurely and regain height for its next attack. Between successive attacks, a hunting tern tracked back and forth over the entire island but no parasitism was ever seen out at sea and it is very likely that the behaviour is confined to the island itself where there was the greatest concentration of potential hosts.

(ii) Seasonal succession of interactions

On Coquet Island, Sandwich Terns usually start egg-laying in the second week of May, Common and Arctic Terns in the fourth week of May, and Roseate Terns in the first week of June. This sequence influences the species composition of terns attacked throughout the breeding season, as shown in Table 13.

Table 13

Changes in the percentage composition of tern species attacked by parasitic Roseate Terns in 1968 and 1969.

Study period	No. of attacks	Host species Sandwich Tern	Common Tern	Arctic Tern	Roseate Tern
May 1968	79	94.9	3.8	1.3	0.0
June 1968	19	63.2	36.8	0.0	0.0
July 1968	314	2.6	93.9	0.0	3.5
July 1969	648	3.5	93.5	2.8	0.2
Aug 1969	335	1.2	96.4	1.2	1.2

In May, Roseate Terns concentrated most of their robbing effort on the Sandwich Tern which was the only species regularly returning to the colony at that time with fish to feed incubating mates or for presentation in courtship. The resulting concentration of birds alighting and displaying with fish offered an ideal opportunity for ground attacks which were more frequent in May than at any other stage in the season and comprised 23% of attacks seen during two days in May 1968. Since Sandwich Terns nested on very short vegetation or bare soil, Roseate Terns could make fast swoops at birds with no hindrance to manoeuvrability or to their visibility of the host. By mid-July, Common Terns, probably through superiority of numbers on the island, were providing the most plentiful source of fish and were most frequently attacked. Common Terns seemed to spend less time than Sandwich Terns standing in the colony and also nested in much higher vegetation (50-80cm in July) which may explain why ground attacks were almost entirely abandoned for mid-air attacks when Common Terns succeeded Sandwich Terns as the most frequently attacked host. Undoubtedly Arctic Terns were also being attacked in July and their low representation in Table 13 is explained largely by the predominance of Common Terns in the study area. Roseate Terns were not averse to intraspecific robbing and one Black-headed Gull was also attacked. All tern species, therefore, were potentially vulnerable to attack but because of differences in the relative abundance and breeding times of the four tern species, seasonal changes occurred in the species composition of birds attacked.

(iii) Robbing intensity

Robbing occurred throughout the day but was most evident early in the morning, just after mid-day, and in the late evening. At these times, both the number of Roseate Terns involved and the frequency of their attacks were highest (Figure 9). However, there were never more than five birds making robbing sorties over the island at any one time and the total number was usually less than this.

A close relationship exists between the fluctuating intensity of

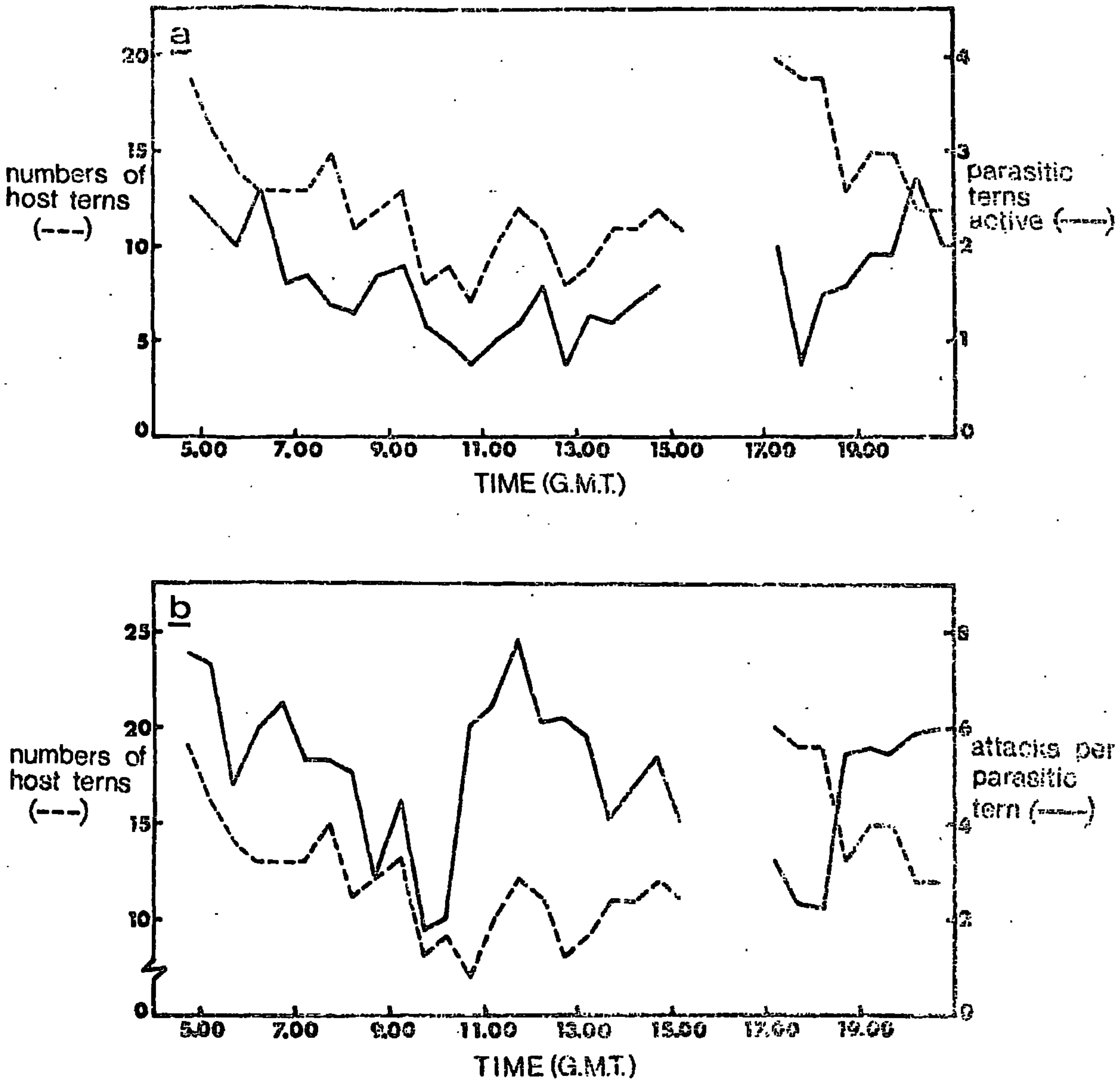


Figure 9

Diurnal patterns of host availability and robbing intensity ((a) the number of parasitic terns active and (b) the frequency of their attacks). Points represent half-hourly means for several days' observation.

cleptoparasitism and the variation in the numbers of potential hosts carrying fish (Figure 9). More birds brought fish into the colony at dawn, mid-day and early evening than at other times of day. This basic diurnal pattern has been demonstrated for terns and other seabirds (Pearson 1964, Boecker 1967, Langham 1968). It is interesting that after 1800 (Greenwich Mean Time) robbing intensity continued to increase despite a steady decline in the availability of fish in the colony. It is likely that Roseate Terns try to accrue as much food as possible by robbing in the evening to maintain their chicks and themselves overnight.

To examine the relationship between the numbers of terns carrying fish and the numbers of Roseate Terns robbing them, all data collected in the period between 04.45 and 15.15 were taken into account. The period after 17.00 was excluded because the relationship between availability of hosts and robbing intensity altered so radically in the late evening. The total number of cleptoparasitic Roseate Terns showed a positive, linear correlation ($r = + 0.90$, 6 d. f., $p<0.01$) with the number of food hosts in area B (Figure 10). The frequency of attacks also increased with the numbers of fish in the area (Figure 11). It was very noticeable that a failure to dispossess a tern of its fish at the first attempt was usually sufficient to make the parasite break off its attack and switch its attention to another host with the result that the rate of launching fresh attacks was partly dependent on the frequency with which the aggressor encountered a succession of new host terns. This lack of perseverance in attacking any host more than once suggests that a Roseate Tern which fails at the first attempt is unlikely to succeed by attacking the same bird immediately afterwards, possibly because the latter's vigilance has increased. The adaptation of robbing strategies for surprising rather than harassing hosts is consistent with this absence of pursuit. Figure 11 shows that, after an initial increase, the attack rate began to level off at 6 attacks per parasite per 15 minutes, and finally dropped below this asymptote. However, the considerable variation in performance indicates that this decline

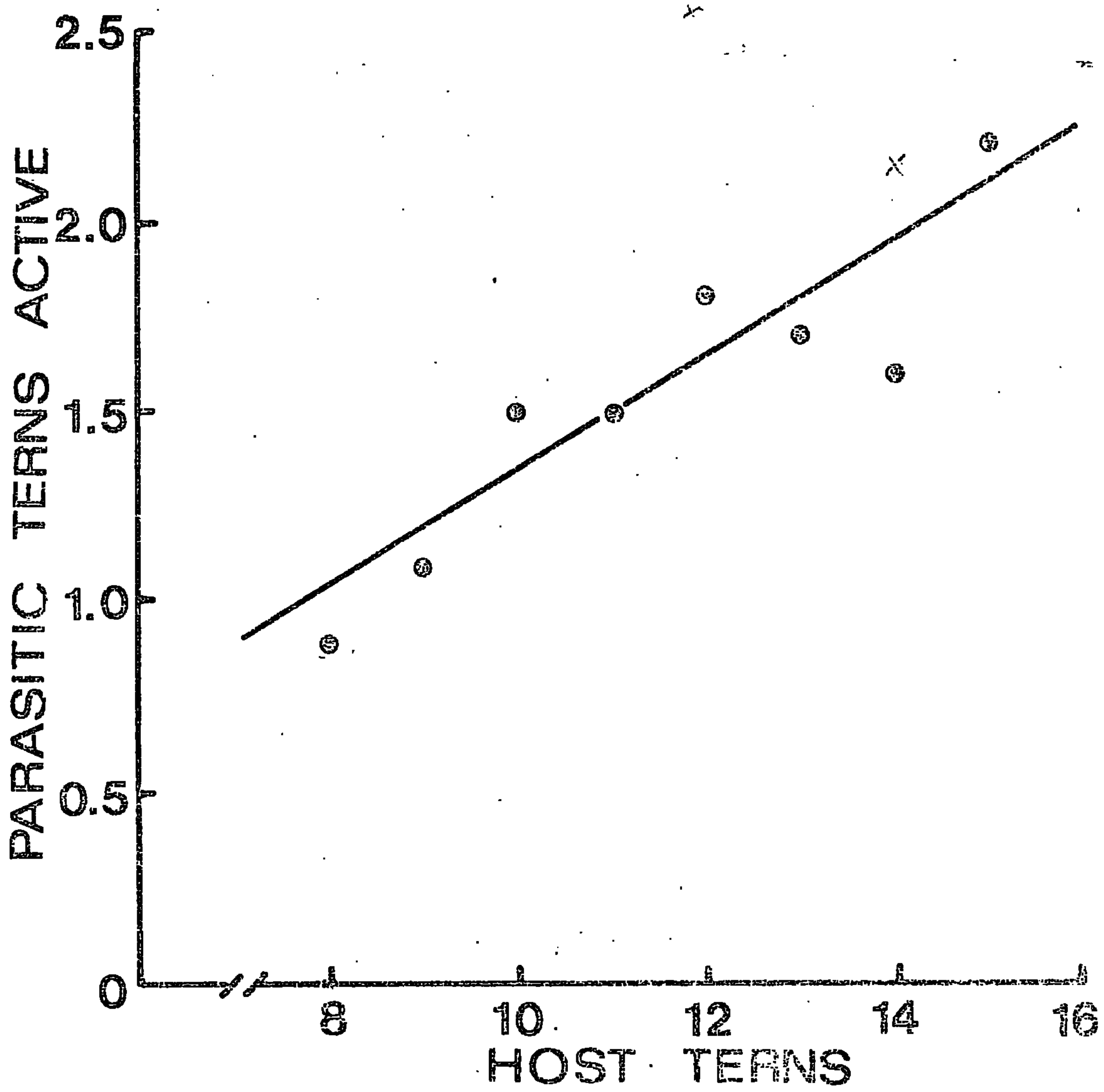


Figure 10

Relationship between the number of host terns and the number of parasitic terns active. The regression line (y = 0.15x - 0.16) is shown.

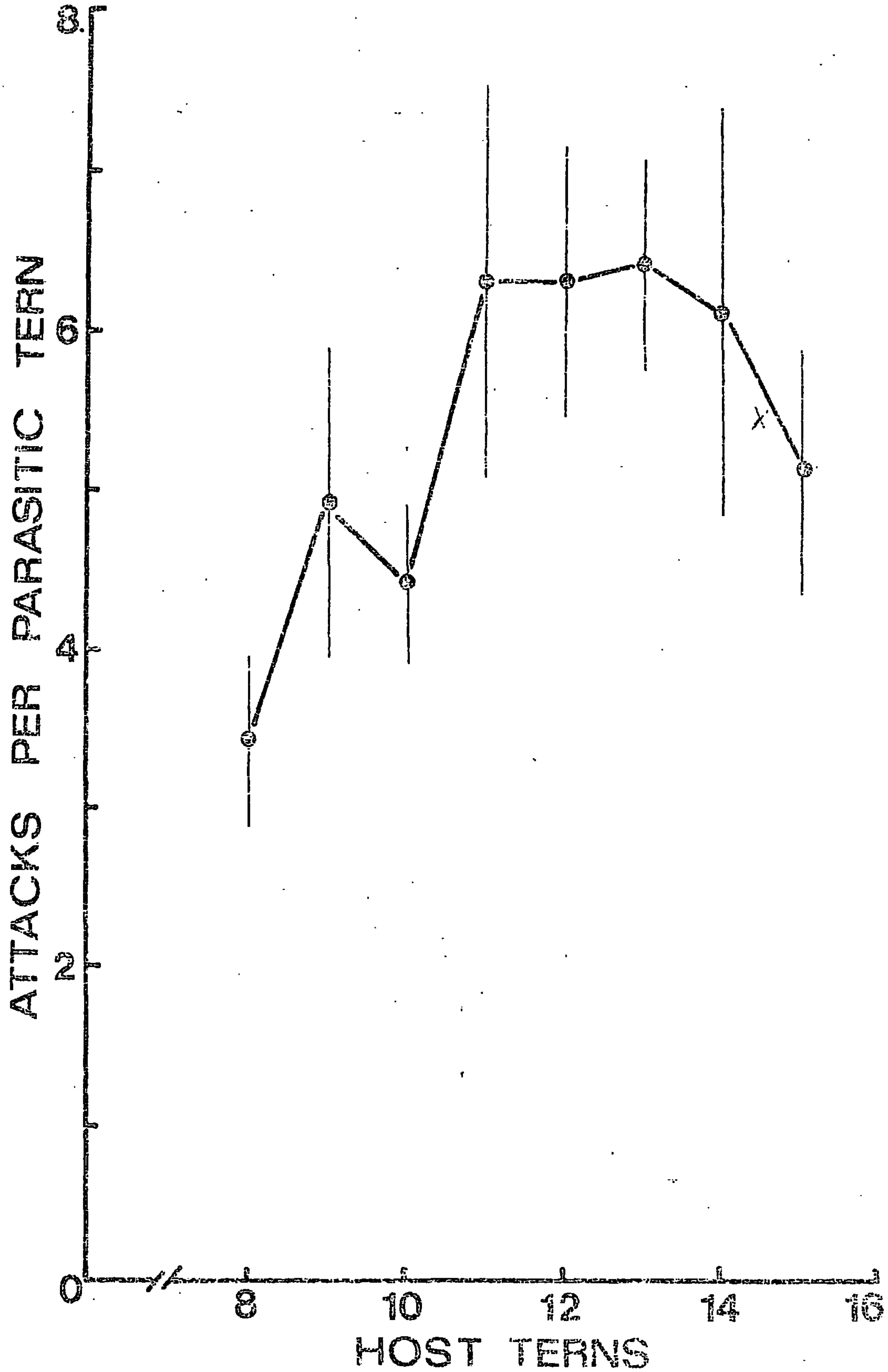


Figure 11

Relationship between the number of host terns and the frequency of attacks by parasitic terns.

One standard error is given on either side of each mean.

may not be significant. It should also be pointed out that these rates are certainly conservative since the rate during each watch was calculated by dividing the total number of attacks witnessed by the number of parasites active in area A. Underestimation arises because the parasitic terns foraged over the part of the island not visible to the observer so that not all individuals were active in area A throughout the watch.

(iv) Robbing success

(a) Quantity

Table 14 shows the percentage robbing success on 15 days in 1968 and 1969; the mean success was 7.5% ± 1.1% (standard error). The more terns there were entering the area (B) with fish, the higher was the subsequent robbing success ($r = +0.98$, 3 d. f., $p<0.01$) as shown in Figure 12. A large number of terns entering the colony with fish was consistent with intense and seemingly congested aerial activity to which birds both with and without fish contributed. At such times, the hunting strategy of the parasitic terns may have been relatively inconspicuous so that those birds returning with meals were possibly less likely to detect and anticipate the threat above them. It is suggested, therefore, that the greater surprise element afforded by dense air traffic enhanced robbing success.

A large number of terns carrying fish into the colony was probably elicited by a strong stimulus to provision chicks. It is possible that the drive to obtain food was also high in Roseate Terns at these times, and consequently they attacked more tenaciously. If the will to attack is related to the likelihood of being successful, then a positive correlation between robbing success and host density might arise independently of the "confusion" factor suggested above. The evening period offers an opportunity to examine this possibility. After 17.00, there was a distinct decline in host density and yet Roseate Terns showed an increase in attack frequency, presumably in an effort to obtain as much food as possible before nightfall. If the parasites had been attacking more tenaciously for this reason, one might expect their robbing

Table 14

Daily robbing success in 1968 and 1969.

Date	Number of attacks	Number successful	Robbing success (%)
May 20, 1968	26	3	11.5
May 21, 1968	43	3	7.0
July 16, 1968	52	1	1.9
July 17, 1968	158	7	4.4
July,18, 1968	105	11	10.5
July 23, 1969	96	12	12.5
July 24, 1969	140	24	17.1
July 25, 1969	187	17	9.1
July 27, 1969	235	21	8.9
July 29, 1969	484	18	3.7
July 31, 1969	209	11	5.3
August 4, 1969	167	8	4.8
August 5, 1969	305	24	7.9
August 6, 1969	.182	12	6.6
August 7, 1969	109	2	1.8
Totals	2,498	174	Mean 7.5 ± 1.1 (standard error)

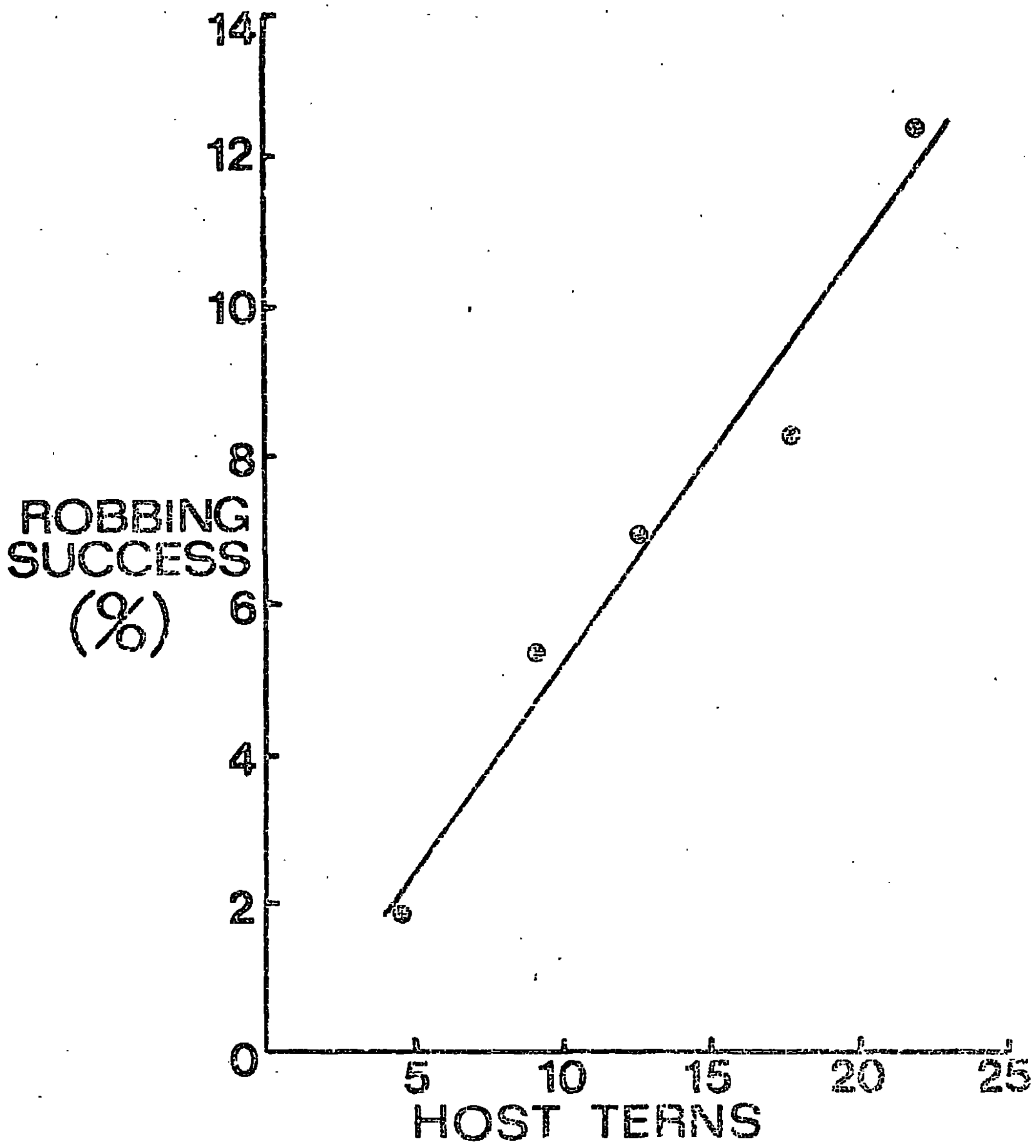


Figure 12

Relationship between the number of host terns and the robbing success of parasitic terns, based on 1,791 attacks. The regression line ($y = 0.55x - 0.32$) is plotted.

success to have remained level or even increased, in spite of the reduction in host birds. However this did not happen (Figure 13). Despite considerable variation due to small samples, it is clear that the apparent urge to accrue food did not improve robbing success. The strength of motivation to attack may well affect robbing success, but the observations are more in accord with the "confusion hypothesis."

(b) Quality

Of 723 attempts to rob fish in 1969, only 15 concerned fish other than sprats or sand-eels. From data collected during 10 days, the mean robbing success was calculated for each length category of these fish types. Robbing success was found to be inversely proportional to fish length ($r = -0.94$, 4 d. f., $p<0.01$) such that attacks on hosts carrying the smallest fish (up to 2.5cm) were about 15% more successful than attacks on hosts with the largest fish (10cm) (Figure 14).

By combining the information in Figure 14 with the known weights of sprats and sand-eels of given length, it is possible to calculate the weight of fish a Roseate Tern could expect to derive by attacking hosts that carry fish of varying length (Table 15). It is clearly more profitable to challenge for large fish in spite of the greater success at robbing terns with small fish.

Table 15

Yield of fish (g) to parasitic terns when they attack hosts carrying sprats and sand-eels of varying length. Yield = weight of fish x robbing success appropriate to the fish's length.

		Length of fish (cm)			
		2.5	5.0	7.5	10.0
SPRATS	Weight (g)	0.20	0.55	2.50	-
	Success (%)	21.6	14.5	9.9	-
	Yield (g)	0.04	0.08	0.25	
SAND-EELS	Weight (g)	-	0.25	1.30	3.00
	Success (%)	-	16.9	6.8	7.4
	Yield (g)	-	0.04	0.09	0.22

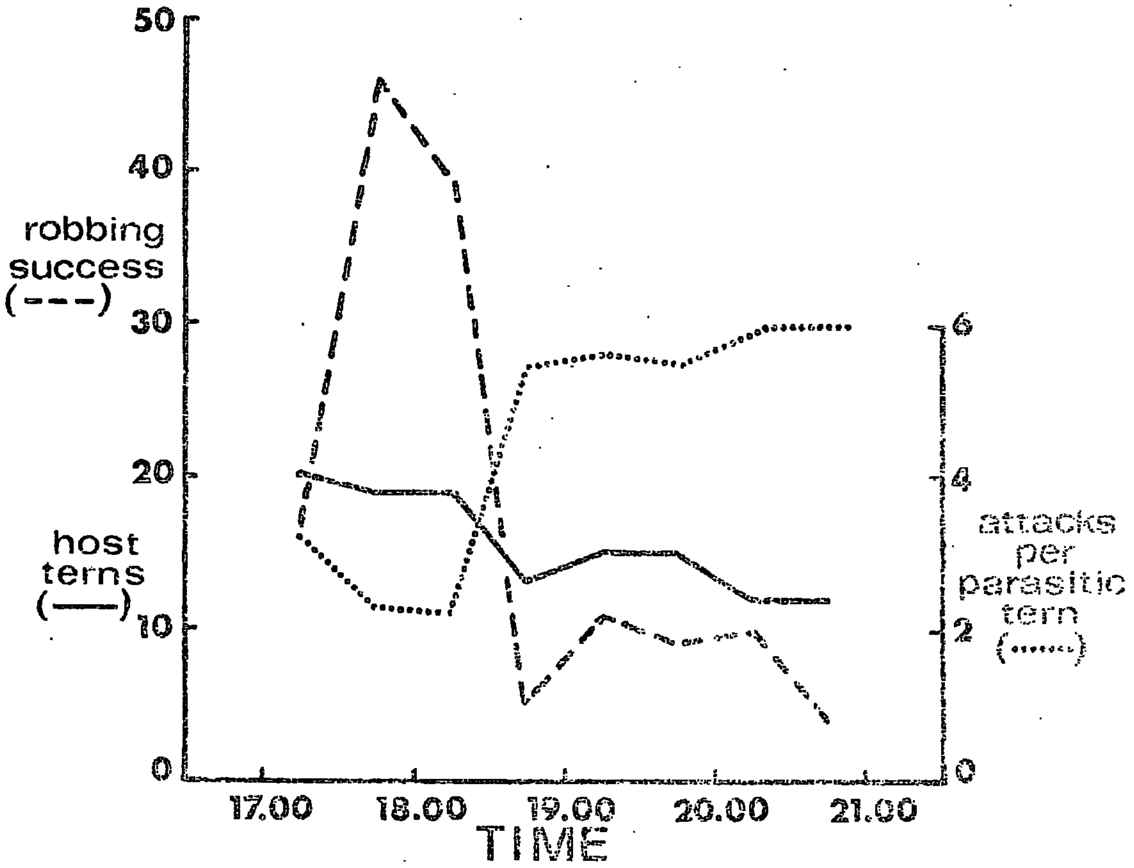


Figure 13

Evening patterns of host availability, robbing success and attack rate.

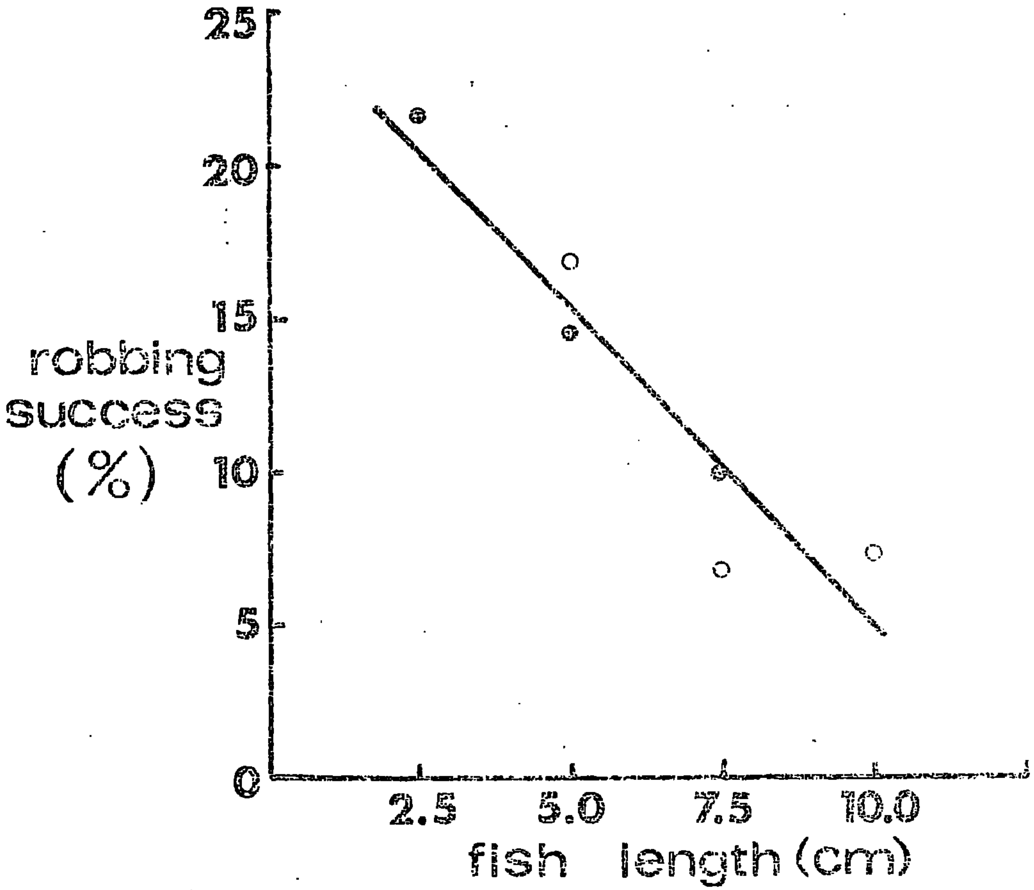


Figure 14

Robbing success for different lengths of sprats (⊕) and sand-eels (o) carried by host terns. The regression line ($y = -2.08x + 25.85$) is shown.

(v) Selection of hosts

Although fish available in area B were categorised by species and length, these are scarcely likely to be the visual cues recognised by parasitic Roseate Terns. Selection of hosts was more likely to be made in response to the general size of the fish as indicated by the silhouette area. Thus a sprat presents a more substantial image than a sand-eel of the same length. For instance, compared with a 5cm sand-eel, a 5cm sprat is about half as large again in silhouette area and is about twice as heavy (Table 15). In Figure 15, the various length categories of sprats and sand-eels are ranked along the x-axis by increasing weight. (These rankings correspond to their sequence by silhouette area.) The histogram shows the total number of attacks actually made on each size class of fish in area B with the number expected if parasites encountered and attacked fish of different sizes at random in the area, i. e. according to their known frequencies of occurrence (availability). The Figure is compiled from data only for Common Terns which received 95.3% ± 1.1% (standard error) of attacks during the 10 days studied. The remaining attacks were made on the other three tern species and were too few for separate analysis. There was no indication that the likelihood of encounter varied spatially for different size classes and it can be assumed that parasites had equal access to all Common Tern hosts. The expected size frequency of fish attacked was first calculated for each of the 10 days and the resultant sets of values summed to give the overall expected distribution shown in the Figure. There was a highly significant difference ($X^2 = 135.05$, 6 d. f., $p<0.001$) between the observed and expected numbers of attacks on various sizes of fish. The relative contributions to the total X^2 value show that there was selection for 5cm sprats at the expense of smaller fish (2.5cm sprats and 5cm sand-eels) and larger fish (10cm sand-eels). Discrimination was strongest against fish smaller than 5cm sprats. However, 7.5cm sprats and 7.5cm sand-eels were attacked about as often as expected. The strong preference for 5cm sprats is reflected in the composition of the 128 fish successfully robbed: the mean length of these was 5cm and

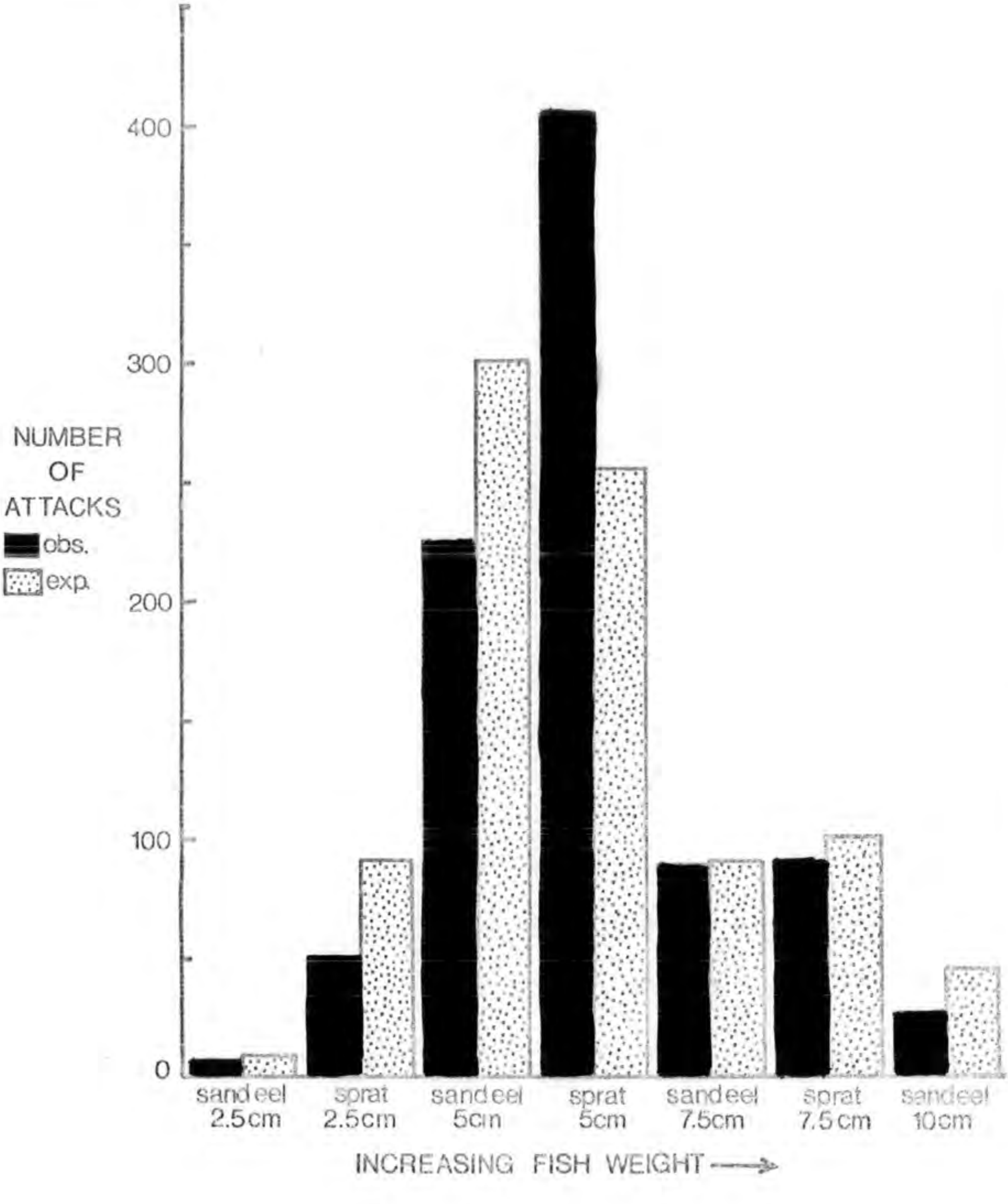


Figure 15

Frequency distributions of the number of observed and expected attacks on sprats and sand-eels of varying length (and weight), based on 896 attacks.

they comprised 62% sprats and 38% sand-eels.

Discussion

(i) Robbing intensity

The parasitic behaviour of Roseate Terns is obviously a highly ordered activity which responds to a variety of subtle changes in the numbers and types of potential prey carried by hosts. The responses to changes in host (i.e. prey) density are generally consistent with those described by Holling (1959a) for various predator-prey and parasitic-host relationships (for a recent summary, see Royama 1970). Thus the number of Roseate Terns engaged in robbing at any one time shows a direct numerical response to changes in the numbers of host terns (Figure 10). Moreover, the attack rate indicates a functional response such that the number of attacks launched per unit time shows a progressively decreasing rate of increase, rather than a constant one, as host density increases (Figure 11).

The small number of active parasitic terns compared with the number of hosts suggests that the limitation of attack rate was not imposed by competition for hosts but by handling time (Holling 1959b) which would result from swooping, wresting the fish from the host's bill (if the attack was successful) and then regaining height for the next attempt. As the rate of attack increased, the time taken to perform these manoeuvres would ultimately impose constraints on the maximum rate at which attacks could be mounted. My own handling time, i. e. time to record data, also showed a slight increase as host density increased but was not sufficient to account for the marked rate of decline in attack rate.

(ii) Robbing success

It seems plausible that the parasitic terns benefited from the confusion factor introduced by high densities of host terns in the colony. With relatively high attack rates and robbing success at greater host densities, it follows that robbing of this kind may be generally more successful in large tern colonies with a dense concentration of breeding birds.

It is less obvious, however, why robbing success should be better for smaller fish than for larger ones. Since almost all (99.8%) unsuccessful attacks were characterised by curtailment of the attack just short of actual physical contact with the host, an increase in the length of fish carried by hosts effectively resulted in a greater probability of disengagement from attacking manoeuvres. An aborted attack by the parasitic tern was sometimes seen to be preceded by anticipatory avoiding action by the host in the form of a slight downward or sideways deviation from the horizontal flightline. Lower robbing success when fish are large may, therefore, be related to more frequent or more effective (e. g. earlier) avoiding action by the host tern. Such a relationship could arise in various ways; firstly host terns with large fish were also liable to be pursued by Black-headed Gulls while terns with very small fish could pass by gulls with impunity (pers. obs.). Furthermore, Common Terns with large fish seemed more likely to be accosted by small bands of their own species which resort to robbing on Coquet Island during times of food shortage. Thus there is ample stimulus for promoting special caution in a tern that carries a large fish through the colony. This suggests that the host may learn that there is danger inherent in carrying a conspicuously large fish and so may be better prepared to forestall attack from Roseate Terns in these circumstances. A second possibility is that terns which bring in large fish are older, more experienced individuals which could be more adept at taking avoiding action, but there is no evidence for or against this.

Since the method of data collection inevitably underestimated attack rate, it is not possible at this stage to synthesise attack rates and robbing success to produce a realistic rate of food capture for comparison with Roseate Terns that forage at sea by conventional plunge-diving methods. However, the study indicates that this would be a rewarding area for further investigation.

(iii) Selection of hosts

Selecting a host for attack appears to be associated mainly with the dimensions of the fish being carried. Although 5cm sand-eels were the most abundant size class on 7 days out of 10, they were less preferred than 5cm sprats on each of these days. It seems likely, therefore, that fish smaller than 5cm sprats were suboptimal prey and that Roseate Terns searched selectively for larger items. Root (1967) suggested that Blue-grey Gnatcatchers Polioptila caerulea "overlooked" small prey because their energy yield was too low to warrant the effort involved in their pursuit, and parasitic Roseate Terns seem to adopt a similar policy. I frequently recorded that Roseate Terns and other tern species plunge-diving at sea would catch and eat a succession of very small fish but would not return to the colony until a larger fish had been caught. The validity of this observation was tested for Sandwich Terns in July 1969 when 130 successful dives were scored according to whether the fish was (a) swallowed on the spot or (b) retained in the bill and carried towards the colony. In each case the length of the fish was estimated and fortunately this assessment could usually be made before I knew if the fish was going to be swallowed or not. The change of behaviour in category (b) is very characteristic; after emerging from the water, the bird usually shakes itself free of water once or twice and then flies strongly in the direction of the colony, and I have little doubt that these fish were delivered to chicks. The mean size of fish swallowed was 5.3 ± 0.1cm (N=110) compared with 7.6 ± 0.3cm (N=20) for those carried, and the difference was highly significant ($t = 7.59$, 128 d. f., $p<0.001$). This bias was probably related to the food requirements of the chicks and it seems likely that, in the case of fish robbed by Roseate Terns, chicks rather than adults consumed most of the fish. Of 146 successful attacks, only 16 fish (11%) were swallowed by the parasitic tern on the spot. The rest were carried towards parts of the island occupied by breeding Roseate Terns and whenever a successful parasite was seen to alight at its nest-site with a stolen fish, the chick rather than the mate was fed.

The relatively low yield from robbing small prey items, especially in view of the needs of growing chicks, adequately accounts for discrimination against fish smaller than 5cm sprats but it is not clear why a greater preference was not shown for larger fish since these gave a better weight return per robbing attempt (Table 15). The availability of prey over 5cm is relatively low and active selection of these items may involve wasteful searching. In addition, Roseate Terns and their chicks probably experience increasing handling difficulties with prey longer than about 7.5cm. Observations in July 1969 of Roseate Terns plunge-diving at sea showed that they tended to take smaller fish (4.5cm ± 0.2cm, standard error) than Sandwich Terns feeding in the same situation. These and other records (Langham 1968) suggest that 5-7.5cm is the optimum size range for Roseate Terns.

(iv) Number of parasitic Roseate Terns

Since the general availability of both fish and airspace seemed opportune for several parasites to be active simultaneously, it is surprising that never more than five participated at once. If robbing sorties were of short duration, it is possible that many different individuals were parasitic during the course of a day. In 1969, however, there were about 500 Roseate Terns on Coquet Island and it is reasonable to suppose that more than 5 birds would have been active at any time if the robbing habit was at all widespread in the population. It is more plausible that a relatively small number of specialist Roseate Terns was making fairly long or repetitive sorties. Moreover, if robbing was widespread throughout the population as a potential means of supplementing fish capture, it might be expected that the intensity of parasitism would increase when food was scarce. In 1968, strong winds and rain for three days (14-16 July) caused exceptional weight loss and mortality of Roseate Tern chicks through starvation. Parasitic activity was monitored from 16-18 July (when weight gains remained well below average) but was found to be no more nor less intense than usual. Thus parasitism did not increase when food was scarce; on the contrary, it always become more prevalent when food was more abundant. On a day-to-day basis, however, it was striking how consistent the level of parasitic activity turned out to be. This situation was in marked contrast to the sporadic outbursts of piracy by Common Terns.

In July 1968 and in June 1970, widespread intraspecific robbing by this species suddenly started during periods of food shortage (indicated by small numbers of terns returning regularly to the colony with fish, poor growth performance and heavy mortality of chicks) and took the form of small bands of terns harrying other terns that had fish. These tactics were not observed at all in 1969 and obviously appear only when fish are in short supply (Chestney 1970, Hays 1970). The sudden emergence and intense form of this behaviour suggested that many Common Terns were capable of "switching on" to it when the need arose.

Although there is no definite proof, the evidence of the persistently low intensity of robbing by Roseate Terns, even during a food shortage, contrasted with the widespread opportunism of Common Terns in the same situation, strongly suggests that only a few specialist Roseate Terns were capable of utilising the sophisticated robbing strategies observed on Coquet Island. Specialisation of this sort is not uncommon in birds. In a colony of Common Terns in Massachusetts, for example, one conspicuous individual spent much of its time robbing its neighbours instead of catching fish at sea like all the other birds in the colony (I. Nisbet, pers. comm.).

To summarise, it appears likely that robbing behaviour is confined to a relatively small number of specialist individuals among the Roseate Terns that breed on Coquet Island. It is therefore improbable that the colony of Roseate Terns as a whole acquires most of the food required for self- or chick maintenance by regular parasitism of other terns.

SECTION II

FACTORS INFLUENCING FEEDING RATES

This section is concerned with the variables that determine the rate at which terns obtain food. Part 1 describes the influence of diurnal and tidal rhythms on feeding activity. Parts 2, 3 and 4 consider the effects of the age of the bird, prey abundance and wind/sea conditions respectively on the rate of prey capture by plunge-diving.

PART 1. Feeding rhythms

Introduction

Several authors (e. g. Franz 1937, Boëtius 1949) have investigated relative changes in the rate at which food is transported to chicks at different times during the day, and have noted that a similar pattern emerges for many species: there are peaks of feeding activity at dawn and in the evening, with less activity in the intervening period. This diurnal cycle has been previously demonstrated for Common and Arctic Terns on the Farne Islands, (Pearson 1964) and on Coquet Island, (Langham 1968) and is a predictable daily phenomenon. In 1967, however, Boecker reported that the peak foraging times of Common Terns and Arctic Terns at Wangerooge (W. Germany) were dictated more by the tidal than by the diurnal cycle. The purpose of this part of the study was to determine the contribution of both diurnal and tidal components to the feeding rhythms on Coquet Island and to investigate their biological significance.

Methods and study areas

In May 1968, preliminary observations were made on a subcolony of about 200 nests of Sandwich Terns on Coquet Island to determine the rate at which birds returned to feed their mates. During July and August 1969, a fixed area of Coquet Island was chosen and counts made at 15-minute intervals during the course of the day to determine the number of terns of different species that entered the area carrying fish. A total of 80 hours observation was made over 10 days during which time the arrival of 3,011 terns with meals was recorded. Since a major source of variation in the input of fish to a colony is likely to be the success of the adults at finding food, a complementary study was made of terns foraging in Druridge and Newbiggin Bays, using the methods described in Section I. Some additional observations of foraging Sandwich Terns were made at Scolt Head Island in Norfolk (G.R. TF 8046). The phasing of daily tidal cycles at these areas was recorded and checked by reference to appropriate nautical tables.

In addition to plunge dives, records were also kept of those dives that were terminated before reaching the water surface; the tern starts as if to plunge dive but checks its descent in mid-flight, regains height and resumes hunting. These dives are here referred to as "intention dives". From these observations, four parameters of fishing ability were calculated. They are:

(i) fishing success $\left(\frac{\text{number of successful plunge dives}}{\text{total number of plunge dives}} \times 100\right)$

(ii) rate of plunge diving (plunge dives/bird/minute)

(iii) rate of intention diving (intention dives/bird/minute)

(iv) rate of fish capture (successful plunge dives/bird/minute)

Results

(i) Pattern of food input to the colony

Temporal variations in the numbers of Sandwich Terns arriving at Coquet Island with fish on 16 May 1968 are shown in Figure 16a. The pattern is essentially bimodal with peaks at dawn and in the early evening. Apart from a smaller peak around mid-day, the level of activity subsided in mid-morning and late afternoon. In 1969, it was established that a similar bimodal pattern was typical for each of the four tern species that colonise the island (Figure 16b).

When the 1969 data are plotted on a tidal scale, however, not all species adhere to the same pattern (Figure 17). For Common and Sandwich

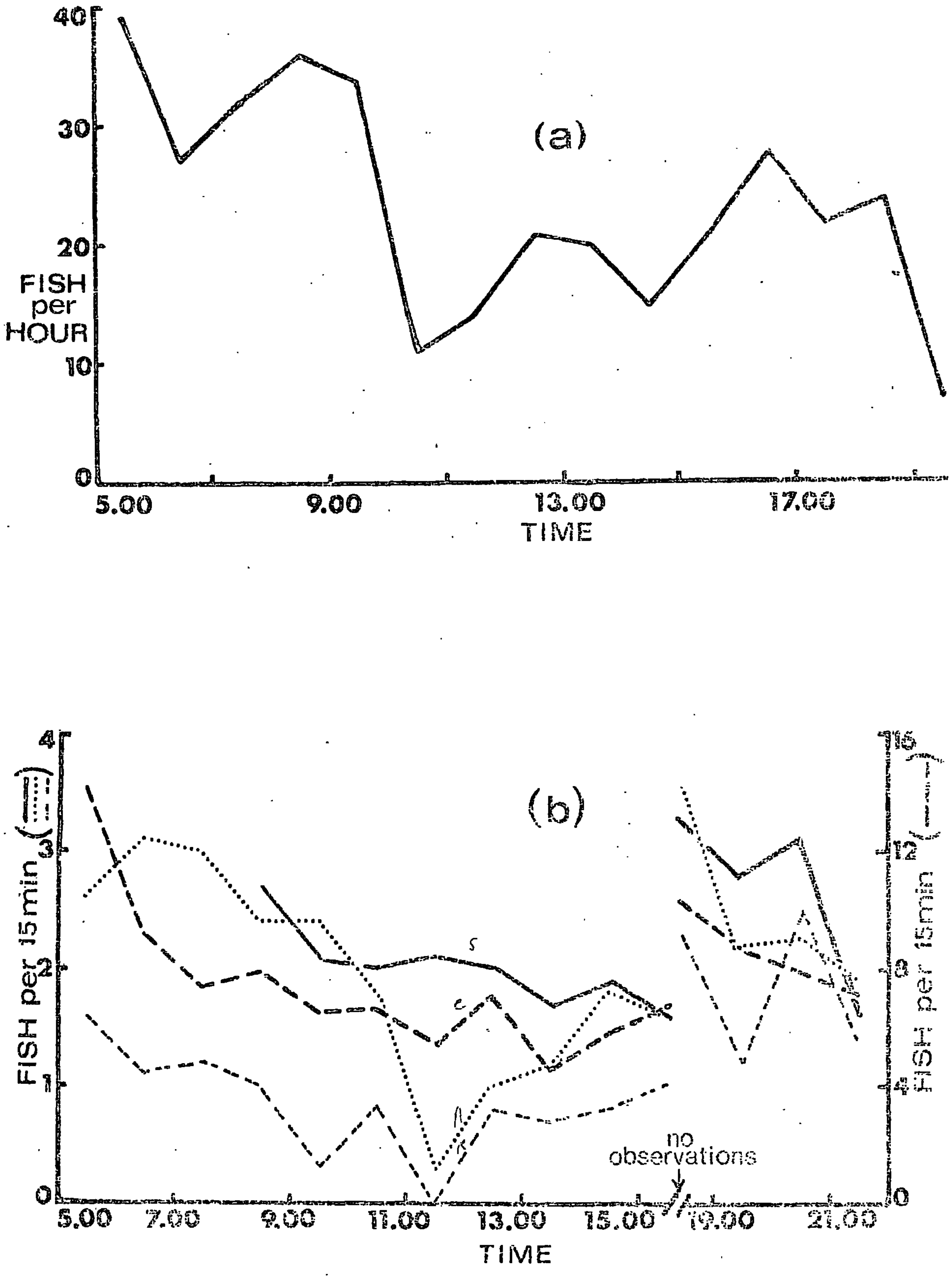


Figure 16

Diurnal patterns of food carrying activity
(a) for Sandwich Terns on 16 May 1968
(b) for all four tern species in July and August 1969.

Key to (b) —— Sandwich
······ Arctic
– – Roseate
----- Common

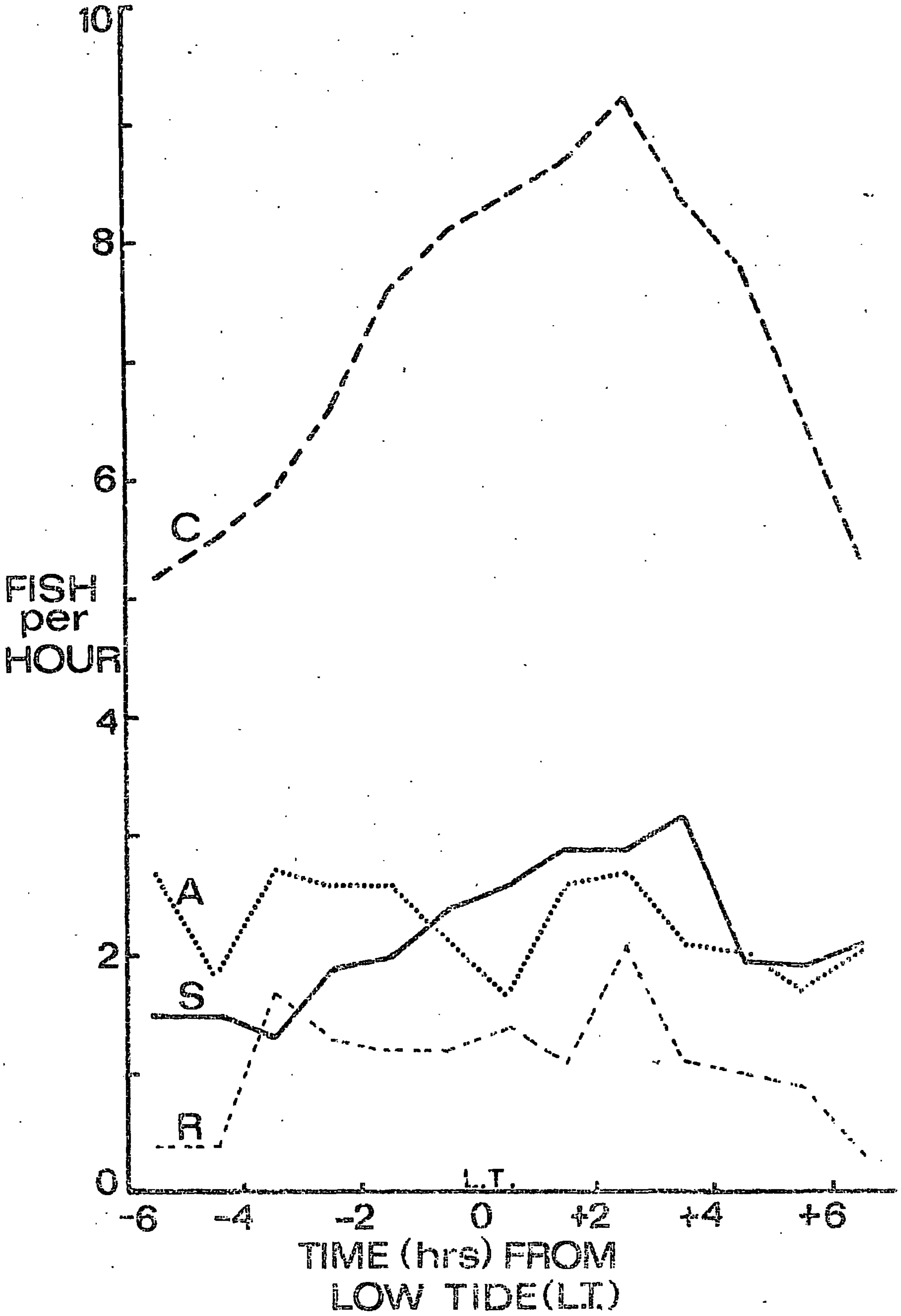


Figure 17

The numbers of different tern species bringing fish into a discrete area of Coquet Island throughout the tidal cycle. Derived from several days' observations - July and August 1969. (C = Common, A = Arctic, S = Sandwich, R = Roseate).

Terns, the pattern is unimodal: Relatively few birds carried food at high tide but, as the tide ebbed, the number increased steadily and reached a maximum 2-3 hours after low water before decreasing again with the approach of the next high tide. While Roseate Terns also showed a reduction in food-carrying at extreme high tide (low water ± 5-6 hours) no distinct pattern was obvious between consecutive high tides apart from a brief burst of activity coinciding with the peak for Common Terns. The pattern for Arctic Terns does not appear to be related to the tidal cycle at all. In summary, the number of terns ferrying food to the colony at any particular times is determined both by the hour of day and the state of the tide; a similar diurnal periodicity is shown by the four tern species but the importance of the tidal influence varies between species.

A convenient way of expressing the interaction of time and tide is to superimpose the effect of a high or a low tide on each portion of the diurnal pattern of activity. There were sufficient data to make this comparison for the Common Tern in 1969 but not for other species. Approximately 6 hours separate the times of a consecutive high and low water in any tidal cycle. A low tide regime was therefore defined as the time 3 hours before to 3 hours after the time of low water and a high tide regime as 3 hours before to 3 hours after the time of high water. On this basis, each hour on any particular day falls into either the low tide or the high tide category. The number of terns entering the colony with fish per 15 minutes was tabulated for state of tide and the values averaged over consecutive 4 hourly periods to provide adequate samples for comparison (Table 16).

Table 16

Effect of high and low tide regimes on diurnal numbers of Common Terns that carried meals into a fixed area of Coquet Island in 1969.

Time	Numbers carrying meals per 15 minutes			
	Low water	No. of hours	High water	No. of hours
Before 8.00	10.3	9	6.5	4
8.01 - 12.00	7.9	7	6.8	16
12.01 - 16.00	6.3	13	5.3	7
16.01 - 20.00	9.0	5	7.0	3
After 20.00	8.0	5	7.3	9

Comparison of the terns' performance under the two tidal regimes was made with Student's paired t-test and shows that, irrespective of the time of day, significantly more birds entered the colony with food per unit times under low tide conditions than under high tide conditions ($t = 2.81$, 8 d. f., $p<0.05$).

(ii) Fishing ability of Sandwich Terns during a tidal cycle

(a) Fishing success

Figure 18 shows the fishing success at Druridge Bay in 1968 and 1970, and at Newbiggin in 1969. Each point is a mean derived from respectively 14 days observation in 1968, 8 days in 1969 and 13 days in 1970. Records for birds feeding in large flocks, presumably on dense shoals of fish, are excluded from this analysis. In each year, the daily information on proportion of plunge dives yielding fish was subdivided according to "tidal hours" (hours before and after time of low water) and then regrouped to give a mean fishing success per tidal hour for the whole season. Figure 18 shows that in 1968 and 1970, fishing success tended to be minimum at high tide and maximum at low tide (1968) or shorty after (1970) although in neither year were the hourly values significantly heterogeneous by a chi-square test. In 1970 there was a brief reduction in fishing success at low water but apart from this, the overall patterns in the two years were remarkably similar. Moreover, although success varied around different levels in 1968 and 1970, the difference in success between maximum and minimum values was 17% in both cases. Tidal changes in fishing success at Newbiggin Bay in 1969 are conspicuous by their departure from the Druridge Bay pattern. Values were relatively high and followed a bimodal distribution with peaks occurring mid-way through the ebb-tide and flood-tide periods.

It is also noticeable that a complete tidal cycle of fishing success is not represented in any of the graphs in Figure 18. The absence of values at high water (LW ± 6 hours) reflects the paucity of terns foraging at this time. Thus it was a common feature of both Newbiggin Bay and Druridge Bay that high tide was associated with a definite lull in foraging activity.

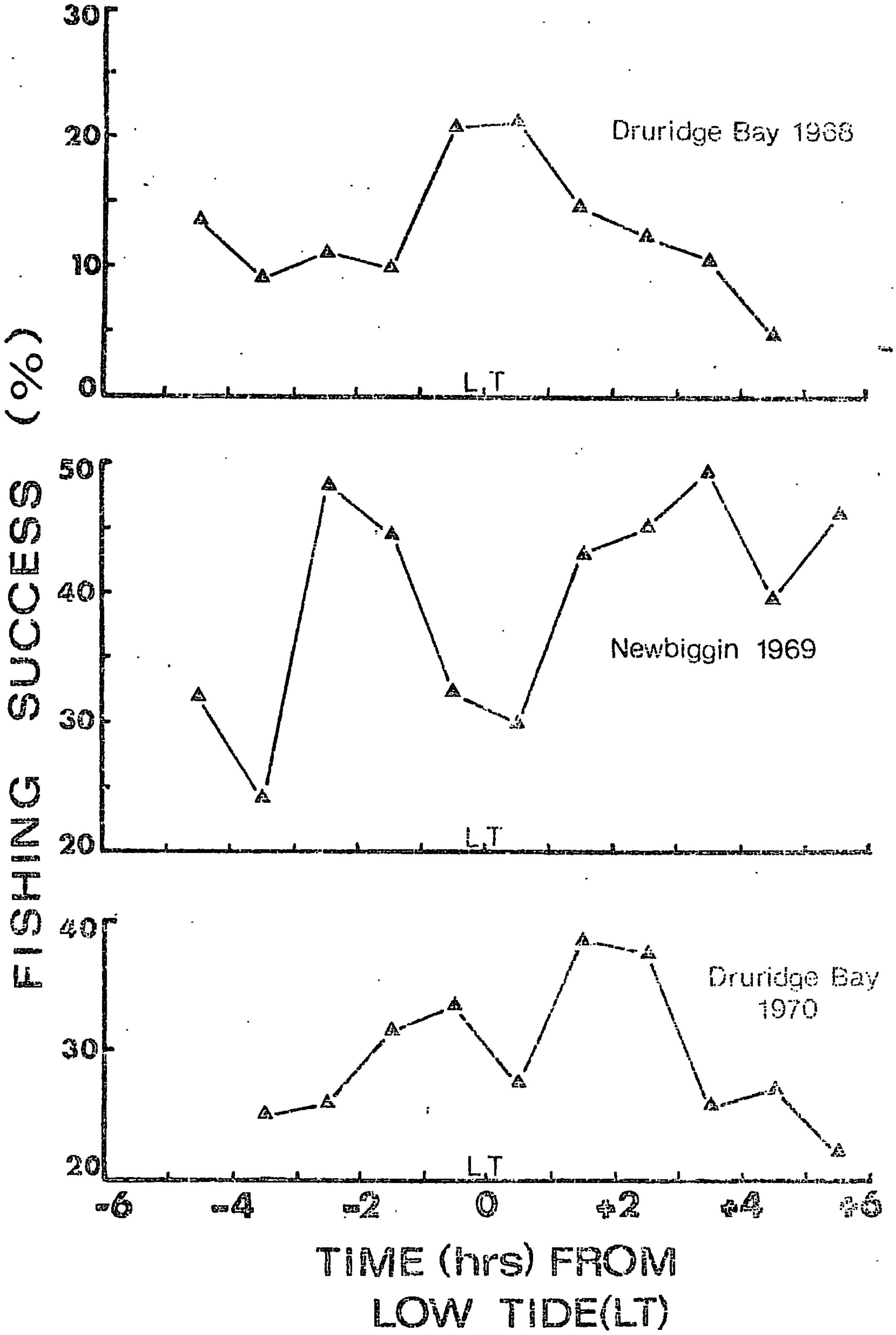


Figure 18

Tidal patterns of fishing success of Sandwich Terns, 1968-1970.

These results suggest that in these areas more fish are available to be caught around low water than at high water. At Druridge Bay, fish could easily be trapped in the shallow backwaters and troughs that form between sandbanks as the tide recedes. These prey would be readily visible and vulnerable to foraging terns. Observations at Scolt Head lend support to this suggestion. A major topographical feature of the beach at Scolt in 1969 was a broad sandbank situated near low water mark. On 19 August 1969, I observed the influence of this bank on fishing activity of Sandwich Terns. As the tide ebbed, terns began to congregate over the bank and started diving, initially in small numbers and with little success (Figure 19). The number of foraging birds and their capture success gradually increased, however, and soon 90 birds were diving intensively (3-4 dives per bird per minute) and achieving over 30% success. The depth of water over the ridge was such that fish were most readily accessible to the terns about 60-70 minutes before low water. Thereafter, numbers and success declined and eventually fishing ceased altogether just prior to the exposure of the sandbank.

(b) Diving rates

When mean daily fishing success of Sandwich Terns was compared with mean daily rate of 'combined' diving (combined = plunge + intention) for 21 days, success was directly correlated with diving rate and the relationship was highly significant ($r = +0.64$, 19 d. f., $p<0.01$). On a daily basis, fishing success was also correlated with the rate of plunge diving ($r = +0.61$, 19 d. f., $p<0.01$) but not with the rate of intention diving. The diving frequency of Sandwich Terns is therefore a good indicator of their fishing success and this relationship should also hold during the course of a tidal cycle. Rates of plunge diving and intention diving in 1969 and 1970, calculated from observations on individual birds, are plotted separately against tidal hours in Figure 20. In both years, the rate of plunge diving declines towards a high water minimum of about 1 dive per 2 minutes, and this corresponds to the decline noted in fishing success at the same stage of the tide. The rate of

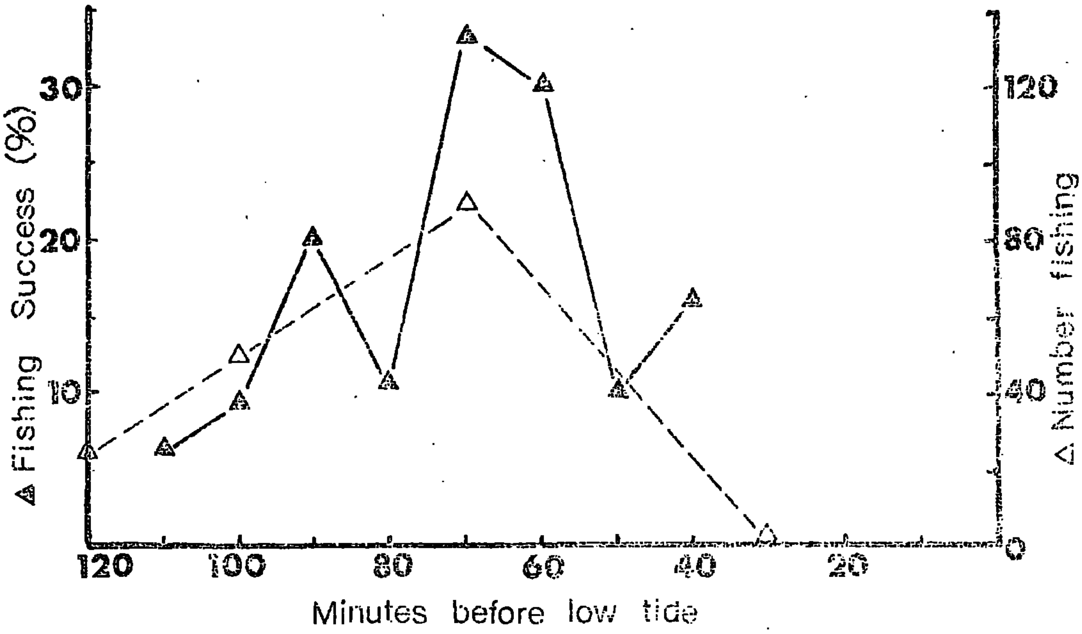


Figure 19

Effect of ebb-tide on the numbers of Sandwich Terns, and their success while fishing over a sandbank at Scolt Head Island on 19 August, 1969.

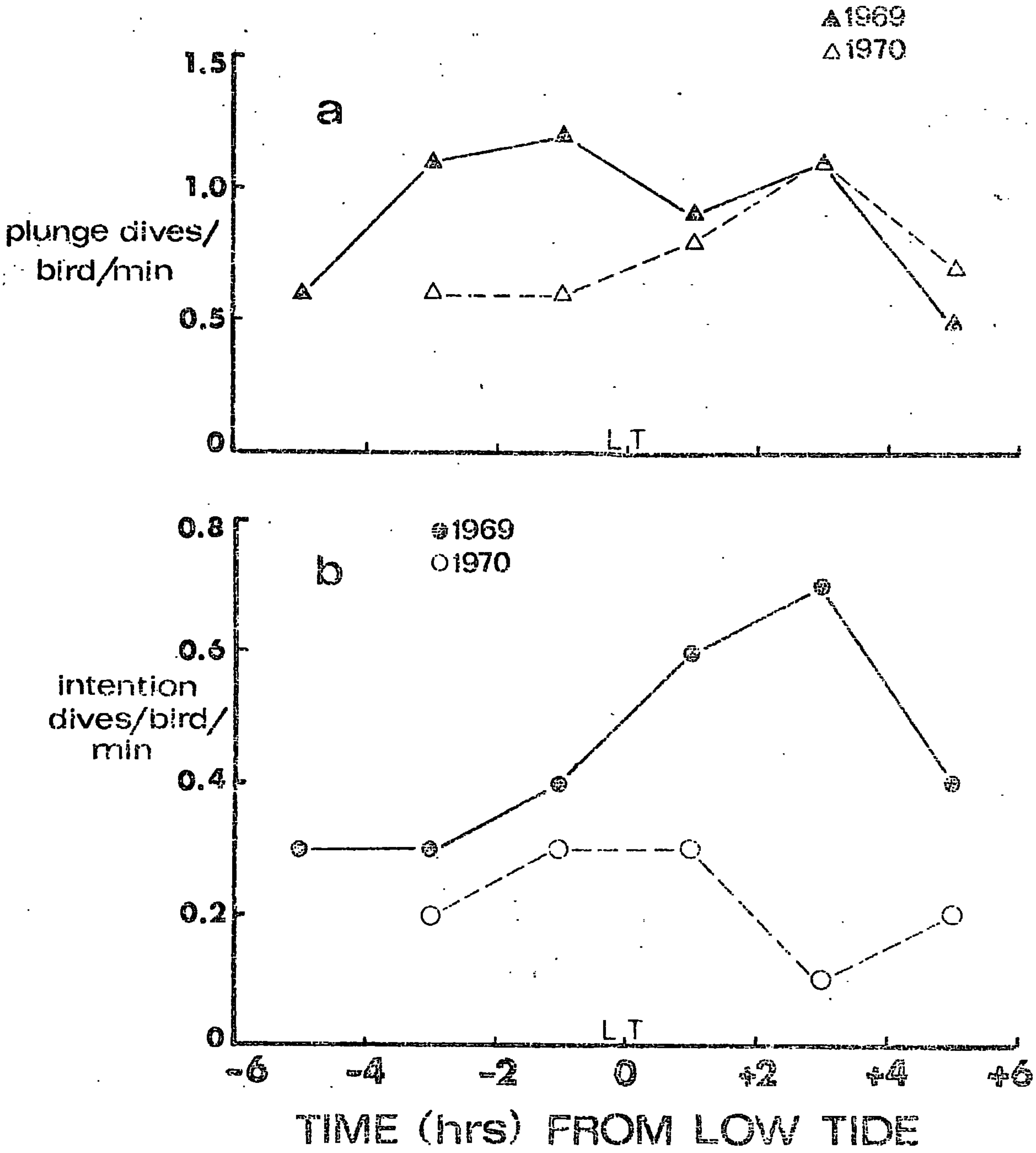


Figure 20

Rate of diving (a = plunge, b = intention)

by Sandwich Terns during a tidal cycle.

intention diving in 1969 followed a unimodal pattern with minima at high water but in 1970 the pattern was less clearly defined.

(c) Rate of fish capture

This measure is effectively a product of fishing success and diving rate and should therefore vary closely with these over a tidal cycle. This prediction is fulfilled in all 3 years; there is a peak at the beginning of flood tide and a general decline towards high tide (Figure 21). At Newbiggin in 1969, the depression in fishing success and plunge diving rate at low water is reversed due to the averaging effect of combining data at 2-hourly intervals. The maximum rate of fish capture (approximately 1 fish every 2 minutes) is almost twice as fast as the maximum rate achieved at Druridge Bay in 1968 and 1970, suggesting that a relatively rich food supply was available to Sandwich Terns at Newbiggin in July 1969. In neither area was there any tidal pattern in the size of fish caught.

(iii) Fishing ability of Common Terns during a tidal cycle

Tidal variations in fishing ability correspond closely with those found for the Sandwich Tern. The pattern of fishing success is shown for 1968 and 1969 in Figure 22. (This species was not studied in 1970). Like Sandwich Terns, success is maximum towards low water and minimum at high water.

Rates of plunge diving and intention diving in 1969 are plotted against tidal hours in Figure 23. The trend in plunge diving rate is similar to that for fishing success. The rate of intention diving appears to be inversely propoetional to the rate of plunge diving but the relationship is not statistically significant. The net effect of these variations in fishing success and diving rates is that the rate of fish capture is smallest at high tide and greatest about 3 hours after low water when peak activity occurred at Coquet Island itself (Figure 24).

(iv) Fishing ability of Roseate Terns during a tidal cycle

It was not possible to make a systematic study of this species which rarely frequents the inshore zone. However Roseate Terns were occasionally

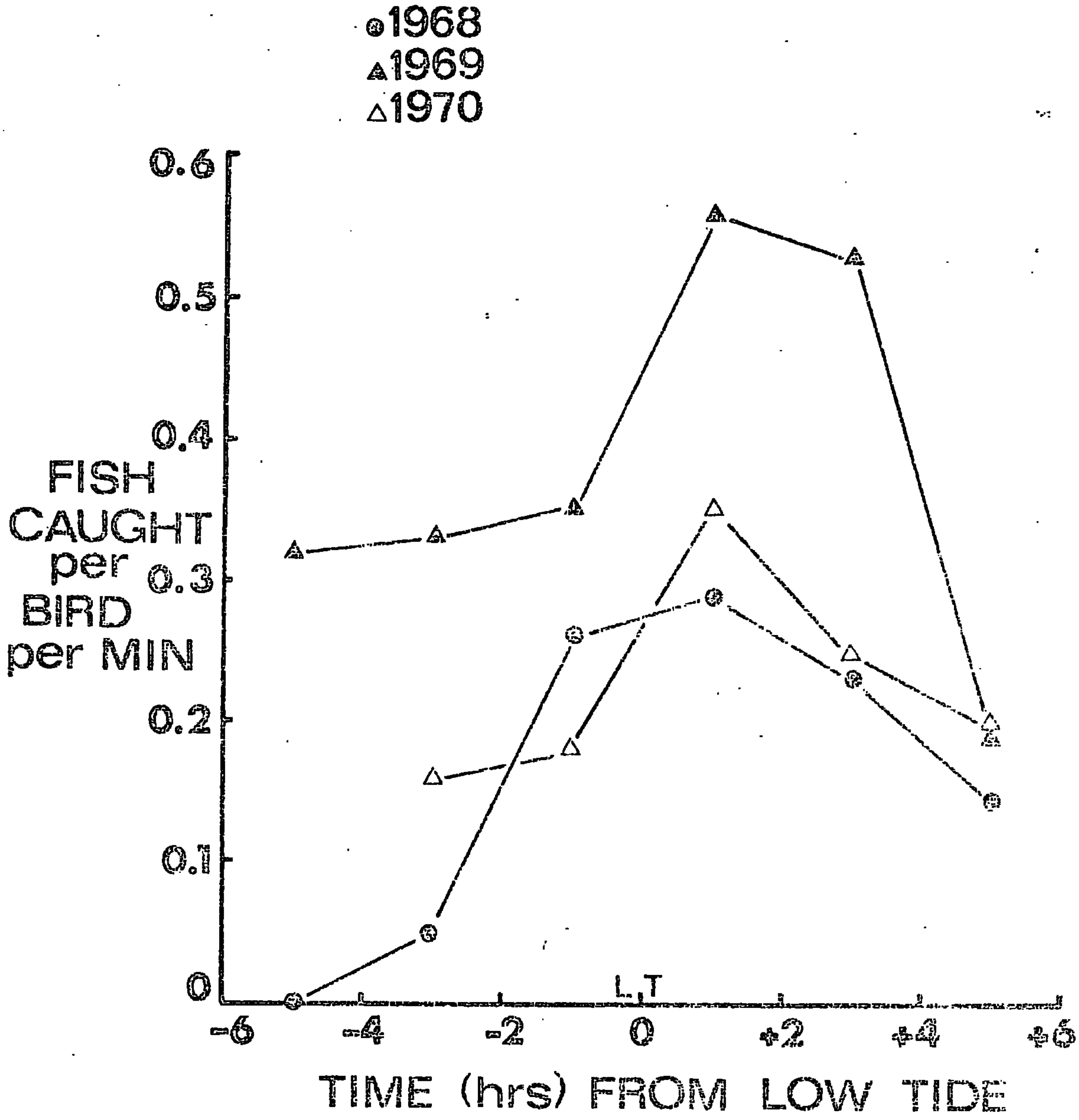
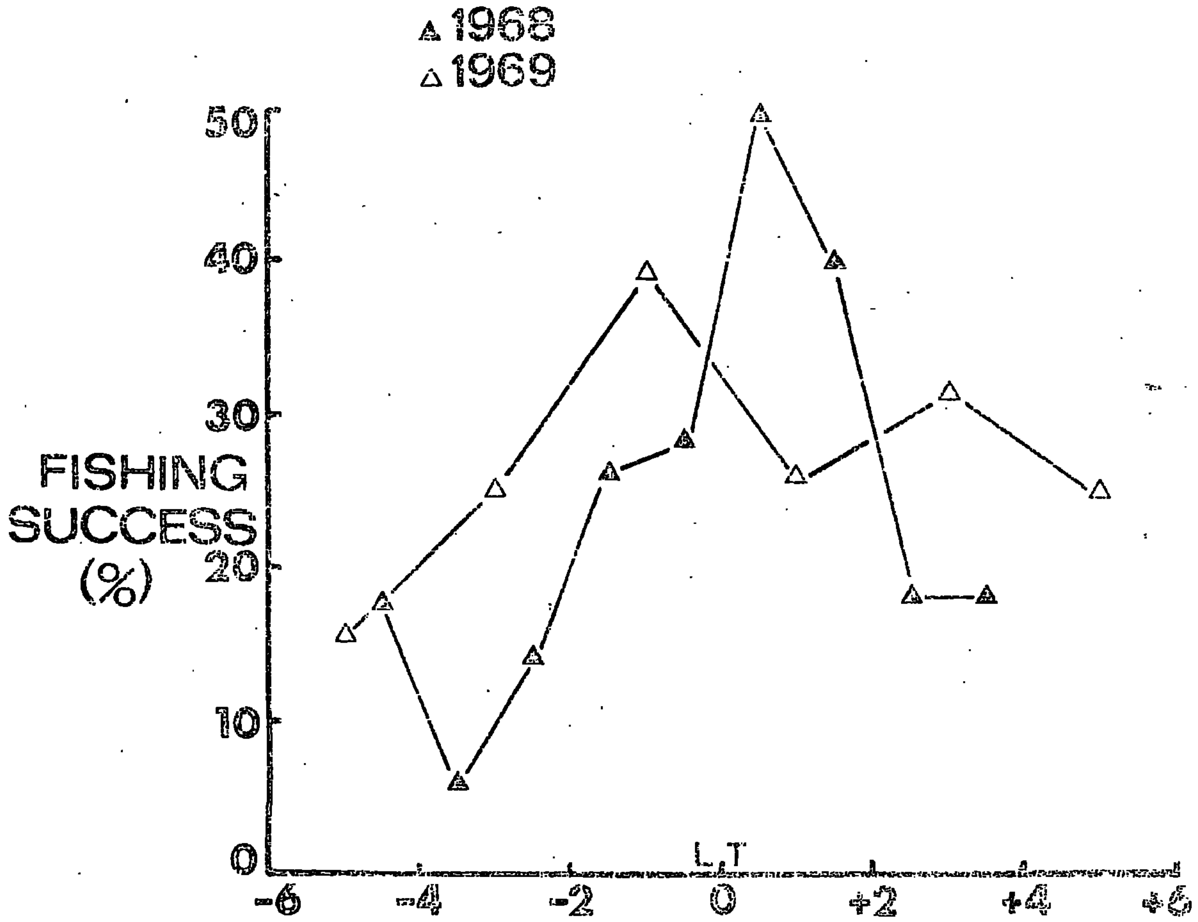


Figure 21

Tidal patterns in rate of fish capture by Sandwich Terns in three different years.



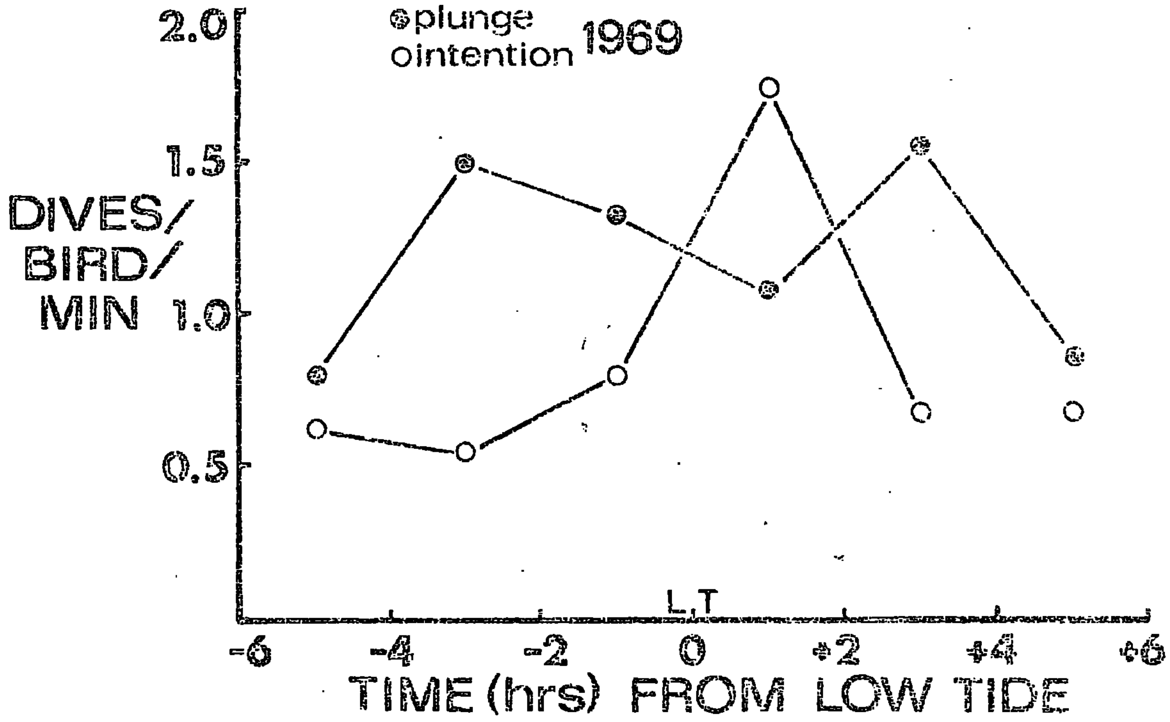


Figure 22 (above): Tidal patterns of fishing success of Common Terns.

Figure 23 (below): Tidal patterns of plunge and intention diving by Common Terns.

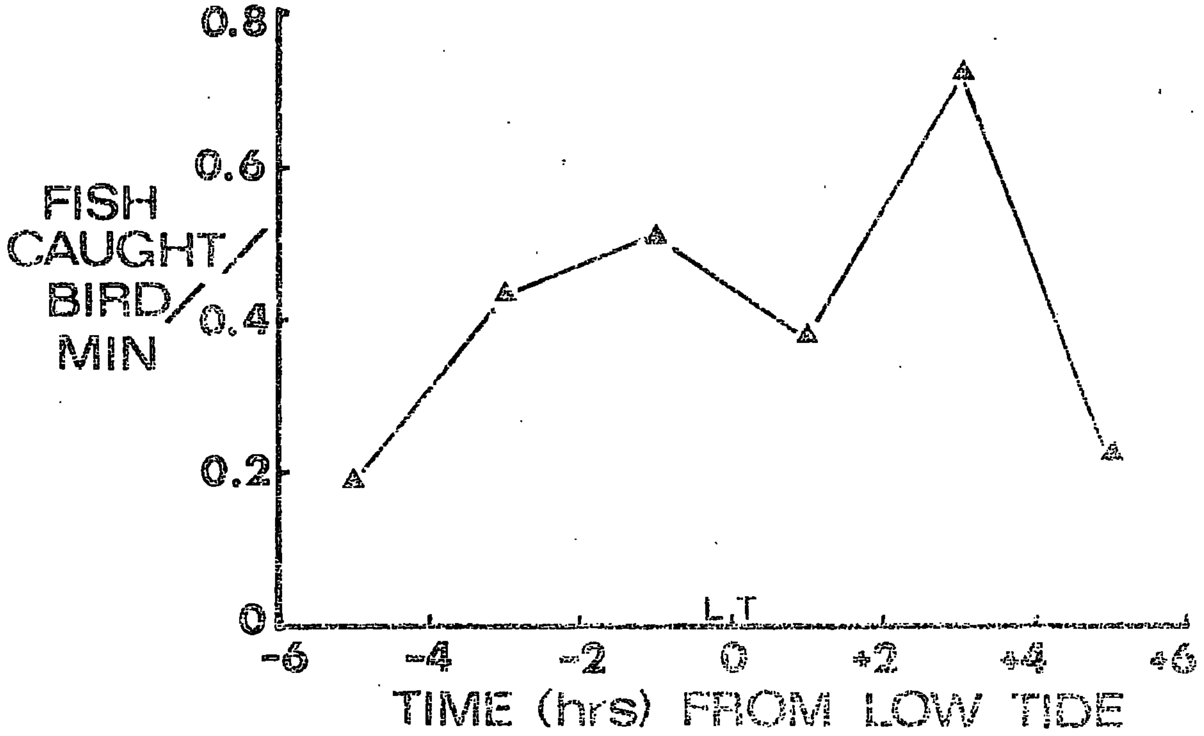


Figure 24

Rate of fish capture shown by Common Terns over a tidal cycle.

found fishing at Newbiggin in 1969 and a few observations were made. These show that this species resembles the others in diving and capturing fish at rates which are lowest at extreme high water and highest about halfway through the flood tide (Figure 25).

(v) Tidal differences between Sandwich and Common Terns

When the patterns of fishing success for Sandwich Terns and Common Terns at Druridge Bay in 1968 are superimposed on the same graph (Figure 26) it is evident that Common Terns were the more successful throughout most of the tidal cycle. Secondly, it appears that this disparity was greater at low water than at high water. Figure 27 shows the hourly tidal differences in success, with 1 standard error either side of the mean. The standard errors were calculated as follows. Each hourly difference in success was first tested for significance by a 2 x 2 chi-square analysis. Where differences proved significant, their standard errors = $\sqrt{\frac{p_1 q_1}{n_1} + \frac{p_2 q_2}{n_2}}$ where p_1 and q_1 are the proportions of successful and unsuccessful dives respectively for one species, n_1 the number of dives for that species, and p_2, q_2, and n_2 are the corresponding values for the other species (Snedecor and Cochran 1967, p. 221). Where fishing success is not significantly different between species, the standard error of the difference is given by $\sqrt{\frac{pq}{n_1} + \frac{pq}{n_2}}$ where p = the combined proportion of successful dives by both species, and q = the combined proportion of unsuccessful dives by both species (Snedecor and Cochran, op. cit., p. 220). Interspecific differences in fishing success were statistically significant at the following tidal stages: 2 hours before low water ($X^2 = 11.79$, 1 d. f., $p<0.001$), 1 hour after low water ($X^2 = 9.88$, 1 d. f., $p<0.01$), and 2 hours after low water ($X^2 = 9.02$, 1 d. f., $p<0.01$); all other differences were statistically insignificant. Inspection of the standard errors (Figure 27) reinforces the validity of a greater interspecific difference in fishing success as the tide ebbs and a decrease in the size of the difference as the tide floods again. In short, Common Terns fished more successfully than

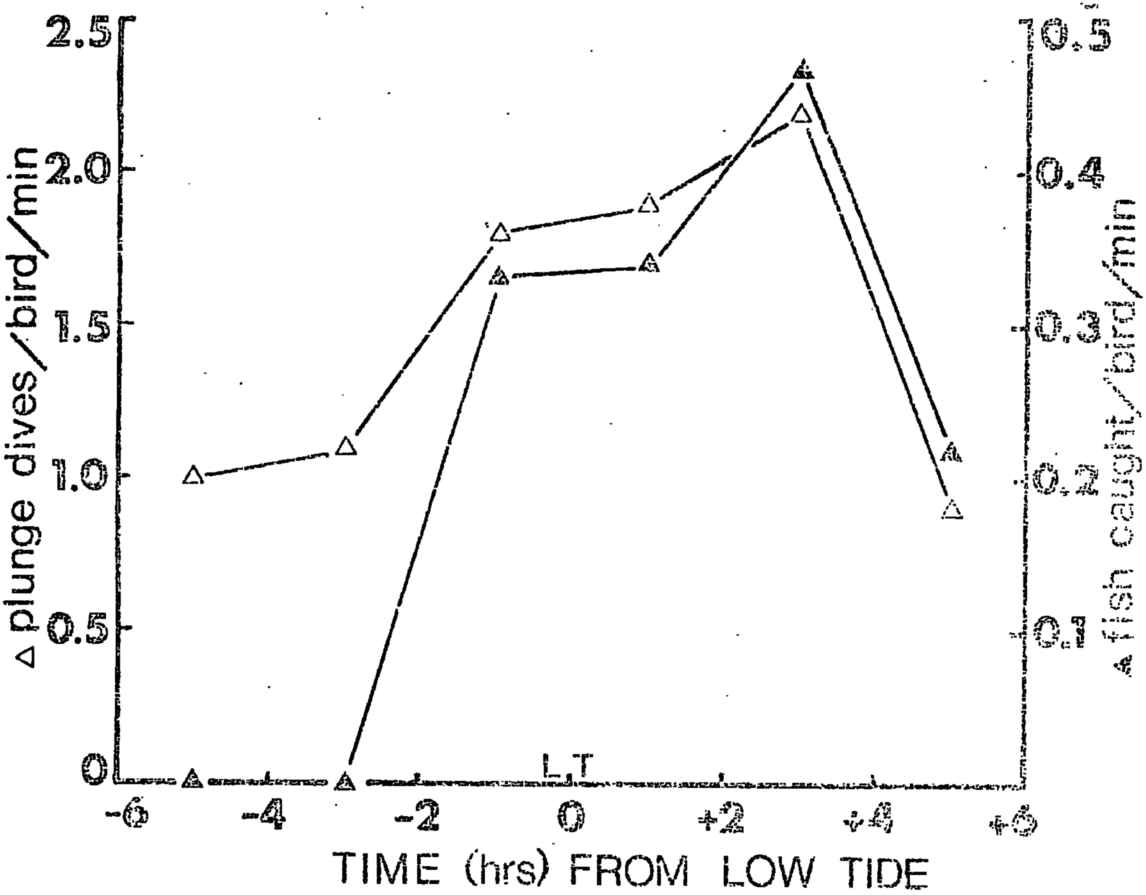


Figure 25

Rate of plunge diving and fish capture by Roseate Terns during a tidal cycle.

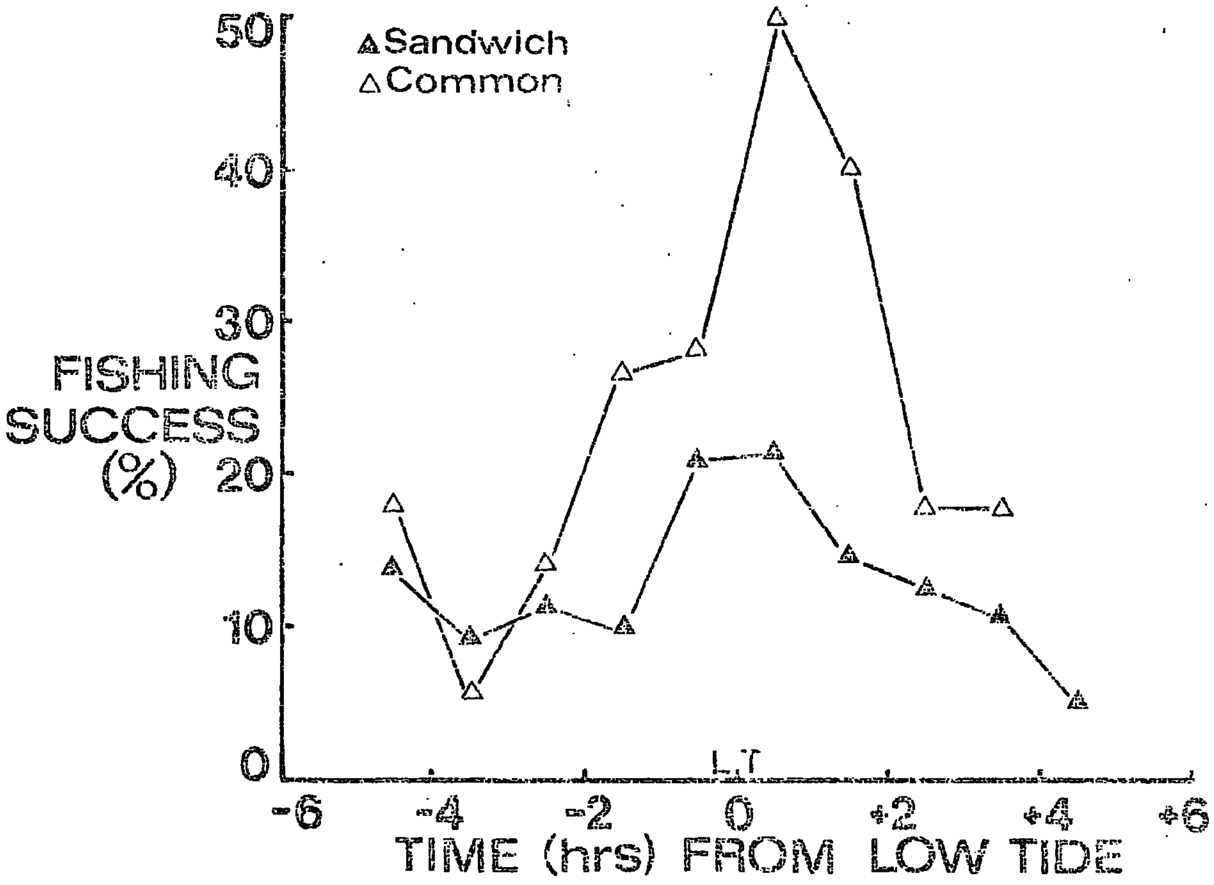


Figure 26

Fishing success of Sandwich and Common Terns during a tidal cycle. Data from Druridge Bay, 1968.

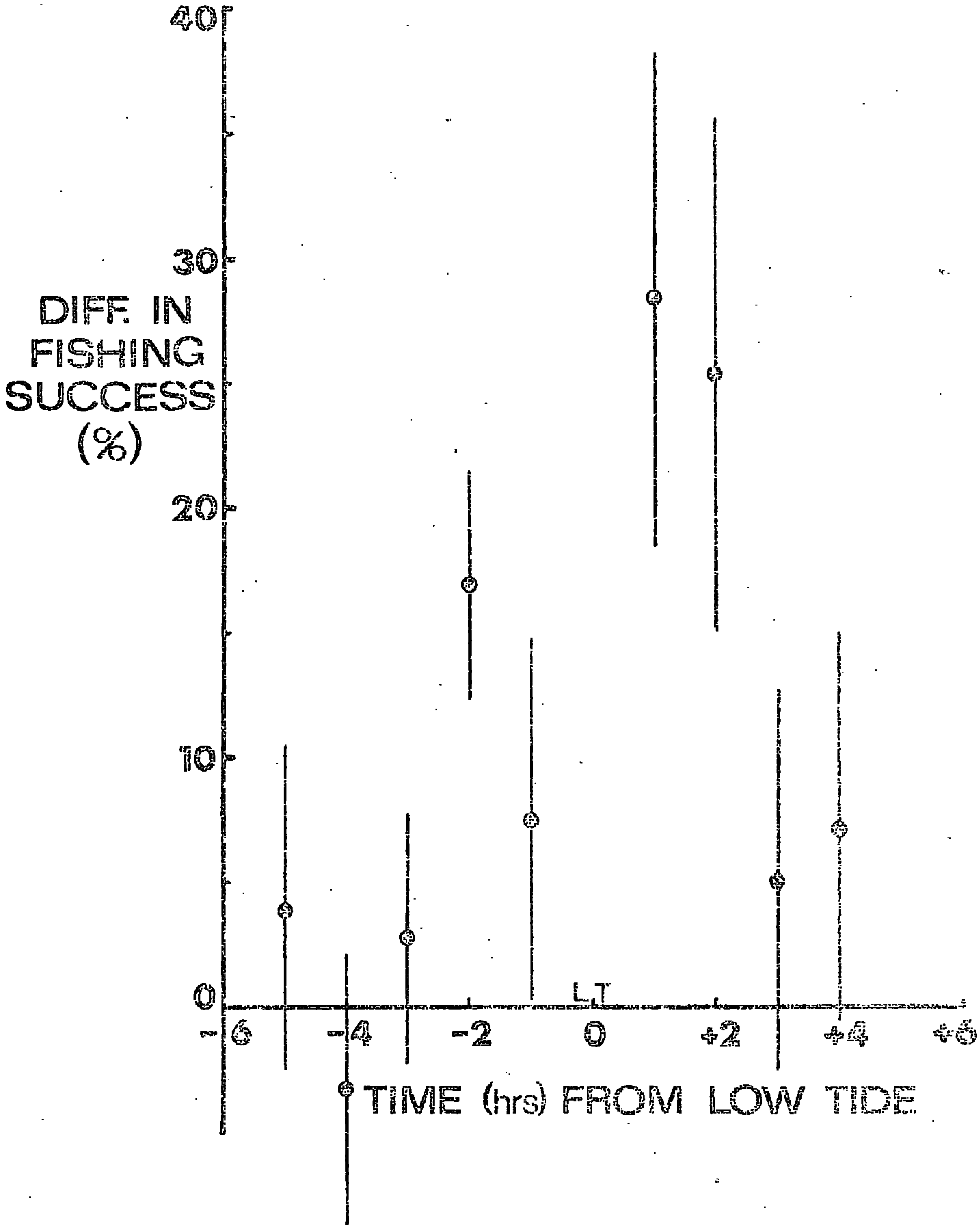


Figure 27

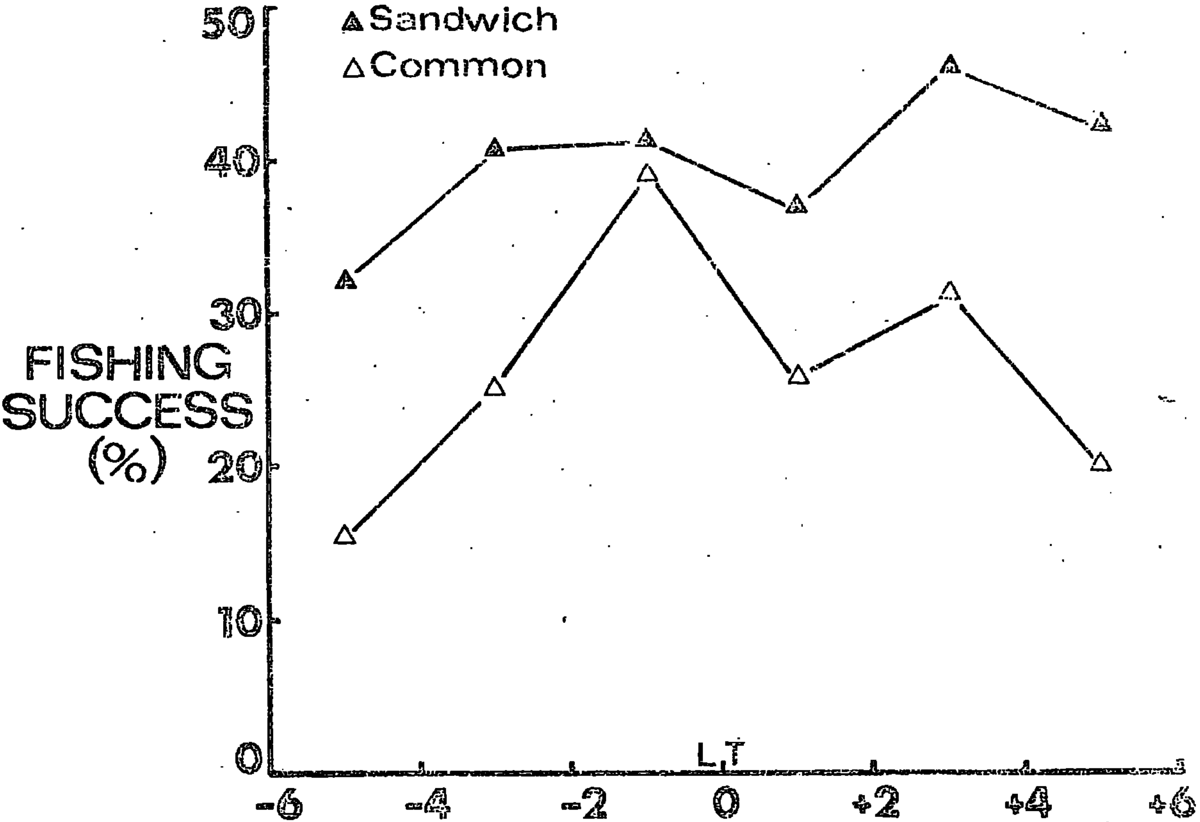
Difference (± 1 standard error) in fishing success between Common and Sandwich Terns at hourly intervals in the tidal cycle (Druridge Bay, 1968).

Sandwich Terns over the tidal cycle at Druridge Bay and also achieved proportionally better success at low tide than Sandwich Terns.

In 1969, the situation was totally reversed and Sandwich Terns tended to catch fish more successfully than Common Terns at all stages of the tide (Figure 28). However, the sample sizes for Common Terns were appreciably smaller than those for Sandwich Terns and the only significant differences occurred during flood tide between 3 and 4 hours after low water ($X^2 = 7.21$, 1 d. f., $p<0.01$) and between 5 and 6 hours after low water ($X^2 = 4.33$, 1 d.f., $p<0.05$). Interspecific differences tended to be least at low tide and greatest at high tide (Figure 29) but the variability was high and the only significant disparities occurred between low water and the latter portion of the flood tide phase.

Discussion

The results show that both diurnal and tidal factors influence the intensity of food-carrying activity of terns on Coquet Island. The diurnal variation in this activity was very similar to the changing rate at which chicks of Common Terns are fed during the day on Coquet Island (Langham 1968). Similar diurnal rhythms are characteristic of several other species of seabirds, notably Shags Phalacrocorax aristotelis and Eider Ducks Somateria mollissima (Rollin 1968) and Kittiwakes Rissa tridactyla (Pearson 1964). Moreover, the same bimodal pattern of feeding rate also emerges for various land-birds, e. g. White-backed Woodpecker Dendrocopos leucotos (Franz 1937), Robin Erithacus rubecula (Boëtius 1949) and House Sparrow Passer domesticus (Summers-Smith 1963, pp. 84-85). The widespread occurrence of this rhythm suggests that it is motivated by basic maintenance requirements. Thus, the dawn peak of feeding activity probably arises from the hunger of the adults and chicks on awakening. The diminishing hunger which results from this early burst of intense activity may induce the mid-day lull although this may also be a necessary rest period. Finally, the evening peak is consistent with the need for a final bout of feeding before the onset of nightfall.



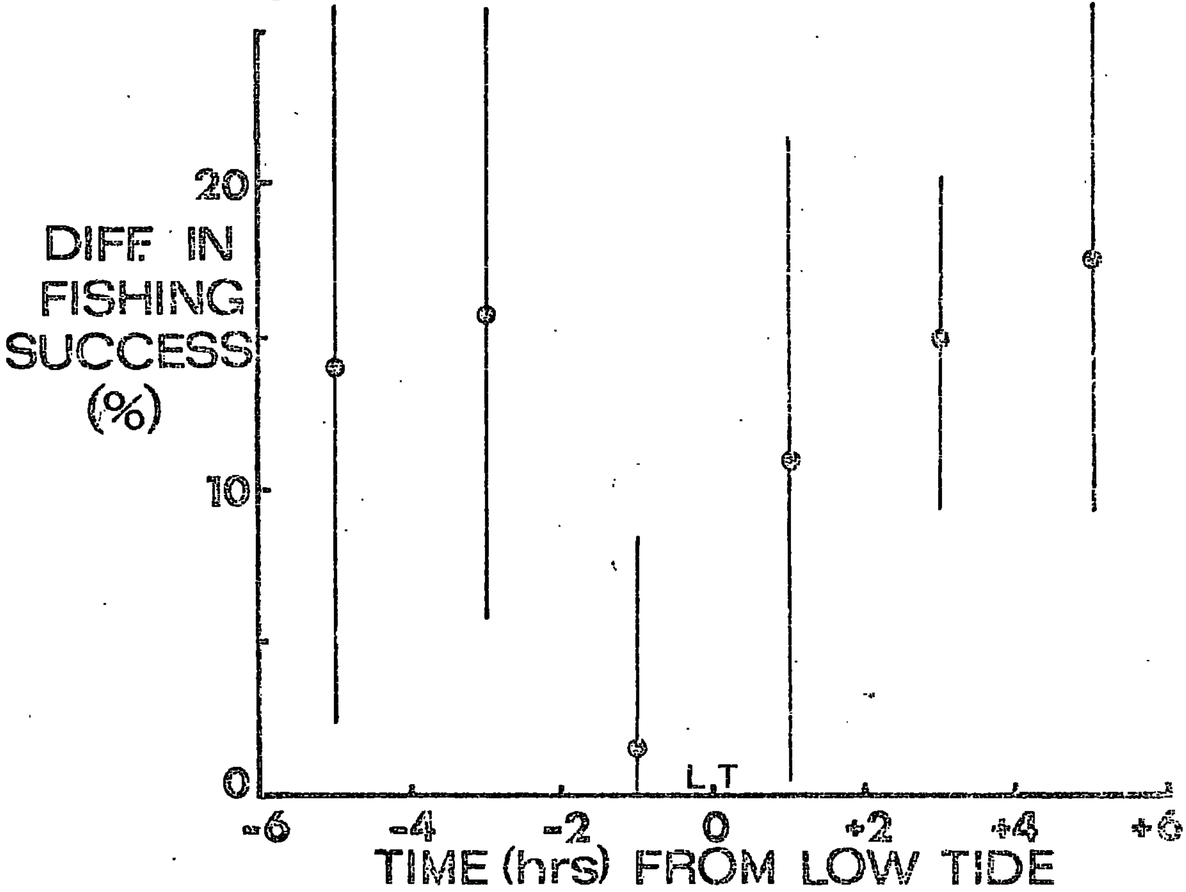


Figure 28 (above): Fishing success of Sandwich and Common Terns during a tidal cycle. Data from Newbiggin, 1969.

Figure 29 (below): Difference (± 1 standard error) in fishing success between Common and Sandwich Terns at hourly intervals in the tidal cycle (Newbiggin, 1969).

Superimposed on this fixed diurnal pattern is a tidal component and since the times of high and low tide vary from day to day, the phasing of its effect on feeding activity will also shift over successive days. The nature of this component is that more birds arrive at the colony with food at low tide than at high tide. This finding is in direct agreement with Boecker's (1967) observation that the chicks of Common and Arctic Terns at Wangerooge (W. Germany) received more feeds per hour at low tide than at high tide, and that the numbers of birds feeding out at sea was also much higher at low tide. Boecker found that foraging terns were attracted to a spot centred over an offshore submarine ridge. As the tide ebbed, the water overlying the ridge became progressively shallower and presumably made the fish relatively more accessible to the diving terns than in the deeper water elsewhere. Salt and Willard (1971) found that Forster's Tern S. fosteri did not disperse evenly over the entire surface of a non-tidal pond near San Francisco but tended to hunt along the gradually sloping margin. The authors saw no reason to suppose that fish were more common at the edge and speculated that there must have been a greater probability of capture there. Unfortunately, neither Boecker nor Salt and Willard tested the implications of these dispersion patterns by measuring fishing success.

The tidal changes in fishing ability demonstrated in the present study suggest that, for those terns that foraged close inshore, the shallow littoral zone had an enhancing effect on their hunting success. Since such changes cannot effect offshore feeders (except in places where a reef comes close to the surface) it is not surprising that Roseate Terns showed only a weak tidal response at the breeding colony. That there was a marginal tidal influence on this species is consistent with inshore feeding by a small number of individuals in July 1969. The Arctic Tern was seen even less frequently close inshore and, in keeping with its almost exclusive offshore distribution, the effect of tide was not discernible at all in this species.

The interaction of tidal change and local shore topography will dictate the time when fish are most readily available to diving terns. In Boecker's study, the number of terns fishing over the ridge was maximum two hours before and two hours after low water which suggests that the depth of water was optimum at those times. At Scolt Head, a large sand-bar produced the greatest fishing activity and highest success about one hour before low tide while the tidal feeding patterns recorded at Coquet Island and on the adjacent coast suggest that optimum conditions prevail during flood-tide. This may be due to the fact that, along much of this coast, and notably at Druridge Bay, backwaters continue to empty by gradual drainage after the tide has stopped ebbing and fish may be most available to diving terns about 1-2 hours after low tide.

Such area differences, combined with interspecific differences in feeding behaviour, probably account for the variations observed between Druridge Bay and Newbiggin Bay. In 1968, Common Terns foraged more successfully than Sandwich Terns throughout the tidal cycle and their rate of increase in fishing success between high and low water was faster than that of Sandwich Terns. This implies that Common Terns were better able to profit from the opportunities presented by tidal changes at Druridge Bay. Although there are no quantitative data, it was evident that Common Terns utilised shallow channels and pools for plunge diving more frequently than Sandwich Terns which were more often seen feeding 50-100m offshore. Moreover, when water was ebbing from a channel, Sandwich Terns usually abandoned it and moved into deeper water before Common Terns. This suggests that when water depth drops below a threshold level, Common Terns, with their lighter build and more buoyant flight, are better adapted for fishing than Sandwich Terns, and since it is in shallower water that fish have least opportunity for concealment or escape, Common Terns show the greater improvement in fishing success around low water. The Little Tern <u>S. albifrons</u> can capitalise on even shallower water—often only one or two inches deep—than the Common Tern, and a similar hierarchy exists in many sympatric, tropical Kingfishers (Alcedinidae). Newbiggin Bay shelves downwards from high water mark about twice as steeply as the shore at Druridge Bay with the result that the littoral zone of shallow water produced by the ebbing tide is relatively narrow at Newbiggin. This may partly account for the much more erratic patterns of fishing ability in both Sandwich Terns and Common Terns at Newbiggin, although the latter species again showed the better improvement in fishing success between high and low tides. However, a major difference from the results at Druridge was the absolutely greater fishing success of Sandwich Terns throughout the tidal cycle. It was noticeable that Sandwich Terns were catching fish very successfully with dives from 5-6m whereas Common Terns, diving from 3-4m, were less successful, suggesting that fish may generally have been at a more suitable depth for capture by the former species.

In conclusion, it is suggested that the changing rate of food input to the tern colony is dictated by a combination of diurnal and tidal factors. The diurnal pattern probably arises from habitual feeding times and these seem to be common to all four tern species. On the other hand, the change in rate of food-carrying due to tide is only conspicuous in those species that frequent the shoreline. The tidal variations correspond with variations in the rate at which these species capture fish in the littoral zone, where the availability of food seems to vary systematically with tidal changes in water depth. These findings may have general application for tern species that use shorelines for foraging.

PART 2. Effect of age on the fishing ability of Sandwich Terns

Introduction

Biologists have suspected for some time that the ability to obtain food improves with age and experience in some birds (Lack 1954, 1966, Ashmole 1963) but not till recently has this been demonstrated. For example juvenile Little Blue Herons *Florida caerulea*, up to at least 9 months old, miss prey more frequently than do adults (Recher and Recher 1969), as do immature Brown Pelicans *Pelecanus occidentalis* up to 18-24 months old (Orians 1969). Norton-Griffiths (1968) has shown that young Oystercatchers *Haematopus ostralegus* take three years to become as efficient as adults at eating Edible Mussels *Mytilus edulis*. These studies strongly suggest that the period needed to learn feeding skills is long among those species whose foraging methods demand careful judgement and co-ordination. Thus it might be expected that the sophisticated plunge diving techniques used by some terns for catching prey would require a protracted period of learning in early life. Ashmole and Tovar S. (1968) provided indirect evidence for this when they observed six month old Royal Terns _Thalasseus_ _maximus_ being fed by adult birds in the wintering area. D. Willard (pers. comm.) has found a comparable length of post-fledging dependence in Caspian Terns _Hydroprogne_ _caspia_ and even at two years old these terns were less successful at catching prey than adults (Willard, quoted by Recher and Recher 1969). Because of these preliminary findings it was decided to investigate the relationship between age and fishing ability in the Sandwich Tern.

Methods

Between January and March of 1970, foraging Sandwich Terns were observed at various sites on the coast of Sierra Leone. The first-winter birds were readily distinguishable by their dark primaries and outer tail webs, from the lighter plumage of birds in their second or subsequent winters. Around March-June, at the end of their first winter, the immature birds undergo a complete moult and assume a plumage indistinguishable in the field from the winter plumage of older birds. Thus it becomes impossible to age any Sandwich Tern older than about 10 months during the winter period.

Data were collected to enable calculation of fishing success, diving rates (plunge and intention), rate of fish capture, prey length and dive height for the two age groups. For the purpose of this analysis, records were used only when first-winter and older birds were found fishing alongside each other, i. e. under apparently identical conditions. When a flock of terns was fishing, or if birds remained only briefly in the area before flying out of sight, details were recorded for any dives made by birds of known age and were added to the data derived from timed watches of individuals to provide a mean daily fishing success for each age group. In this way, many different birds could contribute to the mean values, thereby reducing the likelihood of one outstandingly proficient or inept individual biassing the results. The Wilcoxon matched-pairs signed-ranks Test used in this analysis is described in Siegel (1956).

Results

(i) Prey size and fishing success

When a tern rises from the water after a successful dive, it usually has to re-orientate the fish in its bill in order to swallow it. In four instances, first-winter birds dropped fish before they could be swallowed and these were scored as unsuccessful dives. In each of these cases the fish was about 5cm long, a size which did not usually present first-winter birds with any detectable difficulty. No birds older than first-winter dropped fish and although such mishandling was rare it may indicate slightly poorer manipulating ability by some younger birds. The mean length of fish caught and eaten by both age groups was 5cm (N = 134) and it did not appear that older birds were catching heavier fish (e. g. deeper bodied species).

The fishing success of first-winter birds was, on average, 3.2% less than that of older birds and the difference between daily scores was significant (Table 17, p = 0.02). The gap did not increase when the success of the older birds was low (<20% success). In other words, when the experienced birds had relative difficulty in catching fish, the less experienced birds did not do exceptionally badly.

Table 17

Fishing success of first-winter and older Sandwich Terns.

	First-winter			Older than first-winter		
Date	Dives	Number Successful	% Success	Dives	Number Successful	% Success
25 Jan	61	6	9.8	37	3	8.1
11 Feb	49	10	20.4	68	16	23.5
19 Feb	73	4	5.5	58	7	12.1
21 Feb	54	4	7.4	37	9	24.3
23 Feb	96	9	9.4	53	5	9.4
24 Feb	161	31	19.3	67	15	22.4
25 Feb	43	10	23.3	24	8	33.3
2 Mar	89	9	10.1	118	15	12.7
4 Mar	152	21	13.8	117	18	15.4
Totals:	778	104		579	96	
Means:			13.4			16.6

Note: % Success of first-winter vs. older birds: $Z^* = -2.24$, p = 0.02

*Z = Normal deviate transformation for Wilcoxon test.

It is also notable that fishing success varied markedly from day to day in both age groups. This is best explained by reference to the days when success was comparatively high. The data for 11 Feb were collected during a spell of intense diving activity by several terns in a shallow estuary, implying that a shoal of fish was available to them. This bout of diving stopped as abruptly as it had begun as would be expected if a shoal suddenly became inaccessible, e. g. by escaping into deeper water as the tide flooded. All the other data in Table 17 were collected in a truly marine situation. On 24 and 25 Feb predatory fish, probably tuna (F. Scombridae), were seen to periodically break the water surface, driving before them shoals of small fish which were heavily predated by the terns. The behaviour of fish and terns under these circumstances is characteristic and instantly recognisable (see Ashmole 1963, Ashmole and Ashmole 1967). It is therefore reasonable to conclude that fishing success was enhanced by the activity of predatory fish on these two days. Except for the older birds on 21 Feb, fishing success was generally lower on the remaining days when none of the behaviour associated with shoals in shallow water or with predatory fish was observed.

Additional data were collected at Cockerill Bay, near Freetown, where beach seining operations attracted large numbers of terns. As the seine net was hauled ashore, terns dived to capture the countless small fish trapped inside it. Most of the fish were either picked up from the tideline or water surface by contact dipping or else were caught with a shallow plunge from a height of 1.5-3m. The fish were obviously easily accessible and could be caught with a minimum of skill. Consequently diving rates (about 2-3 dives per minute) and fishing success were high (first-winter birds = 66.0% and 90.6% on the two days; 65.7% and 88.5% respectively for older birds). These results show that first-winter birds were not at any disadvantage in this abnormally rich feeding situation.

(ii) Diving rates

One way by which first-winter birds might compensate for their lower fishing success in normal feeding situations would be to dive at a faster rate than the older birds. From observations on performances of individuals, daily diving rates are shown for the two age groups in Table 18. In terms of the potential rate of fish capture, the important comparison is in the rate of plunge diving between the two groups; the first-winter birds did not differ, significantly ($p = 0.90$), from older birds in this respect. Similarly there were no significant differences between the two age groups in their rates of intention diving ($p = 0.53$) or combined diving ($p = 0.92$).

(iii) Rate of fish capture

Since fishing success differed significantly between age groups while diving rates did not differ, it may be inferred that the rate of fish capture also differed. However, a more direct measure is desirable and to obtain this, the number of successful dives per minute was compared for the two age groups (Table 19). Older birds captured fish at a significantly faster rate than first-winter birds ($p = 0.04$). The difference is such that older birds would, on average, capture 14 fish during each hour of sustained foraging activity compared with 10 fish per hour for first-winter birds.

(iv) Foraging behaviour

A conspicuous feature of the behaviour of newly fledged juveniles in Britain when they first start hunting by themselves is the low height from which they dive compared with adults (pers. obs.). In Sierra Leone, the overall difference in dive height of the two age groups approached, but did not reach significance ($t = 1.73$, $0.05 < p < 0.10$); of 327 dive heights recorded for each group, the means were 6.0m and 6.2m for first-winter and older birds respectively. The only significant daily difference ($t = 286$, $p < 0.01$) occurred on 21 Feb when the mean height for adult birds was 5.9m ($N = 44$) but only 5.4m ($N = 71$) for first-winter birds.

During 65 hours observation of first-winter and older birds in fishing and roosting parties, no instances were recorded of older birds feeding first-winter birds. On 25 Jan, however, one first-winter bird was seen persistently following an older bird throughout a fishing session. As it did so, the younger

Table 18

Rates of plunge, intention and combined (plunge + intention) diving by first-winter and older Sandwich Terns, derived from observations on individual birds.

	First-winter[2]					Older than first-winter[2]				
Date[1]	Plunge dives/min	Intention dives/min	Combined dives/min	Birds	Total obs. time (min)	Plunge dives/min	Intention dives/min	Combined dives/min	Birds	Total obs. time (min)
19 Feb	1.9	0.1	2.0	8	23.0	1.7	0.4	2.1	7	20.5
21 Feb	1.0	0.7	1.7	8	27.5	1.2	0.3	1.5	7	29.5
23 Feb	1.4	0.3	1.7	8	23.0	1.2	0.7	1.9	7	26.5
24 Feb	2.2	0.2	2.4	6	17.0	2.2	0.1	2.3	5	20.5
2 Mar	1.6	0.5	2.1	9	25.5	2.0	0.3	2.3	12	35.5
4 Mar	2.1	0.7	2.8	11	42.5	1.9	0.2	2.1	11	45.0
Totals:				50	158.5				49	177.5
Means:	1.7	0.5	2.2			1.7	0.4	2.1		

[1] No data are included from the Cockerill Bay site or for 25 Jan, 11 Feb or 25 Feb, when adequate observations were made on only one of the two age groups.

[2] First-winter vs. older:
Plunge dives/min: $Z = 0.13$, $p = 0.90$
Intention dives/min: $Z = -0.63$, $p = 0.53$
Combined dives/min: $Z = -0.10$, $p = 0.92$

Table 19

Rate of fish capture by first-winter and older Sandwich Terns.

	First-winter				Older than first-winter			
Date	Successful dives	Total obs. time (min)	Successful[1] dives/min	Birds	Successful dives	Total obs. time (min)	Successful[1] dives/min	Birds[2]
19 Feb	2	23.0	0.09	8	4	20.5	0.20	7
21 Feb	1	27.5	0.04	8	7	29.5	0.24	7
23 Feb	3	23.0	0.13	8	3	22.0	0.14	6
24 Feb	2	17.0	0.12	6	6	20.5	0.29	5
2 Mar	5	25.5	0.20	9	8	35.5	0.23	12
4 Mar	13	42.5	0.31	11	13	42.0	0.31	10
Totals:	26	158.5		50	41	170.0		47
Means:			0.16				0.24	

[1] Successful dives/min for first-winter vs. older birds: $Z = -2.02$, $p = 0.04$.

[2] The total is smaller than the corresponding one shown in Table 18 because two birds were so far from the observer that the success of their dives could not be determined.

bird uttered the high-pitched peeping sound characteristic of food begging; this call was also noted by Monroe (1956) for immature Elegant Terns Sterna elegans and Caspian Terns. Other first-winter Sandwich Terns (and likewise the older birds) gave a monosyllabic "krik" call while foraging. It is worth noting that the double note "kirrik" characteristic of adult Sandwich Terns in the breeding season was not heard until 2 March when it was produced by a bird entering full summer (breeding) plumage. It has not previously been realised that this call is lost from the Sandwich Tern's repertoire outside of the breeding season.

Discussion

From personal observations in Britain it is known that newly fledged Sandwich Terns begin to develop hunting skills by making shallow plunge dives or 'contact dips' to the water surface. These early efforts were never seen to be rewarded with edible prey and usually pieces of algae or inanimate objects were picked up. The young of many tern species seem to practice hunting in this way and Ashmole and Tovar S. (1968) have described similar behaviour by juvenile Inca Terns Larosterna inca. The inefficiency of juvenile Sandwich Terns in obtaining food by their own efforts makes them strongly dependent on parental feeding, at least up to the time of migration to the wintering grounds (Tinbergen 1953, p. 229, Nørrevang 1960). At some subsequent stage during the first winter of life, however, the immature birds become self-sufficient and also acquire a fishing technique which is, at least superficially, indistinguishable from that of the older birds.

The evidence presented here shows that between fledging and the end of their first winter, Sandwich Terns improve considerably in fishing ability but do not consistently capture prey as successfully as older birds (Table 17). However, equally high success was achieved by the two age groups under apparently easy fishing conditions when both were able to exploit the fish supply resulting from man's activities. In this situation, the fish prey were in very shallow water and all dives were made from a height of 1.5 - 3m. The disparity in fishing success only appeared when dives had to be made from much higher than this, usually from about 6m, which indicates that the fish were generally further below the water surface in the natural foraging sites. In these cases, older birds tended to dive from greater heights than did first-winter birds and it is interesting to note that on 21 Feb when the only significant daily difference in dive height between the two age groups was recorded, the greatest difference (16.9%, $X^2 = 5.13$, $p<0.05$) in fishing success also occurred.

Clearly, a more rigorous measure of dive height is necessary for a detailed enquiry into this relationship but in view of the lack of information on the causes of differential feeding ability in birds, it is worth speculating about the way in which dive height might contribute to the age difference in fishing success among Sandwich Terns. Because of the rapid attenuation of light intensity in water and the displaced-image effect due to refraction, a tern should generally encounter greater difficulty in seeing a fish and judging its precise position the deeper it is below the surface. Moreover, higher dives are needed to gain the impetus for reaching deeper fish and the demands on the bird's accuracy of aim may increase accordingly. It is suggested that these skills of judgement and co-ordination develop gradually and that the range of dive heights commonly used by a tern will increase with age as it learns to successfully handle progressively deeper prey. This will enable the tern to exploit a greater range of water depths and hence a greater choice of potential prey items. On 21 Feb and on other days when the older birds had better fishing success, the fish may have therefore been vertically distributed in such a way as to be more accessible to the older and more experienced divers. The rate of ossification—especially of the skull—may also be associated with increasing dive height during early development, but this point requires further study.

Since it was not practicable to ascertain the fishing success of individuals under a variety of conditions, the possibility cannot be excluded that many first-winter birds were as efficient as, or even more so, than their elders and had been since much earlier in development. The apparent improvement in fishing success during the first winter might then be partly an artefact caused by the interim mortality of less efficient individuals (cf. Orians 1969). However, as newly fledged birds have a negligible fishing success, it seems reasonable to suppose that the observed differences between age groups were due, at least in part, to a process of progressive, but still incomplete, improvement in the immature birds.

Although some first-winter birds must inevitably catch fewer fish per unit time than older terns, it does not necessarily follow that the former also have a lower net of intake (i. e., total intake less energy expended) of food per day. It is possible that the younger birds compensate for their low capture rate by devoting a longer proportion of the day to foraging. D. Willard (pers. comm.) has found that on days when their fishing success is high, adult Caspian Terns feed only till mid-morning and spend the remainder of the daylight hours roosting, whereas immature birds often hunt for longer and may make sporadic feeding sorties in the afternoon. No differences in hunting time were detected for Sandwich Terns in Sierra Leone but this aspect requires further study, especially in view of the relatively short day available for finding food in the tropics.

PART 3. Effect of prey abundance

It is usually impossible, without a sophisticated sampling programme, to make any statement about the absolute numbers of fish present. Occasionally, however, mixed species flocks of terns are found fishing and these aggregations undoubtedly indicate that fish are present in dense shoals. After one such bout of flock-feeding at Druridge Bay on 5 July, 1969, it was actually possible to verify that a dense shoal of sand-eels Ammodytes marinus had attracted the terns. The flock dispersed as the tide receded and it was found that many of the sand-eels had embedded themselves in the sand, presumably to escape detection. However, many of the fish were buried only up to their gills, with the head protruding; 74 of these were recovered from about 10m^2 surface area of sand. Commonly, fishing success of all tern species examined approaches 50% in shoal situations and may be even higher than this (Table 20).

Table 20

Fishing success of terns feeding in flocks when shoals of fish were presumed to be present.

Date	Fishing success for different tern species							
	Sandwich	N[1]	Common	N	Arctic	N	Roseate	N
5.6.68	51.7	209	53.8	533	-	-	-	-
5.7.68	30.0	50	30.0	40	48.2	27	18.2	33
12.7.68	-	-	49.8	227	-	-	-	-
13.7.68	-	-	51.3	80	-	-	-	-
17.7.69	66.4	125	56.9	123	-	-	47.8	46
20.6.70	34.4	96	25.4	142	-	-	-	-

[1] Number of dives.

Comparison of fishing success of terns feeding both in flocks and as dispersed individuals on the same day confirms that the presumed presence of fish shoals significantly enhances the ability to catch fish. Table 21 makes such a comparison for Sandwich Terns and Common Terns on 4 days; fishing in flocks was significantly more successful than fishing alone for both Sandwich Terns (Student's paired t-test: $t = 3.18$, 6 d. f., $p = 0.02$) and for Common Terns ($t = 6.18$, 4 d. f., $p < 0.01$).

Table 21

Daily comparison of fishing success of Sandwich and Common Terns feeding in flocks and feeding as solitary (spaced out) individuals.

	SANDWICH TERN				COMMON TERN			
	Success in flock	N	Success alone	N	Success in flock	N	Success alone	N
	51.7	209	18.1	160	49.8	227	29.4	17
	30.0	50	14.8	135	39.9	148	26.5	68
	66.4	125	46.7	66	56.9	123	44.4	18
	34.4	96	28.8	66				
Totals:		480		427		498		103
Means:	45.6		27.1		48.9		33.4	

Note: Flock versus solitary comparisons for Sandwich Terns are not on the same days as comparisons for Common Terns.

Birds feeding in flocks also showed a higher rate of plunge diving that those feeding as solitary individuals; this is illustrated for Sandwich Terns and Common Terns in Table 22. The observations in this Table were all made on 17 July, 1969 when intense flock feeding continued for an hour, followed by solitary feeding when the shoal had either dispersed or escaped into deeper water. The net effect of better fishing success and a higher diving rate in the flock was an 8-fold increase in the Sandwich Terns' rate of fish capture compared with solitary feeding, and a 5-fold increase for Common Terns.

Table 22

Comparison of fishing ability of Sandwich Terns and Common Terns feeding in flocks and feeding alone (17 July, 1969).

Species of tern	Type of feeding	Fishing success (%)	Rate of plunge diving (dives/min)	Rate of prey capture (fish/min)
Sandwich	Flock	66.4	6.1	3.8
	Solitary	46.7	1.2	0.5
Common	Flock	56.9	5.2	2.8
	Solitary	44.4	1.6	0.6

PART 4. Effect of wind and sea conditions

Introduction

Although the feeding methods of many seabirds, and particularly plunge-diving species, expose them to rapid alterations in both air and sea conditions, the influence of such variables on the ability to catch prey has not been studied systematically in the past and only a few isolated comments, based more on intuition than observation, exist in the literature. Against this background, it was decided to investigate the fishing ability of terns in a variety of wind and sea surface conditions.

Source of weather and sea records

Details of windspeed were obtained from records kept at the Meteorological Station of R. A. F. Acklington, Northumberland. The station is situated 6.4km (4 miles) south-west of Coquet Island and 4.8km (3 miles) inland from Druridge Bay. The flatness of the land between the airfield and the coast suggested that the windspeeds monitored at the station would provide a realistic record of conditions prevailing in the inshore zone. This assumption was proved correct by comparing windspeed readings from Acklington with simultaneous readings from a portable anemometer situated on Coquet Island and at various parts of the adjoining coast. The Acklington data were available in the form of 3-hourly values, and those which fell within the time span of a daily watch on foraging behaviour were averaged to give an index of the windspeed during that period. Windspeed is recorded in knots (1 knot = 1 nautical mile per hour = 1.15 statutory miles per hour = 1.85km per hour).

Daily records were kept on the sea surface conditions in the foraging areas under observation. Three categories of surface quality were recognised:

> <u>calm</u>—surface unbroken; no "wind-chop" (at the very most, a slight surface ripple).
>
> <u>moderate</u>—wind chop ± light swell.
>
> <u>rough</u>—wind-chop ± heavy swell, producing "white water".

It is important to note that a light swell in itself did not constitute "moderate" conditions unless the water surface was distinctly ruffled. Thus it was the localised texture of the surface (smooth or choppy) that chiefly dictated the distinction between "calm" and "moderate". Due to the difficulty of access from Coquet Island to the feeding areas when conditions were "rough", very few records were collected in this category and this account therefore concentrates on "calm" and "moderate" conditions.

In this analysis, fishing ability in different sea and wind conditions is compared over an equivalent portion of the tidal cycle on different days, first for Sandwich Terns, then for Common Terns.

Results

(i) Sandwich Tern

(a) Sea conditions

The fishing success of Sandwich Terns was significantly greater on days when the sea was moderate than when it was calm in both 1968 ($t = 2.71$, 9 d. f., $p<0.05$) and 1969 ($t = 3.85$, 6 d. f., $p<0.01$) (Table 23). Although fishing success was appreciably higher under all conditions in 1969 than in 1968, the proportional improvement from calm to moderate seas was comparable in both years, being 53% in 1968 and 61% in 1969. The effect of a roughening sea surface, at least up to moderate conditions, would therefore appear to be an enhancement of fishing success among Sandwich Terns.

A detailed analysis of diving rates was made in 1969 and showed that Sandwich Terns tend to dive more frequently when the surface is moderate than when it is calm (Table 24); however the difference was not statistically significant.

The combined effect of a better fishing success and faster diving rate in moderate seas is illustrated in Table 25 which compares the number of fish captured per minute by Sandwich Terns in the two categories of surface quality in 1968 and 1969. Fish were caught at a significantly faster rate in moderate seas ($t = 3.72$, 9 d. f., $p<0.01$). The difference is such that an average of 6 fish would be obtained per hour's fishing effort in calm waters compared with 18 fish per hour in moderate waters. In 1969, the relative difference in cap-

Table 23

Relationship between fishing success (%) of the Sandwich Tern and sea surface conditions in 1968 and 1969. Standard errors of means are shown.

1968

CALM			MODERATE		
Date	Success	N*	Date	Success	N
12.6	7.9	101	31.5	13.0	46
28.6	14.5	110	3.6	12.0	84
29.6	8.5	94	5.6	18.1	160
1.7	9.4	64	17.6	17.5	40
5.7	14.8	135	10.7	21.6	37
			13.7	18.5	168
Totals:		504			535
Means:	11.0 ± 1.5			16.8 ± 1.5	

1969

CALM			MODERATE		
Date	Success	N	Date	Success	N
10.7	32.1	56	9.7	70.8	130
11.7	39.0	100	14.7	61.7	81
15.7	34.9	86	17.7	46.7	66
16.7	36.7	109	18.7	50.6	85
Totals:		411			362
Means:	35.7 ± 1.5			57.5 ± 5.5	

*N = number of plunge dives.

Table 24

Relationship between plunge diving rate of Sandwich Terns and sea surface conditions in 1969. Standard errors of means are shown.

CALM

Date	Dives/min	No. of birds[1]	Total obs. time
10.7	0.9	11	44
11.7	0.8	29	103
15.7	0.6	14	65
16.7	1.4	6	22
Totals:		60	234
Means:	0.9 ± 0.17		

MODERATE

Date	Dives/min	No. of birds	Total obs. time
9.7	1.4	15	61
14.7	0.7	12	45
17.7	1.2	6	29
18.7	1.6	6	16
Totals:		39	151
Means:	1.2 ± 0.19		

[1] Individual birds were kept under observation for not less than two minutes.

Table 25

Rate of prey capture by Sandwich Terns foraging in calm and moderate seas in 1968 and 1969. Standard errors of means are shown.

1968

CALM				MODERATE			
Date	Fish/min	Birds	Obs.time	Date	Fish/min	Birds	Obs. time
12.6	0.18	14	22	31.5	0.20	9	10
28.6	0.14	5	7	3.6	0.17	6	6
29.6	0.17	5	6	5.6	0.33	6	6
1.7	0.00	4	5	17.6	0.40	3	5
5.7	0.00	5	11	10.7	0.36	7	11
				13.7	0.25	26	41
Totals:		33	51			57	79
Means:	0.10 ± 0.04				0.29 ± 0.04		

1969

CALM				MODERATE			
Date	Fish/min	Birds	Obs. time	Date	Fish/min	Birds	Obs.time
10.7	0.32	9	37	9.7	1.05	12	51
11.7	0.40	23	81	14.7	0.64	8	28
15.7	0.18	13	61	17.7	0.54	5	26
16.7	0.39	5	18	18.7	0.70	4	10
Totals:		50	197			29	115
Means:	0.32 ± 0.05				0.73 ± 0.11		

ture rates between sea categories was less than in 1968 but, due to the very good fishing success in 1969, the absolute difference is substantial ($t = 3.35$, 6 d. f., $p<0.02$); thus, in moderate seas, Sandwich Terns could potentially catch as many as 44 fish per hour of sustained foraging activity as against 19 fish per hour in calm seas.

(b) Windspeed

In Figure 30, 33 values for fishing success, collected during 1968-70 and each representing the mean of one day's observations, are plotted against appropriate daily windspeeds. Fishing success is directly correlated with windspeed ($t = 2.61$, 31 d. f., $p = 0.02$).

Plunge-diving rates were not significantly correlated with windspeed when plotted in the same way as in Figure 30.

The rate of fish capture is directly correlated with windspeed ($t = 2.57$, 17 d. f., $p<0.02$) when the daily 1968 and 1969 values are combined. The correlations of capture rate and fishing success with both surface conditions and windspeed emphasise the essential problem of distinguishing the effects of wind *per se* from those of surface conditions which are often causally related to windspeed. Fortunately the extent of disturbance on the sea surface is not always related to *prevailing* windspeeds because of the delayed response of the sea to changes in windspeed, e. g. on two successive days the wind may drop from gale force to a breeze so that a rough sea coincides with a low windspeed on the second day. These discontinuities between windspeed and surface conditions make it possible to compare fishing ability over a variety of windspeeds with differing surface conditions for each. Figure 31b incorporates the same data and axes as in Figure 31a but points are differentiated according to whether the sea surface was calm or moderate on the various days. It is notable that for any particular windspeed, moderate sea conditions are generally associated with a higher capture rate than are calm conditions. To test the significance of this difference, the two regressions (fish/min against $\text{windspeed}_{\text{calm}}$ and against $\text{windspeed}_{\text{moderate}}$) were calculated. Neither regression is

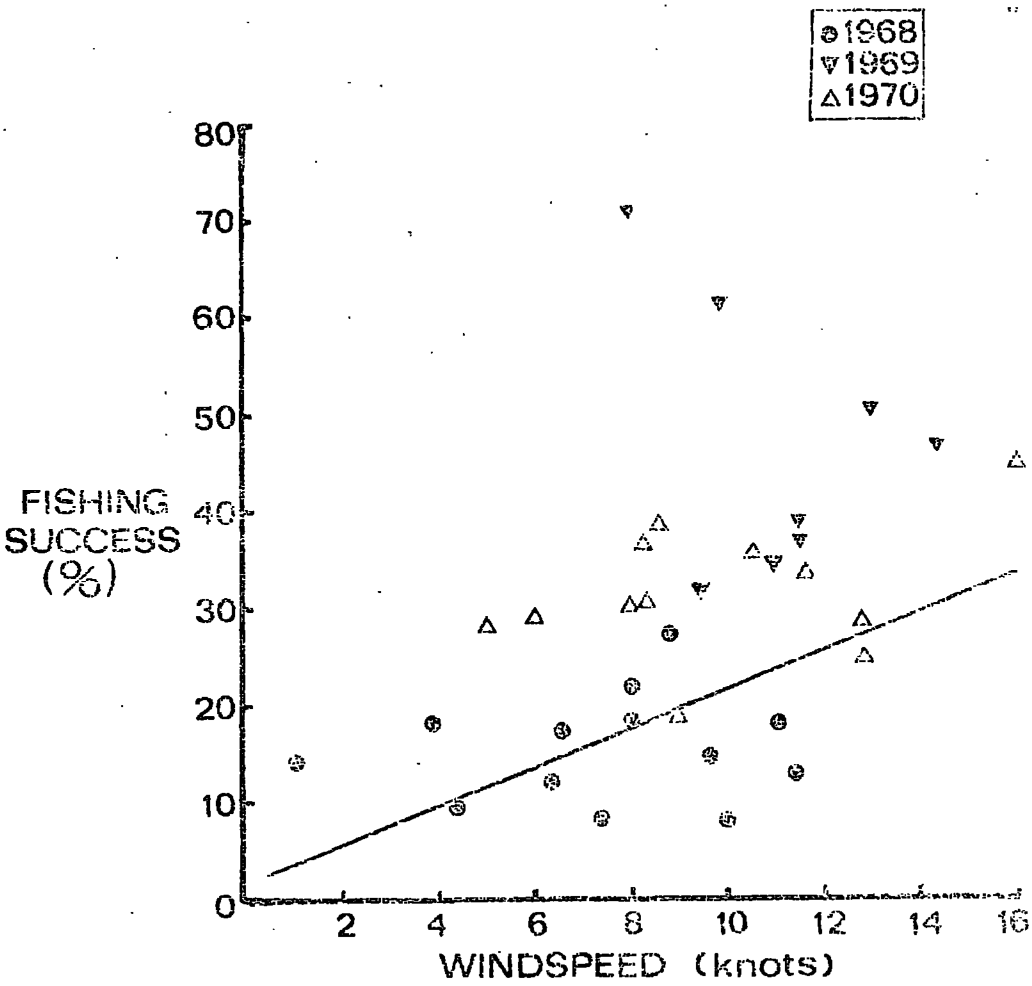


Figure 30

Relationship between fishing success of Sandwich Terns and daily prevailing windspeed. The calculated regression ($y = 2.01x + 1.54$) for the three years' data is shown.

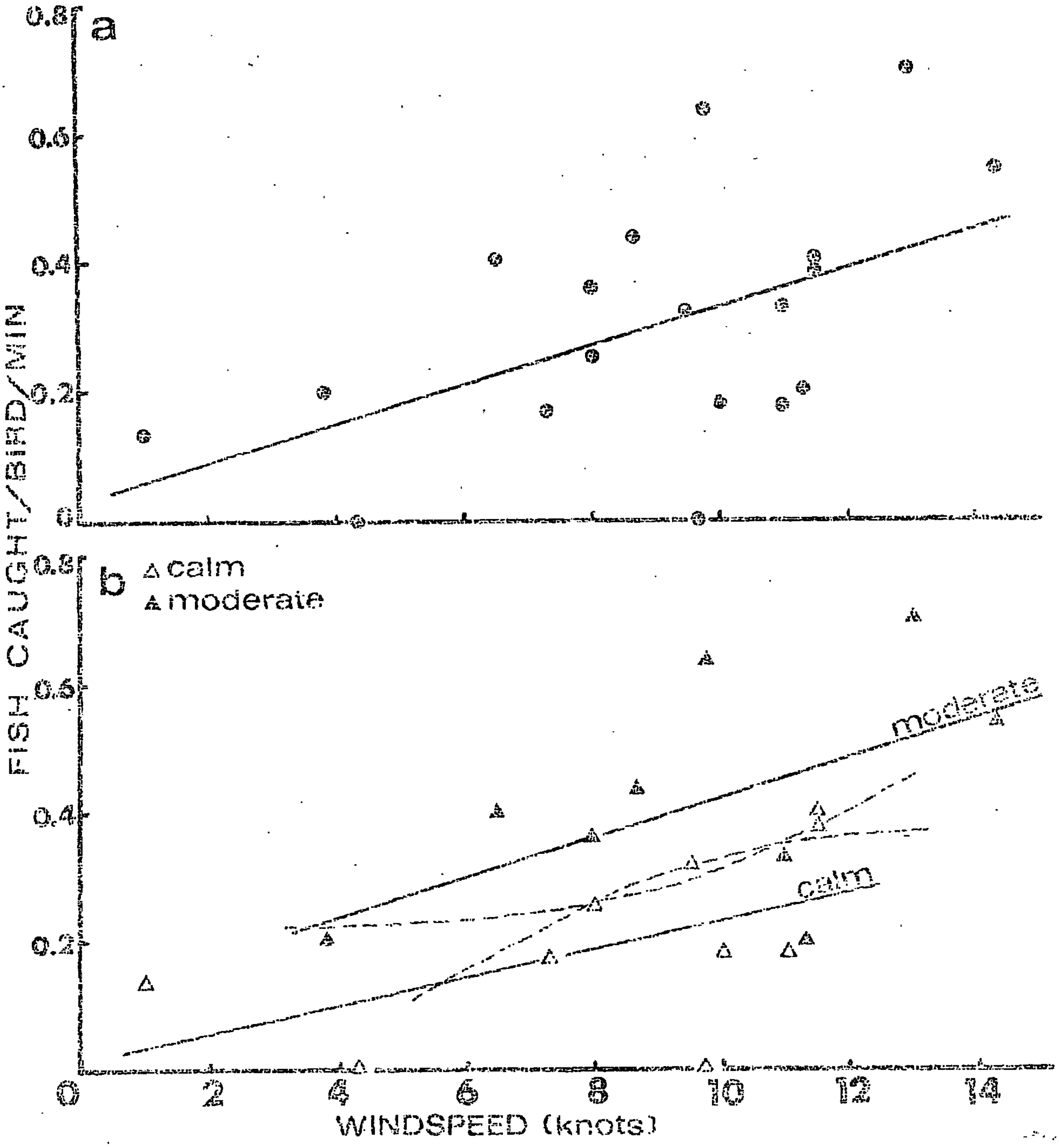


Figure 31

Rate at which Sandwich Terns capture fish in different windspeeds. In (a), no distinction is made for sea conditions and a single regression line ($y = 0.03x + 0.03$) is shown. In (b), separate regressions are calculated for calm ($y = 0.02x + 0.01$) and moderate ($y = 0.03x + 0.11$) sea conditions. The 95% confidence limits are shown by the broken lines. Note the region of non-overlap between 8 and 11 knots.

statistically significant; for the calm conditions, $t = 1.69$, 7 d. f., $p > 0.1$, and for moderate conditions, $t = 1.94$, 8 d. f., $p > 0.05$. However, the two regressions are approximately parallel and the critical test is the difference in elevation between them. To examine this difference, the 95% confidence limits were calculated for each regression. These are plotted between the regression lines and are characteristically hyperbolic (Snedecor and Cochran 1967, pp. 153-155). There is complete separation of the curves within the range 8.0-10.5 knots of windspeed, i. e. about the mean (actually 9.0 knots). This strongly suggests that sea surface conditions contribute independently of windspeed to influence the fish capture rate of Sandwich Terns.

(ii) Common Tern

(a) Sea conditions

In both 1968 and 1969, the fishing success of Common Terns was better on "moderate" days than on "calm" days; the difference was significant in 1969 ($t = 2.60$, 6 d. f., $p < 0.05$) but not in 1968 ($t = 1.59$, 5 d. f., $p > 0.1$) (Table 26). Like Sandwich Terns, the proportional improvement in success from calm to moderate conditions was comparable in both years—64% increase in 1968 and 78% in 1969. These values are respectively 11% and 17% greater than the equivalent values for Sandwich Terns so that, of these two species, the Common Tern would seem to benefit more by a change from calm to moderate conditions. More importantly, however, the two species obviously respond in the same direction to daily changes in their foraging situation. Figure 32 shows how the fishing success of Common and Sandwich Terns varies in unison from day to day; the regression is significant ($t = 2.89$, 14 d. f., $p < 0.02$).

Like Sandwich Terns, Common Terns also tended to dive at a faster rate under moderate conditions (Table 27) but the difference was not significant when calm and moderate values were compared.

There were too few data to compare capture rates of Common Terns with respect to sea conditions in 1968 but this was done in 1969 (Table 28). Moderate conditions produced a significant improvement in capture rates over calm conditions

Table 26

Relationship between fishing success (%) of the Common Tern and sea surface conditions in 1968 and 1969.

1968

	CALM			MODERATE	
Date	Success	N	Date	Success	N
28.6	8.1	37	31.5	37.8	82
29.6	11.0	82	10.7	19.4	62
1.7	25.6	86	13.7	26.5	68
5.7	23.3	60			
Totals:		265			212
Means:	17.0 ± 4.4			27.9 ± 5.4	

1969

	CALM			MODERATE	
Date	Success	N	Date	Success	N
10.7	28.6	14	9.7	50.0	50
11.7	20.4	49	14.7	39.1	69
15.7	22.6	31	17.7	44.4	18
16.7	16.1	62	18.7	22.2	54
Totals:		156			191
Means:	21.93 ± 2.6			38.93 ± 6.0	

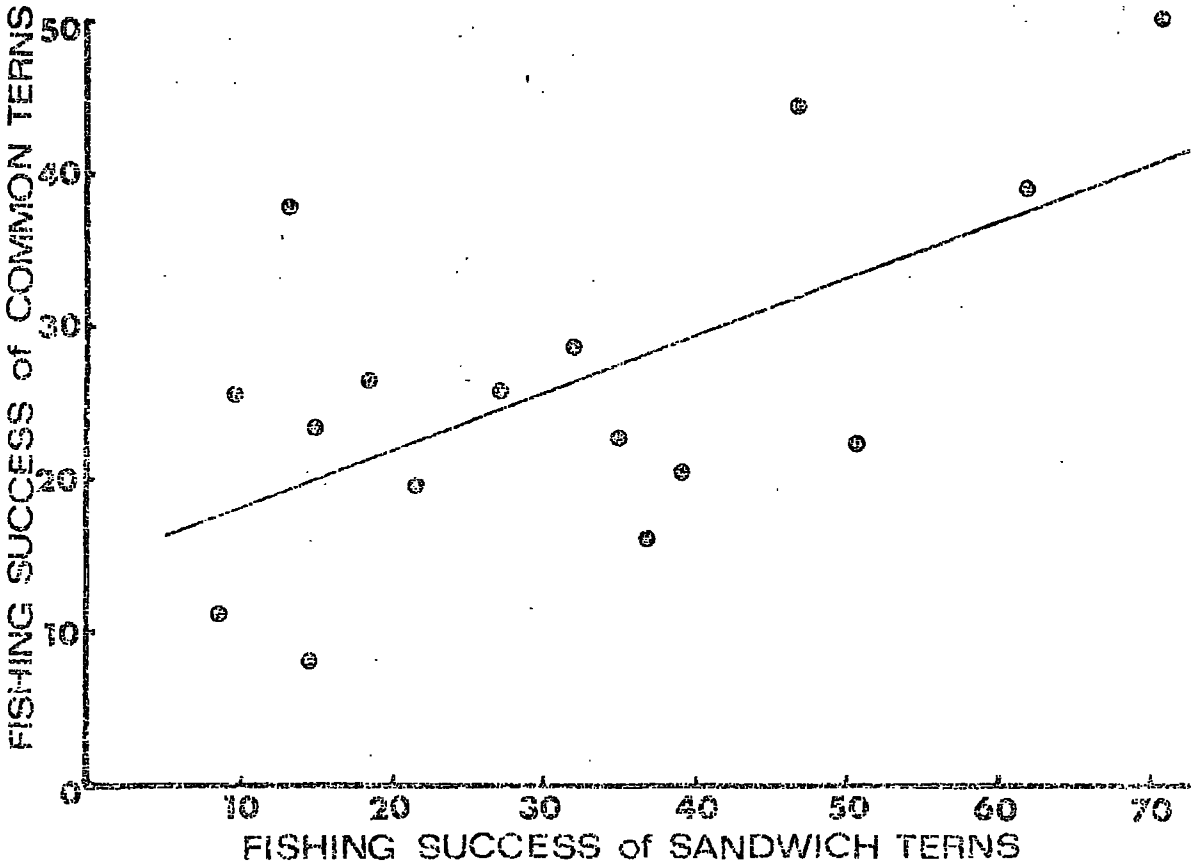


Figure 32

Relationship between fishing success of Common Terns and Sandwich Terns. The regression line ($y = 0.37x + 14.75$) is plotted.

Table 27

Relationship between plunge diving rate of Common Terns and sea surface conditions. (1969)

CALM

Date	Dives/min	No. of birds	Total obs. time
10.7	0.9	2	15
11.7	0.8	14	53
15.7	1.3	6	23
Totals:		22	91
Means:	1.0 ± 0.15		

MODERATE

Date	Dives/min	No. of birds	Total obs. time
9.7	1.2	6	40
14.7	1.4	10	30
17.7	1.6	3	8
18.7	1.8	5	17
Totals:		24	95
Means:	1.5 ± 0.13		

Table 28

Rate of prey capture by Common Terns foraging in calm and moderate seas in 1969.

CALM

Date	Fish/min	No. of birds	Total obs. time
10.7	0.27	2	15
11.7	0.19	13	48
15.7	0.22	6	23
Totals:		21	86
Means:	0.23 ± 0.02		

MODERATE

Date	Fish/min	No. of birds	Total obs. time
9.7	0.60	6	40
14.7	0.67	10	27
17.7	0.38	3	8
18.7	0.36	4	14
Totals:		23	89
Means:	0.50 ± 0.08		

($t = 2.81$, 5 d. f., $p<0.05$). In terms of hourly performance the capture rates represent 14 and 30 fish per hour in calm and moderate conditions respectively.

(b) Windspeed

There was no relationship between windspeed and fishing success ($t = 1.64$, 14 d. f., $p>0.1$) when these were compared on a daily basis (Figure 33). A similar comparison proved to be significant for the Sandwich Tern but in the case of the Common Tern, only 16 days' data were collected. The same qualification applies to diving rates and capture rates which were not significantly correlated with windspeed in this species.

Discussion

As far as a tern's ability to catch fish is concerned, it has previously been thought that disturbance of the water surface has no effect (Salt and Willard 1971) or else must always be detrimental. Howard (1968), for example, commented that terns "must continue to fish when wind ripples the surface of the water and makes visibility very poor. As choppy water also makes the bait stay deeper, under stormy conditions terns must spend a large portion of their time off the nest." Burton and Thurston (1959), perhaps thinking along similar lines as Howard, noted that Arctic Terns in Spitzbergen showed a marked preference for feeding on waters sheltered from the wind. It is equally likely, however, that the source of attraction to such waters was quite different, e.g. a plentiful inshore food supply. That any surface disturbance should be detrimental is not an unreasonable proposal and it is scarcely surprising that, without any empirical observation, this view has not been challenged. Indeed the only previous departure from this view is contained in a statement made by Ferens (1962) who studied the activity of seabirds in the Arctic. Contrary to the finding of Burton and Thurston (op. cit.), Ferens recorded that Arctic Terns were most active during stormy weather with hurricane winds and very rough seas, and while this might be explained away by the additional fishing effort alluded to by Howard, Ferens concluded differently from the behaviour of the birds that "they had rich hunting ground in the disturbed sea." To my knowledge,

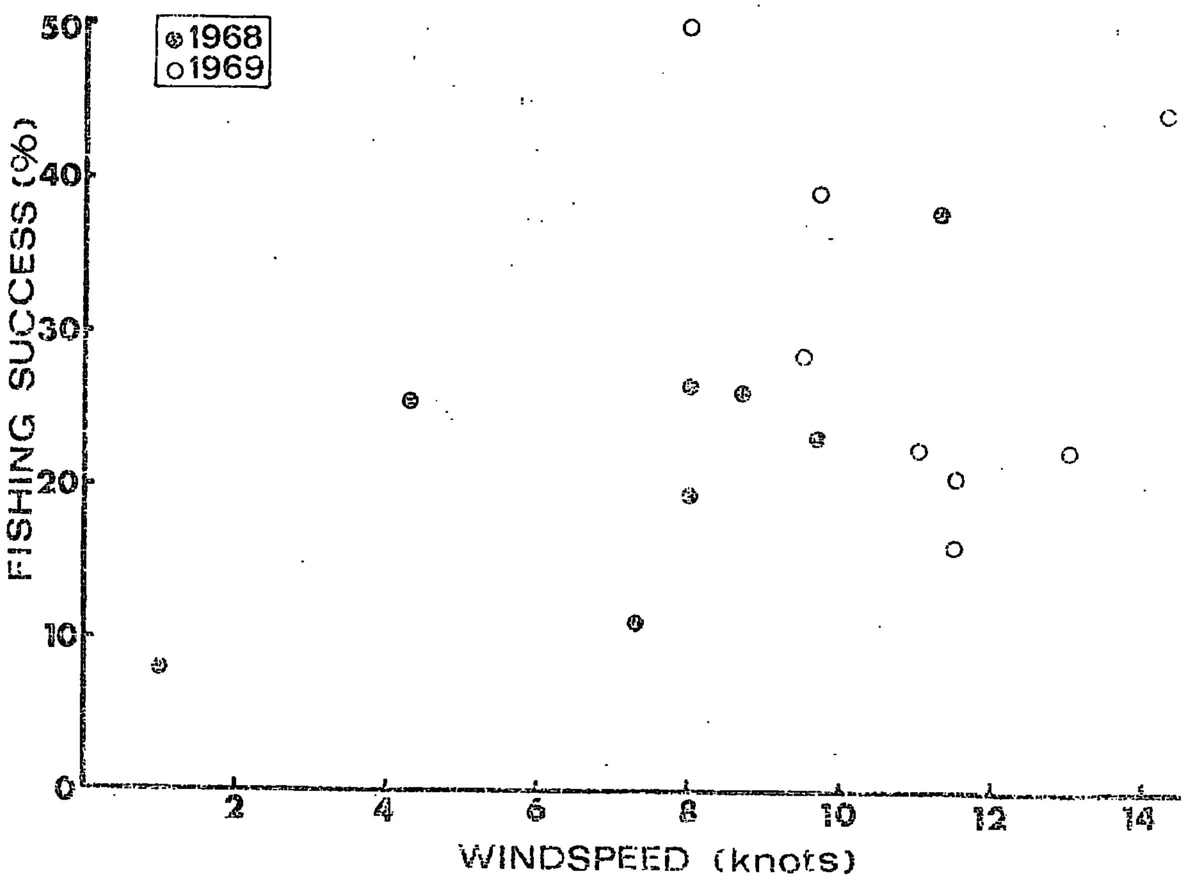


Figure 33

Fishing success of Common Terns plotted against daily prevailing windspeeds. There is no significant correlation.

this is the first suggestion that surface disturbance, or some related factor, might favour rather than depress feeding activity.

The critical factor in discussing the interaction of weather and sea conditions on fishing ability is to define the severity of conditions. If Howard meant to convey gale force conditions by the word "stormy", then she is probably correct in suggesting that terns experience difficulty in obtaining food under these conditions. The same conclusion has been reached by other authors, notably Whitlock (1927), Pettingill (1939) and Boecker (1967). In storms, terns probably find it hard to maintain an accurate diving trajectory and moreover, as Howard suggested, fish may well remain further below the surface in the rough seas that accompany high winds, and so may be less vulnerable to predation by terns. Certainly, persistent gales and high seas in July 1968 produced a marked reduction in the amount of fish being fed to chicks on Coquet Island. This, in turn, led to heavy chick mortality through direct starvation and was probably also responsible for widespread fish-robbing among Common Terns.

But the results of this study indicate that increasing windspeed and its concomitant effects on the sea do not have a linearly depressive influence on fishing ability as Howard supposed. On the contrary, it seems certain that, up to a certain point, increasing windforce and surface disturbance make it <u>easier</u> for terns to catch fish. I suggest, therefore, that these environmental factors reach levels that optimise fishing ability, after which their effect is steadily debilitating. Unfortunately, it was not possible to examine a range of conditions sufficiently broad to determine the optimum point but, according to Figures 30 and 31, this probably involves a windspeed of not less than 15 knots.

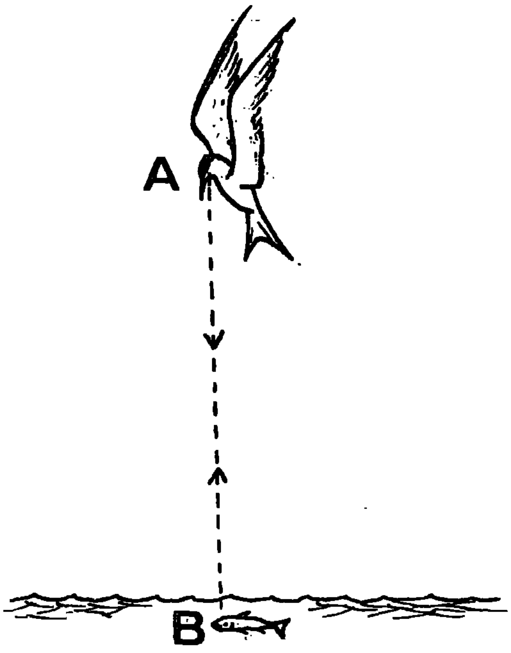
Although the evident inter-correlation of wind and sea state makes it extremely difficult to establish whether each of these factors has an effect when considered independently of the other, the present analysis indicates that <u>both</u> contribute separately (Figure 31), at least in the case of the Sandwich

Tern. It now remains to suggest how these two factors can operate to increase fishing ability over a given range.

Firstly, most plunge dives are preceded by hovering which implies that terns must maintain a reasonably stationary position in the air if they are to dive with any chance of success. By watching terns hovering in a variety of windspeeds it is clear that, the less wind there is, the more vigorously do they have to hover in order to remain stationary. It is not known if fish can detect and respond to the movement of terns hovering a few metres above the surface but they probably do; Phillips (1962) showed that a bird model moving slowly a few feet above water can elicit escape responses from fish. Prey may therefore have a better chance of detecting the presence of terns hunting on days when the lack of a headwind demands conspicuous hovering activity.

Secondly, the effect of the sea surface itself can be considered. Phillips (op. cit.) investigated water-to-air vision under different surface conditions, using an underwater camera directed upwards as a fish substitute and a bird model suspended at various heights above the water surface to simulate a plunge-diving seabird. Photographs from underwater depicted a clear outline of the model when the surface was calm, but when the surface was agitated, the image was very distorted and not recognisable as a "bird". This effect was due to a combination of refraction and internal reflection at the water-air interface. Assuming a fish sees approximately what the camera sees, its ability to distinguish a tern should, therefore, deteriorate as surface disturbance increases. Since light rays are reversible, the tern should also experience greater difficulty in seeing fish through a broken surface. However, it is possible that the tern's visibility of the fish is not impaired as much as the fish's visibility of the tern, and for the following reason: Consider the positions of tern and fish relative to the water surface:

Figure 34



If the water surface is rippled or choppy, a roughly analogous situation for comparison would be a sheet of frosted glass placed between two (human) observers so that their respective distances from the glass were equivalent to those in Figure 34. Person 'A' would then see a distorted but recognisable image of person 'B', but 'B' would be lucky to see 'A' at all. Optically, 'B' is so close to the surface that it (the surface) is very rough and refractive while 'A' is presented with an effectively smoother plane. Personal communications with scuba divers confirm that, as far as human beings are concerned, air-to-water vision is more effective than water-to-air vision when a broken surface intervenes and subjects are positioned as in Figure 34. A final prediction is that Common Terns, since they dive from much nearer the surface than Sandwich Terns, might benefit more by a shift from calm to ruffled water. In fact, Common Terns did show a relatively greater improvement (11% greater in 1968, 17% in 1969) in fishing success than Sandwich Terns between calm and moderate conditions.

To summarise, the combined effects of increasing windspeed and surface disturbance were to improve the fishing ability of Sandwich Terns and Common Terns which probably became less conspicuous to fish. Beyond a certain windspeed, however, fishing ability must decline as diving efficiency becomes impaired, and possibly because fish stay deeper below the surface.

SECTION III

INFLUENCE OF ENVIRONMENTAL FACTORS ON GROWTH OF CHICKS

Introduction

It has been found that the ability of adult terns to catch fish is determined by a complex interaction of factors, notably weather and sea conditions. It is therefore of special interest to monitor the rate at which chicks grow since this might reflect day-to-day variations in the parents' rate of fish capture. Some circumstantial evidence for this was produced by Hawksley (1950, 1957) who showed that Arctic Tern chicks gain weight on clear days but generally lose weight on foggy days. Langham (1968) provided convincing evidence that daily weight changes in chicks of Common, Arctic and Roseate Terns were affected by windspeed, duration of sunshine and amount of rainfall. He used a simplified multiple regression technique in which weight increments were first regressed against wind and sun and then against wind and rain. In order to complement observations of fishing behaviour in the present study, it was decided to make further measurements of growth in chicks of Common and Roseate Terns and to include Sandwich Terns, a species in which development has not been satisfactorily investigated from this point of view in the past. Computer analysis enabled a comprehensive evaluation of the data collected.

Methods

Between 20 and 30 newly-hatched chicks of each species were ringed within 12 hours of hatching and were weighed at the same time each day during their development. A record was kept of the brood size from which each chick originated, and of its hatching order in the brood. At about 19.00 hours, each chick was weighed to the nearest 0.1g on a torsion balance situated in a hide near the nesting area. For Common and Roseate Terns, it was usually feasible to find the same individuals each evening since chicks of these species tend to adopt a fixed hiding place or refuge near the nest-site and so they can be re-located when and as required. Inevitably, some chicks either disappeared or died during the growth study and on two occasions in separate years, most chicks in the sample died from starvation. Whenever this happened, I tried to restore the sample to its original size with new chicks of known age.

A problem peculiar to the Sandwich Tern was the tendency for parents to lead their chicks away from the nest-site about 3-5 days after hatching, probably in response to disturbance caused by my visits into the colony. These chicks soon dispersed widely and assumed a "nomadic" existence during development, rarely staying in any one refuge for more than a day or two. Despite diligent searching, it was difficult to locate the same individual on successive days. Dispersal was partly restricted by erecting wire netting around the subcolony used for growth measurements. Usually, the fence was placed well beyond the boundaries of the nesting group and did not completely encircle it since it was found that total enclosure caused some parents to abandon chicks unable to make an exit. Even with this constraint, many chicks quickly disappeared and to counteract this depletion, as many chicks as possible were weighed on any one evening to ensure that a reasonable proportion would be found again the following evening. Consequently, there was a particularly high rate of turnover among the individuals used but this was not considered to be a drawback since discrete daily growth increments were required rather than long term records for particular chicks. Daily weighings were continued throughout the season until too few chicks were left to maintain adequate sample sizes.

Environmental factors

Details of the following daily weather conditions were obtained from the Meteorological Station at R. A. F. Acklington, Northumberland:

windspeed	(daily values in knots, expressed as the mean of 8 spot readings at 3-hourly intervals).
rainfall	(total precipitation in mm/day).
sunshine	(hours/day).

Acklington is sufficiently close to the coast adjoining Coquet Island to provide a reasonably accurate record of the weather conditions to which foraging terns and developing chicks are exposed. I also scored daily sea conditions on an arbitrary 3 point scale—1 for calm, 2 for moderate, and 3 for rough (see p.71 for descriptions of these categories). Each day was allotted a rating from 1-6 according to how many "low tide hours" it contained. The reason for introducing a tidal factor is as follows. Since the total available foraging time is about 17 hours (4.00-21.00) in mid-summer, and since a tidal cycle (high water low water high water) takes about 12 hours, terns must experience two low tides on some days while on others they experience only one, depending on the time-phasing of the tidal cycle. Since terns fishing along the shore catch fish more frequently around low tide than at high tide, it was thought that some days might yield more fish than others. The method of scoring days to take account of tidal phasing is described in Appendix 3.

Results

(i) Preliminary analysis

In 1968, growth curves of weight against age were produced for chicks of Sandwich, Common and Roseate Terns, using daily measurements obtained on the island. Separate curves were plotted for different brood status (e. g., 1st chick in a brood of two, 2nd chick in a brood of two and so on). Weights of Sandwich Tern chicks older than 20 days fluctuated markedly and were, therefore, omitted from further analysis; the corresponding point on the growth curves of Common and Roseate Tern chicks was 16 days. Since chicks grow at a variable rate depending on their stage of development, it was evident that this could bias the mean daily weight increment of a sample of chicks. To standardise the sample from day to day, the daily increment of each chick was therefore weighted by a correction factor appropriate to its age. Appendix 4 describes the method of calculating these correction factors.

In view of the apparent effect of wind on the fishing ability of foraging terns (Section II, Part 4), the mean daily weight increments (corrected) of chicks were plotted against mean daily windspeed for the three species (Figure 35). In Sandwich Terns, the response of weight change to wind was unpredictable. The data were best fitted by a parabola although the regression was not significant, accounting for only 7.1% of the variation in weight

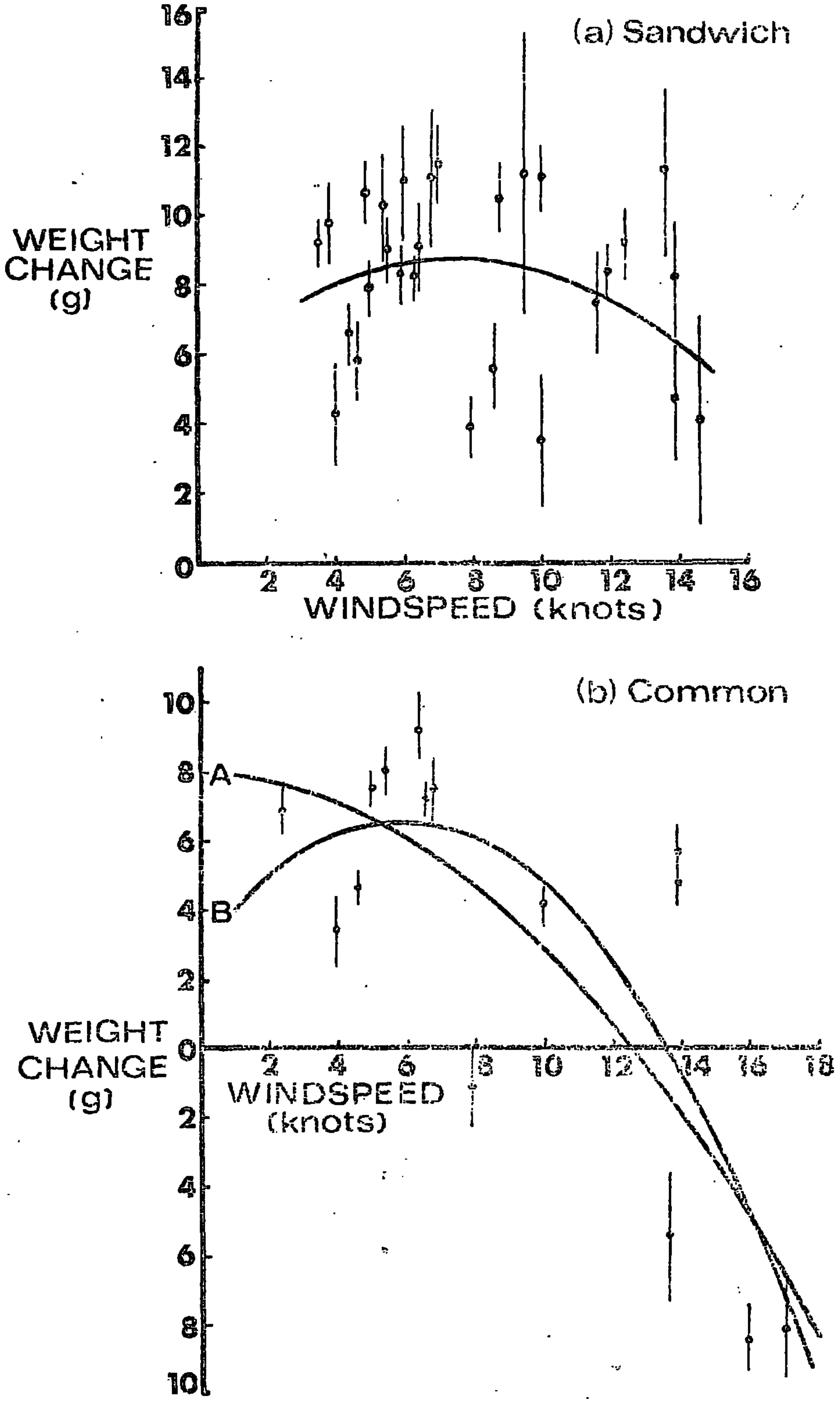
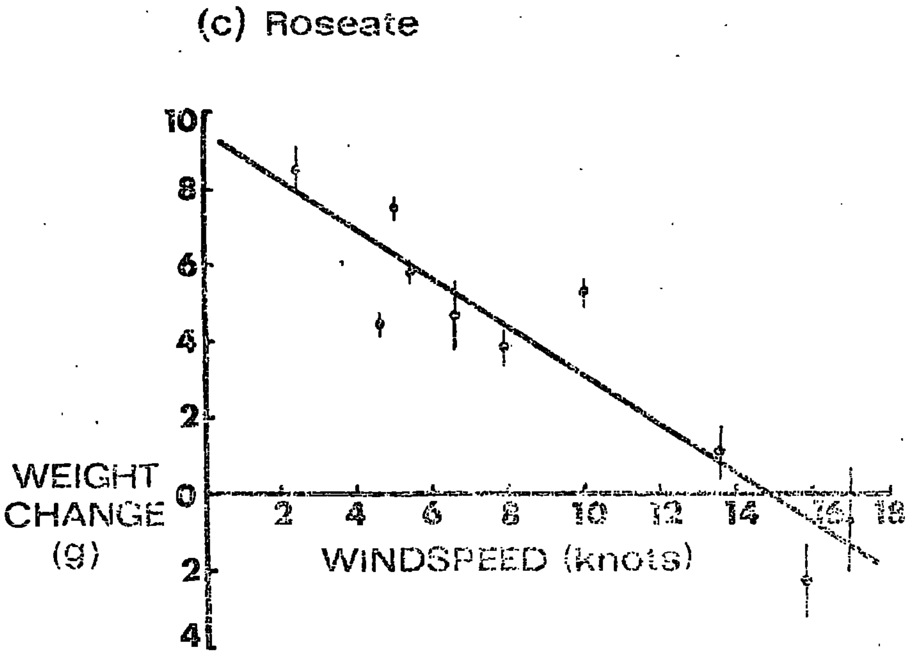


Figure 35

Relationship between mean daily weight changes of Sandwich and Common Tern chicks and mean daily windspeeds in 1968.

Regression equations (a): $y = 5.35 + 0.90x - 0.06x^2$ (not significant).
(b): Curve A: $y = 7.85 - 0.05x^2$ ($p<0.001$).
Curve B: $y = 2.75 + 1.29x - 0.11x^2$ ($p<0.001$).

(Figure 35 continued overleaf).



(c) Roseate

Figure 35c

Relationship between mean daily weight changes of Roseate Tern chicks and mean daily windspeed in 1968. Regression equation: $y = 9.38 - 0.63x$ ($p<0.001$).

increment. Weight increments of Common Tern chicks were inversely correlated with windspeed ($y = 11.10 - 0.90x$, $r + -0.72$, $p<0.01$) but two curvilinear regressions (drawn in Figure 35b) were also significant. It was found by analysis of variance that the reduction in sum of squares achieved by each of these regressions was not significantly different. However, 61.6% (with wind and wind^2 as variables) and 58.5% (wind^2) of the variation were explained by each of the curvilinear regressions compared with 52.4% for the linear regression. The best prediction of weight change in Common Tern chicks is therefore made by curve B in the Figure although it did not represent a significantly better fit than the other two regressions.

In Roseate Terns weight change was inversely proportional to windspeed and the correlation was highly significant ($r = -0.64$, 244 d. f., $p<0.001$), accounting for 41.0% of the observed variation (Figure 35c). For each 1 knot increase in windspeed, the average weight increment decreased by 0.6g. This linear effect was so unequivocal that no attempt was made to fit a curvilinear regression.

The preliminary analysis was designed to answer two questions: (a) Is weight change related to windspeed in the species considered? (b) If it is, what is the form of the relationship? It appears that windspeed had little influence on the growth performance of Sandwich Tern chicks although there is some suggestion that, up to about 7 knots, increasing windspeeds enhanced the rate of growth, after which the effects were unpredictable (see means and standard errors in Figure 35a). In Common and Roseate Terns, however, windspeed was a determinant of weight change in 1968. Moreover, the effect of wind seems to differ in these two species. In Common Terns, as in Sandwich Terns, the possibility cannot be excluded that <u>some</u> wind is more beneficial to weight increase than no wind at all but, above about 7 knots, increasing wind had a depressive influence. On the other hand, <u>any</u> wind at all reduces the size of weight gains in Roseate Terns. These results suggested the inclusion of a transformation of windspeed—in this case windspeed^2—in a more rigorous analysis. Since windspeed and sea surface conditions are closely related, it was also decided to consider the effect of the variable (sea conditions^2).

(ii) Main analysis

Information on growth rates was collected in 1969 and 1970, using the same field methods as in 1968. A series of "step-down" multiple regression analyses was performed, using daily uncorrected weight increments of individual chicks as the dependent variable. The following independent variables were incorporated:

X_1 year
X_2 date
X_3 age of chick
X_4 hatching order
X_5 brood size
X_6 windspeed (knots)
X_6^2 windspeed^2 (knots)
X_7 rainfall (mm)
X_8 hours of sunshine
X_9 sea conditions
X_9^2 sea conditions^2
X_{10} low tide hours

The year was included when all data for any species were combined into one regression but when regressions were calculated for individual years, the year was omitted from the matrix. Dates were calculated from 1 June in each year so that July 4, for example, was entered in the regression as day 34. The inclusion of age as a variable is one way of taking account of varying growth rates at different stages in development, and avoids the need for applying correction factors.

Step-down regression is a procedure for finding the combination of independent variables that most effectively predicts the variation in the dependent variable (y). By this technique, y is first regressed against all variables simultaneously and then individual variables are subtracted successively from the regression equation until the minimum number of significant variables is established. The value of Student's 't' for any particular variable indicates whether it significantly reduces the sum of squares in the overall regression. The variable is retained only if its effect is significant at the 5% level. To determine the percentage of variation accounted for by multiple regression equations, the coefficient of determination (R^2) (i. e. the square of the multiple correlation coefficient x 100) is given. For a test of significance of the regression equation, a standard F-test was used; this tests the null hypothesis that the combination of independent variables exercises no influence on the dependent variable (weight increment). The step-down procedure was then continued to determine the percentage contribution made by each of the significant variables. To do this, the least significant one of these variables was eliminated from the regression and the percentage reduction in variation explained was therefore attributable to the eliminated variable. The next least significant variable was then removed, and so on until there was only one independent variable left. A certain amount of discretion is necessary in the interpretation of the results since each variable on its own could explain more percentage variance than is suggested by this procedure if the variables were highly intercorrelated.

All of the computations were carried out on an ICL 1906A digital computer at Oxford University. I am grateful to R. J. O'Connor for writing preliminary sorting programmes. The mutiple regressions were computed by the Fakad 24 Library programme written by Dr. E. Van Broekhoven and K. I. Macdonald of Nuffield College, Oxford.

In the results of this analysis, there was considerable variation both between species and between years when all the variables were considered simultaneously (Table 29). The maximum percentage of variation in weight increments explained was 39.6% for Common Terns in 1968 and the minimum percentage explained was 1.6% for Sandwich Terns in the same year. Apart from this last case which was insignificant, all regressions were significant at either the 1% or the 0.1% level. The majority of variables contributed very little to the observed variation; factors which never accounted for more than 5% in any species-year category were hatching order, brood size, hours of sunshine and low tide hours. The results will now be examined in detail for each species.

(a) Sandwich Tern

Since very few Sandwich Terns nested on Coquet Island in 1969, weight measurements were inadequate for separate regression but were included in the

Table 29

Summary of step-down multiple regression of various factors on weight increments of tern chicks. Only significant independent variables are included, and the sign of the regression slope is shown in each case.

F-test results were *$p<0.05$, * *$p<0.01$, ***$p<0.001$.

	INDEPENDENT VARIABLE AND % VARIATION EXPLAINED															
Sp. & yr.	Year	Date	Age of chick	Hatch order	Brood size	Wind speed	(Wind speed)^2	Rain	Sun	Sea	(Sea)^2	Tide	% var. expl. by signif. variables	% var. expl. by all x's	Signif.	N*
Sand '68										1.55			1.55	4.00	n. s.	404
Sand '70					-2.52	-2.36							4.88	13.06	**	239
Sand all years	-2.05			-0.88		+0.68	-2.75						6.36	7.52	***	702
Comm '68		-6.23		-0.62	+1.22		-16.92	-8.09		+3.18	-0.68	-2.69	39.63	40.32	***	361
Comm '69			+1.68	-2.19						+1.84	-1.78		7.49	9.94	**	314
Comm '70			+28.35										28.35	33.99	***	132
Comm all years				-0.81	+0.84				+1.22	+2.83	-7.04		12.74	15.69	***	807
Rose '68		-0.73			-0.97	-28.11	+3.59	-0.86				-0.40	34.66	36.20	***	268
Rose '69		+1.95		-3.35									5.30	10.13	**	276
Rose all years	+3.60			-1.22		-7.47	+0.39		+1.91			-0.26	14.85	16.07	***	641

*Number of "chick-days".

combined data for all three years. Simultaneous consideration of all variables explained only 1.6%, 4.9% and 6.4% of the variation in weight increments in 1968, 1970 and in 1968–1970 respectively. Due to large sample sizes, the latter two regressions were statistically significant, but clearly the factors measured had a negligible effect on weight increments in this species.

(b) Common Tern

Table 29 indicates that the balance of factors affecting weight change of Common Tern chicks varied greatly from year to year. In 1968, 39.6% of the variation in weight increment was explained when all factors were included and the regression was highly significant ($p<0.001$). Windspeed itself made no contribution but windspeed^2, with a negative sign, accounted for 16.9% of the variation, so reinforcing the preliminary finding that windspeed was not a simple linear component in 1968. Rain had a depressive effect, accounting for 8.1% of the variation, and the size of weight increments also declined as the season advanced, this influence of date explaining 6.2%. The remaining 8.4% was due to a combination of hatching order, brood size, sea, sea^2 and tide. Thus we can write: $y = 22.75 - 0.69X_2 - 1.58X_4 + 1.00X_5 - 0.06X_6^2 - 0.44X_7 + 12.00X_9 - 1.80X_9^2 - 0.65X_{10}$ where X_2 = date, X_4 = hatching order, X_5 = brood size, X_6 = windspeed, X_7 = rainfall, X_9 = sea conditions, and X_{10} = low tide hours.

In 1969, only 9.9% of the variation in weight increment was explained by the recorded variables and of this, 7.5% was attributable to significant factors. As in 1968, weight change showed a slight positive correlation with sea state and negative correlations with sea^2 and hatching order. In complete contrast with 1968, however, windspeed did not make a significant contribution to the multiple regression. In this connection, it is worth noting that the range of windspeed was smaller in 1969 than in 1968 when both very light and very strong winds were relatively common (Figure 36). The difference in the frequency of strong winds between the two years might have been important since reference to Figure 35b in the preliminary analysis shows that the rate of change of weight increments was greatest when windspeeds were in excess of 12

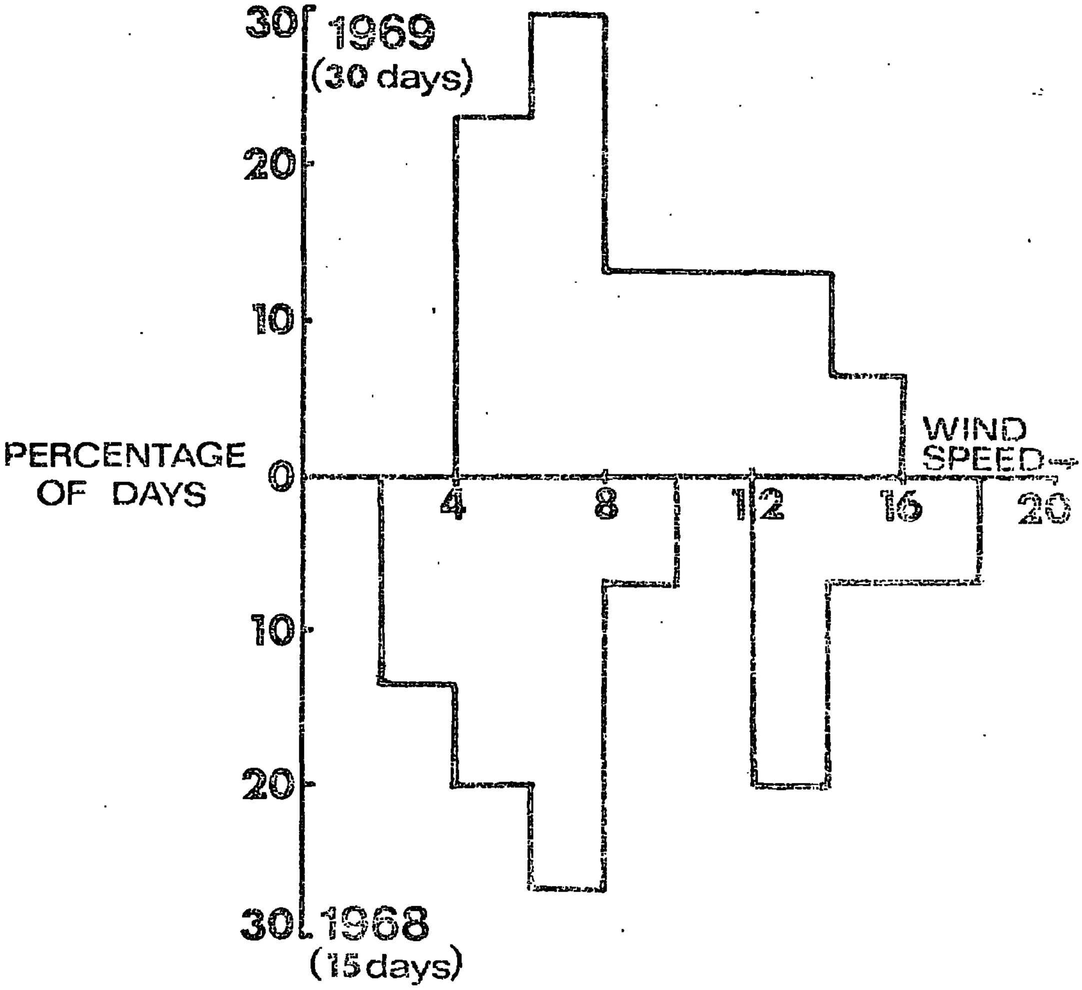


Figure 36

Percentage frequency distributions of days with different windspeeds (knots) during growth study of Common Terns in 1968 and 1969.

knots. Rainfall was another factor which contributed to weight changes in 1968 but not in 1969. However, rain was both more frequent and heavier in 1968. At least a trace of rain fell on 80% of days (12 out of 15) during the 1968 study but on only 53% of days (16 out of 30) in 1969. On days when rainfall was measureable, a mean of 6.2mm fell in 1968 compared with 3.6mm in 1969. Moreover, the calculation of the latter figure includes a day of torrential rain when 27.5mm fell and if this exceptional value is omitted, the average in 1969 drops to 1.2mm.

In 1968, age had no linear influence on weight change and in 1969 it had only a slight positive effect. But in 1970, age was the only significant factor, accounting for a substantial proportion (28.4%) of the variation. In this case, the regression equation simply resolves as $y = 0.68X_3 - 0.80$ which means that, for every 1 day advance in age, weight increments increased by 0.7g. In 1970 weight increments tended to increase steadily in size whereas in 1968 and 1969 they showed a distinct decline in the terminal stages of development as the asymptotic weight was approached (Figure 37). The change of pattern in 1970 was due to growth being retarded at an early age; as early as 6 days old, chicks in 1970 were 10g lighter than those in 1968-69 (34g compared with 44g) and by 10-12 days, this deficit had widened to over 20g. Chicks of 14 days were still grossly underweight for their age and therefore showed little sign of the diminishing growth rate usually associated with this age group.

The retarded development, and consequently the abnormal growth pattern, of chicks in 1970 was not obviously related to any of the environmental factors measured, but other observations made at the time strongly suggest that a shortage of fish affected the species from 22-29 June. Weight measurements were made daily from 24 June-5 July. The following field notes, written in June 1970, provide circumstantial evidence of a reduction in the local food supply:

June 22-23: "Very few birds are bringing fish into the colony and mortality of 3rd chicks in broods of 3 (Common Terns) has been particularly evident.

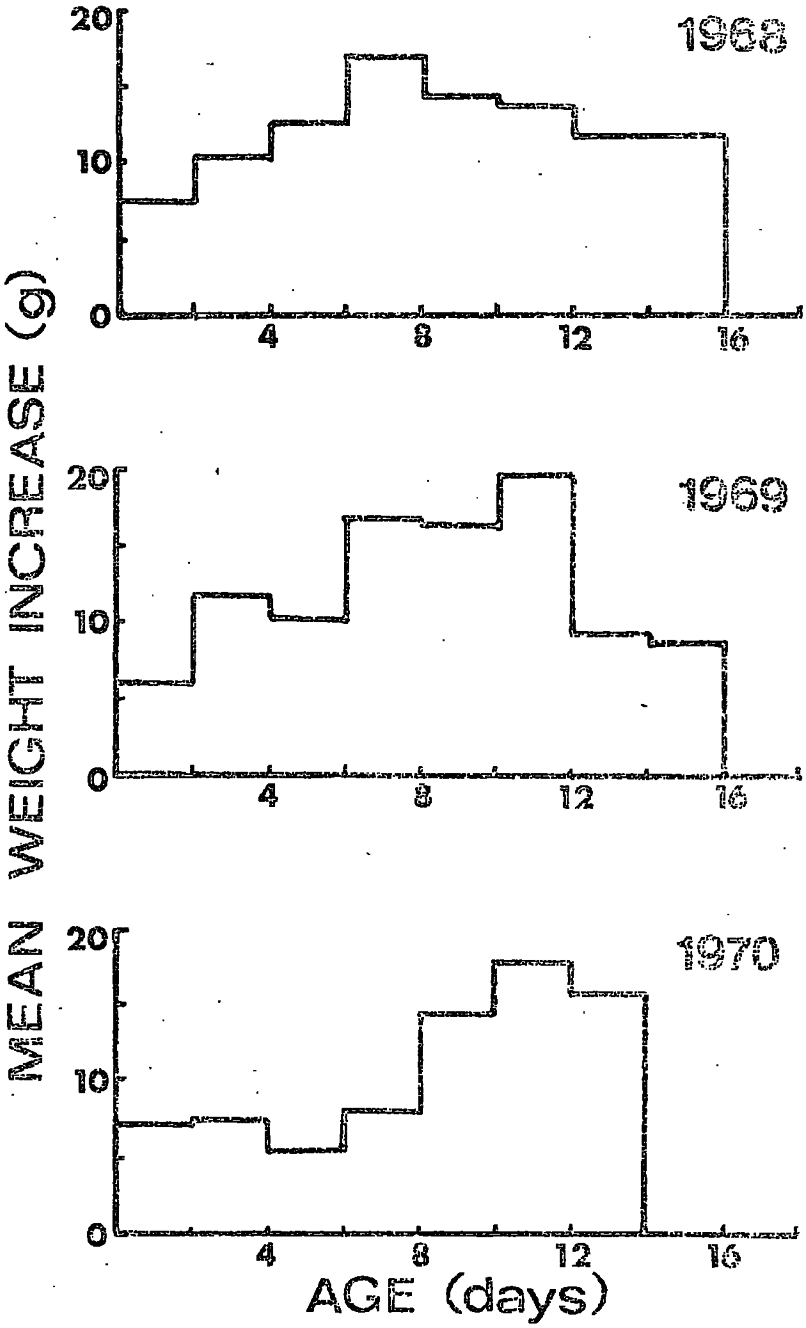


Figure 37

Mean weight increases per two days of Common Tern chicks in different years (weights are not cumulative).

June 29: "Chicks continue to fare badly. Common Terns arriving with fish are harassed by other Common Terns. Also notable is the odd range of prey being brought in, e. g. flatfish and shrimps. (These usually are uncommon in the diet and probably represent suboptimal prey). These items are being found at nest-sites, presumably refused by the chicks. Only Sandwich Terns seem to be bringing in fish in any quantity.

June 30: "Observations of fish-carrying terns entering the colony confirm that food is now more abundant—reflected in larger weight gains of chicks."

Not surprisingly, the heterogeneity between years prevented any increase in the percentage of variation explained when all data for Common Terns were combined. Only 12.7% was explained by significant variables and of these, sea (positive correlation) and sea^2 (negative correlation) accounted for most (9.9%). Using these two factors alone, $y = 11.73X_9 - 3.38X_9^2 - 4.46$; this equation describes a negative parabola which implies that moderate seas are associated with larger weight increments than either calm seas or rough seas.

(c) Roseate Tern

The results of the preliminary analysis of the 1968 figures were not substantially altered by the more comprehensive regression procedure. Wind was still the most important factor, being inversely correlated with weight change and accounting for 28.1% of the total variation explained (34.7%). By comparison, the other significant variables made only minor contributions. While rainfall was responsible for 8.1% of the variation in weight changes of Common Tern chicks in 1968, it had a much smaller depressive effect on Roseate Tern chicks, accounting for less than 1% of the variation. The complete regression equation for Roseate chicks in 1968 was: $y = 48.86 - 0.82X_2 - 0.86X_5 - 1.16X_6 + 0.06X_6^2 - 0.19X_7 - 1.24X_{10}$ where X_2 = date, X_5 = brood size, X_6 = windspeed, X_7 = rainfall and X_{10} = low tide hours.

In 1969, the regression explained very little (5.3%) of the total variation and in this respect it resembled the 1969 regression for Common Terns. Hatching order had a slight negative influence, showing that weight increases of 2nd chicks in broods of two are smaller than those of 1st chicks. Too few data were collected in 1970 to warrant multiple regression analysis but they were added to the data for 1968 and 1969 for analysis of the combined data. The major effect of wind in 1968 was still conspicuous in this latter regression in which windspeed accounted for half (7.5%) of the total variation explained.

Discussion

The results show that windspeed is the major weather factor affecting the size of weight changes in tern chicks although its influence is highly variable both between species and between years. The simple regression equation derived in the preliminary analysis shows that a 10 knot wind would depress weight increase in Roseate Tern chicks by 67.2% which resembles Langham's (1968) estimate of a 55.3% reduction given this windspeed. From the appropriate linear regression equation, Langham calculated a linear reduction of 45.7% in weight increments of Common Tern chicks under these conditions but in at least one year in the present study, the relationship was better described by a curvilinear regression. This showed that, up to about 7 knots, increasing windspeed might enhance the growth rate of chicks. This trend might easily be dismissed as the result of chance, were it not for the evidence presented earlier that, over a similar range, greater windspeeds enhance the fishing ability of Common Terns. As discussed earlier, a moderate degree of disturbance on the sea's surface is also likely to benefit fishing success. It is interesting, therefore, that in the overall (1968-70) regression of Common Tern data, some surface disturbance was associated with higher weight gains than none or too much, although this factor was responsible for only 10% of the observed variation.

In 1968, increasing windspeed also seemed to give an initial boost to the weight increments of Sandwich Tern chicks but this trend was not sustained beyond 7 knots and the overall distribution of points was not significantly related to windspeed or to any other variable. This relative insensitivity to wind compared with the two other species in the same year, could be related to several factors. Firstly, Shestakova (quoted by Borodulina 1960) pointed out that, among the Laridae, an increase in body weight leads to greater flight stability in strong winds. The Sandwich Tern is almost twice as heavy as Common and Roseate Terns and it may therefore be less susceptible to high winds. Furthermore, Pearson (1968) has shown that, among seabirds, the amount of foraging time required to rear a single chick decreases with increase in size of the species and from this he concluded: "Should the available food be less, the large seabirds have a considerable time period which could be exploited to search for food whereas the terns are breeding near the physical limit of their capacity to hunt and find food, and a decrease in the availability of fish must inevitably result in starvation among the larger broods." This size-related phenomenon could also operate within the tern species and then the Sandwich Tern, by virtue of its greater size, would be less vulnerable in fluctuating feeding conditions than the smaller Common and Roseate Terns.

High winds presumably impair the accuracy of diving and may, through surface disturbance, cause fish to become less accessible by moving deeper. It is also possible that, in strong winds, chicks compensate for heat loss by using relatively more food for maintenance and less for growth. However, the latter explanation cannot account for the different patterns of weight change with windspeed in the species studied. Moreover, Roseate Tern chicks which occupy burrow refuges, and are least exposed to wind, show the most direct response to increasing windspeed (Langham 1968). Why Roseate Terns should appear to be more sensitive to wind than Common Terns is not obvious but one possibility is that the former is at the northerly limit of its range in Britain and may be ill-adapted to the capricious climate of temperate latitudes. Langham (op. cit.) has noted the paradox that this species, with its apparent susceptibility to wind, is nevertheless an offshore feeder around Coquet Island and he has suggested that the dictates of food preferences have given rise to this anomaly. However, the difference in exposure between inshore and offshore areas may not be so great as to make the foraging area of this species a major anomaly.

Apart from windspeed, the only other weather variable worthy of note was rainfall which depressed weight increase of Common Tern chicks in 1968. Langham also found that rain adversely affected chicks of Common and Roseate Terns but the effect was much smaller than that of wind (1/5 as great in Common Terns, 1/7 as great in Roseate Terns). Rainfall might influence chick growth in various ways. It is known that one parent is more likely to remain at the nest-site to brood its chicks on rainy days, so preventing them from getting wet and cold. This means that only one parent can fish at a time so the food gathering potential is effectively halved on such days. Moreover, Boecker (1967) stated that when it was raining, a wind of force 6 (22-27 knots) reduced the feeding frequency of foraging Common and Arctic Terns. (Without rain, wind was not thought to be depressive till it reached force 7-8, i. e. 28-40 knots). Thus, on rainy, windy days, chicks are probably handicapped by a severe reduction in their food intake. Chicks more than about a week old are not brooded (pers. obs.) and although Palmer (1941) believed that, at this stage, individuals have a thermoregulatory system adequately developed to resist inclement weather, chicks of all ages on Coquet Island could sometimes be found wet and chilled after heavy rain, which rapidly soaks the dense undergrowth of Rumex acetosa and Festuca ovina. Again, Roseate Terns in their underground refuges are usually immune from such wetting and rainfall was not a significant factor for this species. It should be pointed out, however, that heavy rain is relatively uncommon during the breeding season and is only occasionally harmful. Out of 150 days in June and July between 1968 and 1970, there were only 19 (6%) on which rainfall exceeded 5mm, and only 9 exceeded 10mm.

In any of these unfavourable conditions, one other factor can aggravate weight loss and precipitate starvation. If wind and rain should persist for several, successive days, a vicious circle is started in which chicks get progressively weaker, gradually beg less vigorously, and so become less likely to elicit the appropriate feeding response from their parents (Langham 1968). This chain of events resulted in many chicks becoming so debilitated after a three-day storm in 1968 that, on return of favourable conditions, they were unable to recover and slowly starved to death in the midst of plenty.

The annual variations in the combination of independent variables correlated with weight changes can be attributed partly to fluctuations in the frequency and intensity of the different weather influences described above. In 1969 and 1970, the weather was less extreme than in 1968 and accordingly its effects were smaller and less likely to be detected. A complicating factor between years, and undoubtedly within years also, was the absolute abundance of food which could not be evaluated in any quantitative way. In 1970, for example, there was little doubt that food was in short supply at the peak hatching time for Common Tern chicks and this may have been such an overriding factor that daily fluctuations in weather, however large, could not significantly improve or depress the fishing ability of the adults. In this case, we should expect lower growth rates in 1970, compared with those in other years. After excluding days on which windspeed exceeded 12 knots (i. e., apparently the most deleterious weather factor) it is found that the mean (corrected) weight increase of Common Tern chicks in 1970 was only 4.9g compared with 6.5g in 1968 and 7.7g in 1969. Similarly, the mean weight increases of Sandwich Tern chicks in 1968 and 1970 were 8.5g and 6.1g respectively.

Ideally, these relationships should be tested by a simultaneous monitoring of fishing ability and weight increases. In the present study, logistical problems made this impossible to do satisfactorily. Nevertheless, from the independent observations of parental behaviour and growth performance under comparable conditions, certain trends in weight change can be linked with the food-gathering abilities of the parents. A break-down in provisioning in severe weather conditions can lead to widespread starvation and death but this usually affects only a certain proportion of chicks and may not seriously reduce the production of the colony as a whole. While the inimical effects of stormy conditions are clear, further investigations are required to elucidate the precise influence of very low windspeeds on chick growth since these have previously been overlooked by other authors.

SECTION IV

EFFECTS OF PARALYTIC SHELLFISH POISONING ON BREEDING BIOLOGY

Introduction

In May and June 1968 the marine food chain on the Northumberland coast was seriously affected by a toxin which, in addition to poisoning shellfish (Ingham et al. 1968), caused widespread mortality of other invertebrates and sand-eels Ammodytes (Adams et al. 1968) and various seabird species (Coulson et al. 1968a, b). There is little doubt that a bloom—the so-called 'red tide'—of the dinoflagellate Gonyaulax tamarensis was the source of the toxin which was subsequently transferred through the food chain (Wood 1968).

It was possible to trace the sequence of events back to 13 May when four Shags Phalacrocorax aristotelis died at Amble. At the same time, routine observations were started on the breeding cycle of the tern species on Coquet Island and the fishing success and diet of the birds were monitored at intervals throughout the critical period. It is worth pointing out that, until 23 May when the full extent of the mortality of Shags became apparent, I had little suspected that the events on Coquet Island were exceptional and had no knowledge that they were widespread. Observations were made, therefore, as for the "normal" situation and maximum objectivity was thereby ensured.

The following account describes in detail the results of these observations and draws special attention to the disruption of breeding at the egg stage.

Methods

When egg-laying began, the colonies were visited daily and each nest labelled with a numbered peg. In this way almost all nests of Sandwich Terns and Roseate Terns, and a representative sample of nests of Common and Arctic Terns were permanently marked for further study. A 'nest' was effectively represented by the appearance of an egg; the laying date was noted and similarly the dates for any other eggs added to the clutch were recorded. The desertion, breakage or loss (presumed predation) of eggs were also documented and, where possible, the causes determined. From hatching dates, incubation periods could be ascertained. In calculating these, the day of laying was taken as 'day 1'. A record was kept of eggs that did not hatch, either through being addled or from the chick failing to chip its way out of the shell. With the exception of a few "runts", it was possible to ring all chicks shortly after hatching without subsequent ring loss. A daily search was made for ringed chicks that died before fledging.

Results

(i) Foraging conditions during the red tide period

Since many factors such as failure of the food supply and favourable weather can adversely affect breeding seabirds, it is important to try and determine if any of these factors were inimical to the terns during the period when disruption was attributed to red tide.

The second fortnight in May and the first in June were characterised by dry, sometimes foggy, but mainly sunny weather with fresh onshore breezes prevailing. The weather was therefore apparently ideal for breeding terns and the very early onset of laying by Sandwich Terns (Table 33) provided additional support for this. It was not possible to watch Sandwich Terns foraging during the critical fortnight in May but observations on Common and Arctic Terns ('Comic' in Table 30) showed that their fishing success was uniformly high during this period, reaching 53.1% on 25 May. There is less evidence for early June, but fish seemed to be plentiful since sporadic fishing over shoals was seen along the coast at this time (see 5 June in Table 30). Sandwich Terns were relatively less successful than Common and Arctic Terns during the same spell but the fact that they were foraging consistently within five miles of Coquet Island indicates that they were unlikely to be experiencing any food shortage; the feeding range is generally much greater when fish are scarce locally (pers. obs.). The mean plunge-diving rate for Sandwich Terns, derived from 150 min. observation on 5 June and 12 June was 1.3 dives/bird/min which compares with

1.6 dives/bird/min for July observations. These means are not significantly different and the cumulative evidence strongly suggests that fish were no less plentiful than usual during the red tide period.

Table 30

Fishing success of terns during the red tide period.

Date	Sandwich Tern		Common Tern		'Comic' Tern[1]	
	No. of dives	Fishing success (%)	No. of dives	Fishing success (%)	No. of dives	Fishing success (%)
22 May	-	-	-	-	49	40.8
24 May	-	-	-	-	23	21.7
25 May	-	-	-	-	49	53.1
31 May	46	10.9	82	37.8	-	-
3 June	84	12.0	-	-	-	-
5 June	160	18.1	14	(71.4)	-	-
(shoal)	209	51.7	533	53.8	-	-
12 June	100	8.0	-	-	-	-
17 June	40	17.5	-	-	-	-

[1] Combined performance of Common and Arctic Terns which were not distinguished as separate species on these three days.

During May and June, a detailed record of the diet of Sandwich Terns was obtained by watching birds that brought fish into the colony. The results, listed in Table 31, show that the most frequent fish were sand-eels and clupeoids. The latter comprised about 60% of the diet in late May but almost completely supplanted other species in June. Apart from the unusually large contribution of gadoids in mid May, the relative proportions of fish shown in Table 31 are typical for the Sandwich Tern's diet in which clupeoids usually predominate on Coquet Island, (Langham 1968). In 1969, for example, the diet comprised 44% sand-eels, 52% clupeoids and 4% other food species during the breeding season. Most of the fish caught by Common and Arctic Terns in 1968 between 22 May and 25 May were too small to be easily recognised but seemed to be mainly sand-eels.

On 31 May, Common Terns caught 95% sand-eels and only 5% clupeoids (N = 22) but thereafter clupeoids began to predominate as in the Sandwich Tern's diet.

Table 31

Diet composition of Sandwich Terns during red tide period.

	PERCENTAGE COMPOSITION					
Date	Sand-eels	Clupeoids	Gadoids	Spinachia vulgaris[1]	Flatfish	N
16 May	34.5	40.1	23.9	1.1	0.4	284
17 May	29.9	52.2	17.9	0.0	0.0	67
18 May	16.7	66.7	16.6	0.0	0.0	18
20 May	46.8	42.6	8.5	0.0	2.1	47
21 May	31.4	68.6	0.0	0.0	0.0	35
24 May	32.3	64.5	0.0	0.0	3.2	31
9 June	8.2	91.8	0.0	0.0	0.0	85
11 June	2.5	97.5	0.0	0.0	0.0	40
12-17 June	6.3	93.7	0.0	0.0	0.0	16
Mean:	27.8	57.3	13.9	0.5	0.5	623

[1] Fifteen-spined stickleback.

(ii) Evidence for toxic food supply.

A great deal of diverse evidence has been assembled by the authors cited earlier to show that the side-effects of the red tide manifested themselves most acutely on the Northumberland coast. This was especially true of the seabirds. In addition, two specific kinds of evidence for deleterious effects on the Coquet Island terns can be given. These are: (a) the unusually high mortality of birds and (b) the behaviour of terns that were physically distressed.

(a) When three adult Sandwich Terns were found freshly dead on the island within two days (14-15 May) it was thought unlikely that this frequency would occur by chance. For this reason, a systematic search of the island was made every day and whenever a new corpse was found a note was kept of the species involved and any unusual circumstances. Between 14 May and 17 June, a total of

40 birds was found dead in this way and although this represents less than 1% of the seabirds at risk, it is a substantially higher mortality rate than in the 1969 and 1970 breeding seasons combined when only six corpses were found.

Table 32 suggests that Eider Ducks Somateria mollissima suffered more heavily than any of the tern species. This might well have been a real effect since the mussels Mytilus edulis which constitute the main local food of Eiders were shown by Ingham et al. (1968) to contain an extremely high concentration of toxin (up to 16,680 mouse units/100g at Amble, 1 mile from Coquet Island). On the other hand, Eider Ducks were much more likely to be found dead on the island than terns since the female alone incubates and rarely leaves the nest-site before the eggs hatch. It is probable that several terns escaped detection by dying at sea. In direct support of this, one ailing Common Tern was found at the water's edge and a Roseate Tern in obvious distress was recovered from the sea about 1½ miles offshore.

Table 32

Numbers of seabirds found dead on Coquet Island in relation to the size of the breeding populations at risk in 1968. Column four (from Coulson 1968a) gives the percentages of all birds at risk in Northumberland that were found dead on the coast during 25-31 May.

Species	Number at risk	Number dead	% dead (Coquet)	% dead (Northumberland)
Sandwich Tern	1200	8	0.7	1
Common Tern	2600	20	0.8	1
Arctic Tern	1200	5	0.4	1
Roseate Tern	400	1	0.3	1
Eider Duck	250	6	2.4	2
Total:	6050	40	0.7	1.4

Mortality coincided with several other biological phenomena that were synchronous with the red tide, notably phosphorescence, dying sand-eels, shellfish poisoning and a drastic reduction of the population of Shags on the Farne

Islands (Coulson 1968a). Although the temporal distribution of deaths in each species is based on low figures, these follow the patterns determined for the Northumberland coast as a whole (ibid.). Figure 38 shows that Sandwich Terns were the earliest victims: the first death was recorded on 14 May and the corpse was sufficiently fresh to establish that the bird had not died more than 24 hours prior to its discovery. Of the seven subsequent deaths in this species, six occurred between 23 and 28 May and none were recorded thereafter. Mortality of Sandwich Terns was therefore confined to 14 days in May. By contrast, Common Terns succumbed over a later (24 May-10 June) and rather longer (18-day) period with a diffuse 5-day peak of deaths around 29 May-2 June. Arctic Terns died during an apparently similar spell but one late death (17 June) combined with other evidence (Coulson 1968a) shows that the time span of mortality was more protracted than for the Common Tern. Only one Roseate Tern was found dead and another was found ill on the same day. Nevertheless it is important to note that neither of these individuals fell ill as early as the first recorded Sandwich Terns. The distribution period of mortality in the Eider Duck was generally coincident with that for the Common Tern but was slightly more extended (22 days). In summary, Sandwich Terns died during a relatively short spell in late May. By comparison, the temporal distribution of deaths in the other species began later (9-10 days after the first Sandwich Tern), peaked later (ca. 7 days), and was more protracted (by 4-11 days).

(b) A serious malfunction of the affected birds was indicated from two sources, one behavioural, the other pathological. The first sign of abnormality was noticed in the colony of Sandwich Terns where an unusually high frequency of upflights by incubating birds was evident in May. An 'upflight' as used here refers to the colony rising en masse and circling for a variable period before re-settling on nests; these dispersals suggested a general "nervousness" in the colony. Consequently, birds were off eggs for up to an hour at a time and it was evident that such severe disturbances were not elicited by the usual factors, namely the approach of a person or potential aerial predator (normally Herring

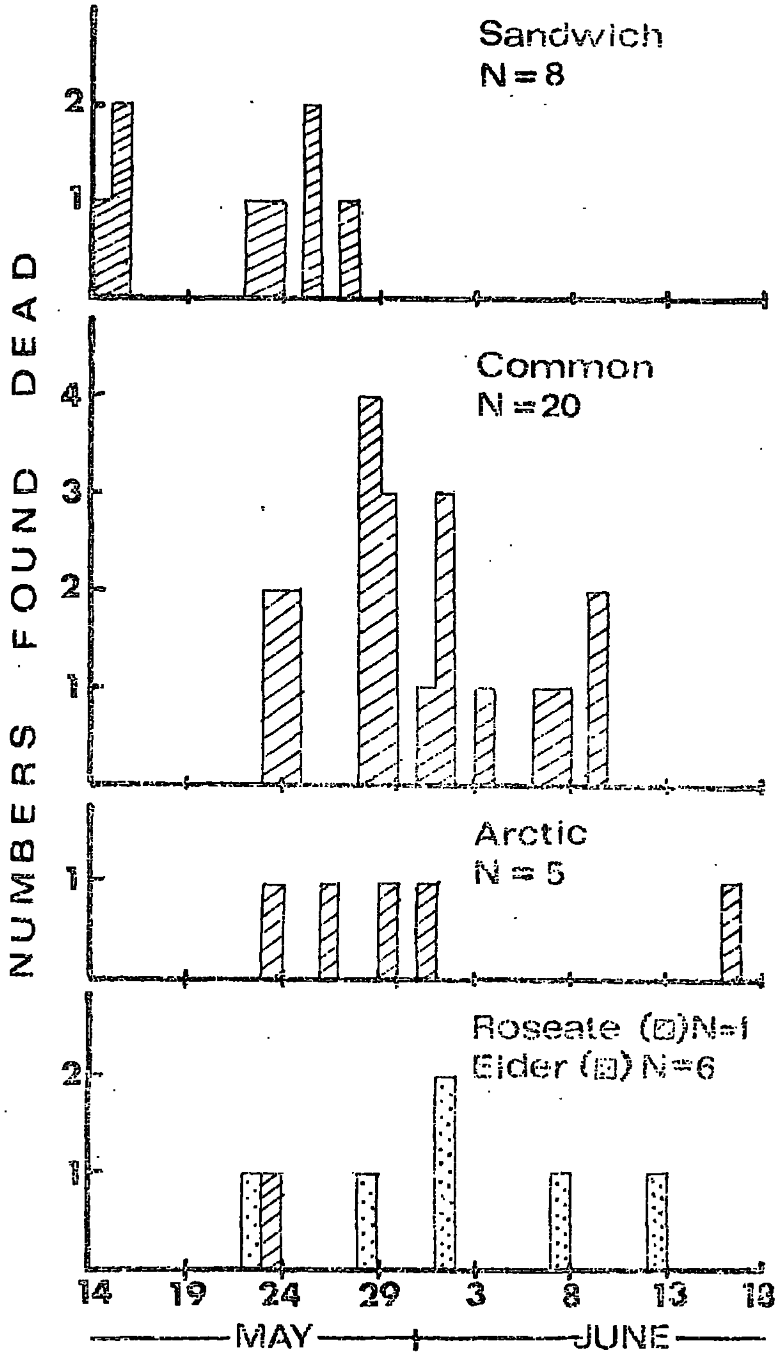


Figure 38

Temporal distribution of dead terns and Eider Ducks found on Coquet Island in May-June 1968.

Gull Larus argentatus), apparent aerial predator (Pigeon Columba livia) or an Eider Duck walking through the colony. Hide observations suggested that at least some of these upflights were associated with the conspicuously abnormal behaviour of distressed birds. The following extract from field notes on 29 May describes one of several similar incidents involving sick birds—in this case a Sandwich Tern—and indicates most of the symptoms and their repercussions:

> "Bird on nest 222 seems to be in a bad way—violent choking movements—wings dropped sluggishly—eyelids half-closed. Failed to return after upflight (15.15) and landed down on rocks. Back on nest (same symptoms) at 15.40. Another upflight at 15.45 puts ailing bird off nest again. Landed nearby but still in distressed condition. It returned to subcolony at 16.05—uncoordinated wing-flapping movements. Settled, but not on nest."

The salient features of this incident are as follows. (i) The main symptoms were the bird's choking and general loss of motor coordination (Figure 39a). (ii) Since the bird's mate was not incubating during the disturbance it is clear that the eggs were susceptible to chilling and predation. (iii) The sight of the sick bird's behaviour visibly unsettled its immediate neighbours and may have been the direct cause of the two spontaneous upflights in the space of an hour. Similarly afflicted birds, especially Common Terns, were discovered by the dense mob of conspecific terns hovering just overhead.

It is notable that the Sandwich Tern ill on nest 222 did not die. Moreover, the two eggs were hatched and one of the chicks was raised to fledging. Other sick birds also seemed to have received a sub-lethal dose of toxin since they recovered after an hour or so without showing any apparent ill effects. The chances of recovery were presumably enhanced by successful regurgitation of the noxious meal and it is interesting that on 24 May the colony of Sandwich Terns was littered with discarded sand-eels. This occasionally happens when the rate of fish capture by adults exceeds the chicks' requirements but does not normally occur during the incubation phase.

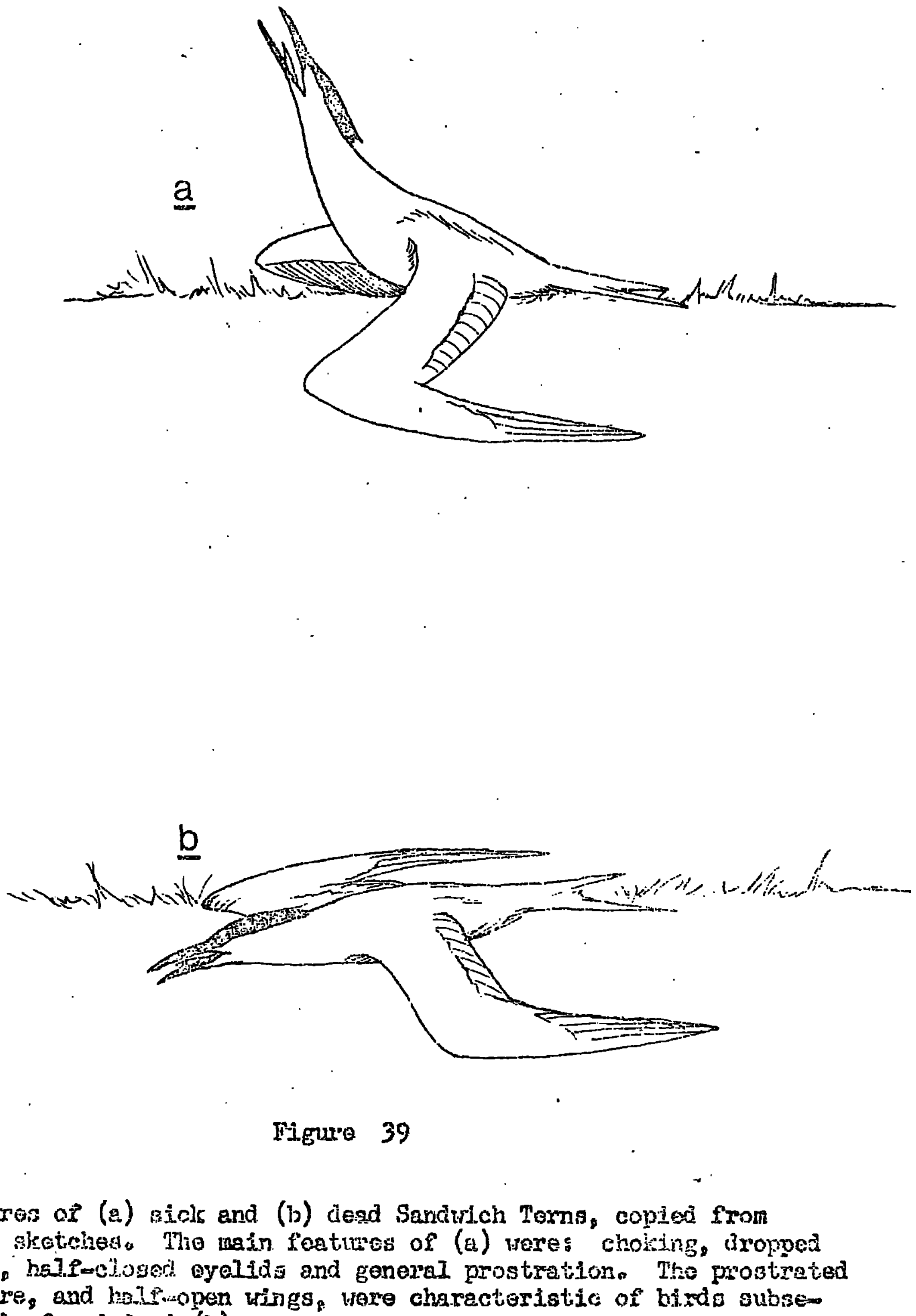


Figure 39

Postures of (a) sick and (b) dead Sandwich Terns, copied from field sketches. The main features of (a) were: choking, dropped wings, half-closed eyelids and general prostration. The prostrated posture, and half-open wings, were characteristic of birds subsequently found dead (b).

Only superficial pathological evidence could be collected in situ and a complete diagnosis of affected birds is described by Coulson (1968a). Birds that had died with the symptoms described above were recognised by their characteristic posture, i. e. prostrated on the ground with wings half-outstretched (Figure 39b). Several of these birds were found on examination to be 'egg-bound' and were presumed to have died in the process of egg-laying. A post-mortem of one of these corpses showed that the bird, a Sandwich Tern, was in good condition (weight: 282g) but was affected by egg peritonitis: there was a partially shelled egg impacted in the oviduct which was congested. This implied that the toxin may have been more hazardous to females than to males. Autopsy of corpses collected elsewhere in Northumberland confirmed that four times as many female terns succumbed as males and that malfunction of the oviduct was implicated as the cause of death in 86% of females (from Coulson 1968a).

(iii) Breeding performance during the red tide period

(a) Sandwich Tern

Pattern of egg-laying

As already shown, the Sandwich Tern was the first species to show exceptional mortality (Figure 38) and abnormal behaviour. Its breeding performance in 1968 will now be examined in detail and compared with other years, especially 1970, when red tide effects were apparently absent. On Coquet Island, the Sandwich Tern is normally the first tern species to start breeding and 1968 saw the earliest onset of egg-laying recorded in six years' continuous observations (Table 33).

Table 33

Annual breeding statistics for the Sandwich Tern

Year	Total nests	Date when 1st egg was found	Spread of laying (days)	Mean clutch size	Reference
1965	313	11 May	64	1.41	Langham (1968)
1966	797	13 May	72	1.15	"
1967	c1750	11 May	44	1.24	"
1968	593	8 May	55	1.12	Present study
1969	206	2 June	33	1.05	" "
1970	708	16 May	22	1.50	" "

As regards the present study, laying was highly synchronous in both 1968 and 1970 (Figure 40) but not in 1969 when the birds did not commence breeding until very late in the season (Table 33). In 1970 the breeding population was about 100 pairs larger than in 1968 and the terns started laying 8 days later than the 1968 birds. Nevertheless the patterns of egg-laying in these two years are basically very similar, sharing in common a marked unimodal peak shortly after the onset of laying. Moreover, in both years the subcolonies were relatively large which is a characteristic feature of the Sandwich Tern (Langham 1968) when it breeds as synchronously as it did in 1968 and 1970. In short egg-laying patterns in these years resemble each other in several fundamental respects and this is a strong case of referring to 1970 as a 'control' year for assessing the normality or otherwise of certain aspects of the breeding performance of Sandwich Terns in 1968.

Figure 40 also shows that the early marked peak of laying in 1968 was followed by a long "tail-off" but comparison with other years (Table 33) indicates that the spread of laying was by no means exceptional. Langham (1968) also found that in 1965 and 1966 small numbers of Sandwich Terns continued to begin clutches long after the major peak of egg-laying. Despite widespread desertion and loss of clutches in May 1968 (see later), there was no evidence of repeat laying and it seems unlikely that the laying pattern was influenced by the abnormal circumstances described. However, the marked susceptibility of birds to death during egg-laying is reflected in the similar spread of mortality and laying.

Egg loss

A remarkable feature of the Sandwich Terns' colony in 1968 was the widespread desertion and loss of eggs in May. Casual observations indicated that eggs were first abandoned and then eaten by Black-headed Gulls Larus ridibundus and less commonly by Oystercatchers Haematopus ostralegus and Herring Gulls Larus argentatus. It seemed unlikely that these desertions were a consequence of my occasional presence in and around the colony since comparable

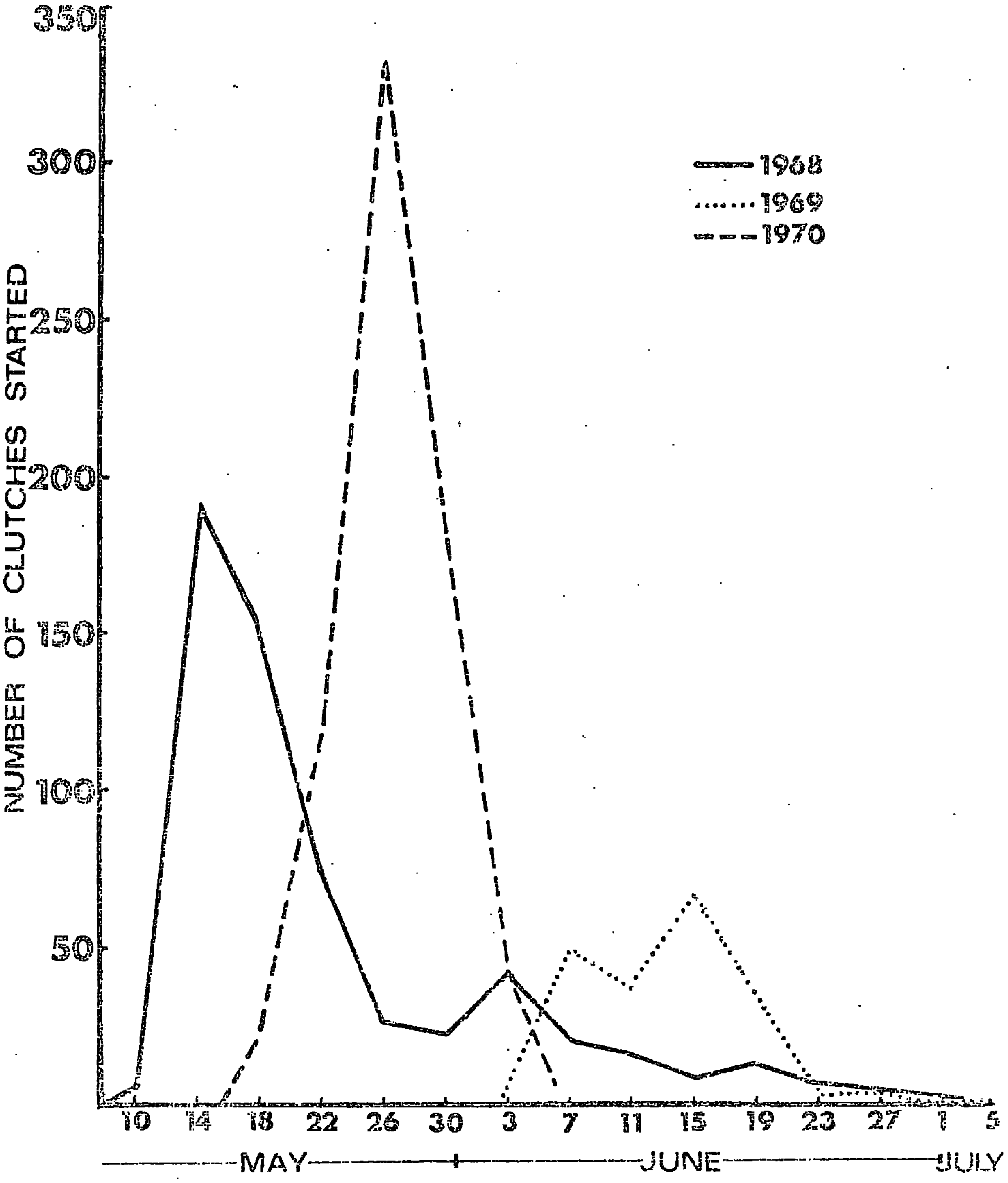


Figure 40

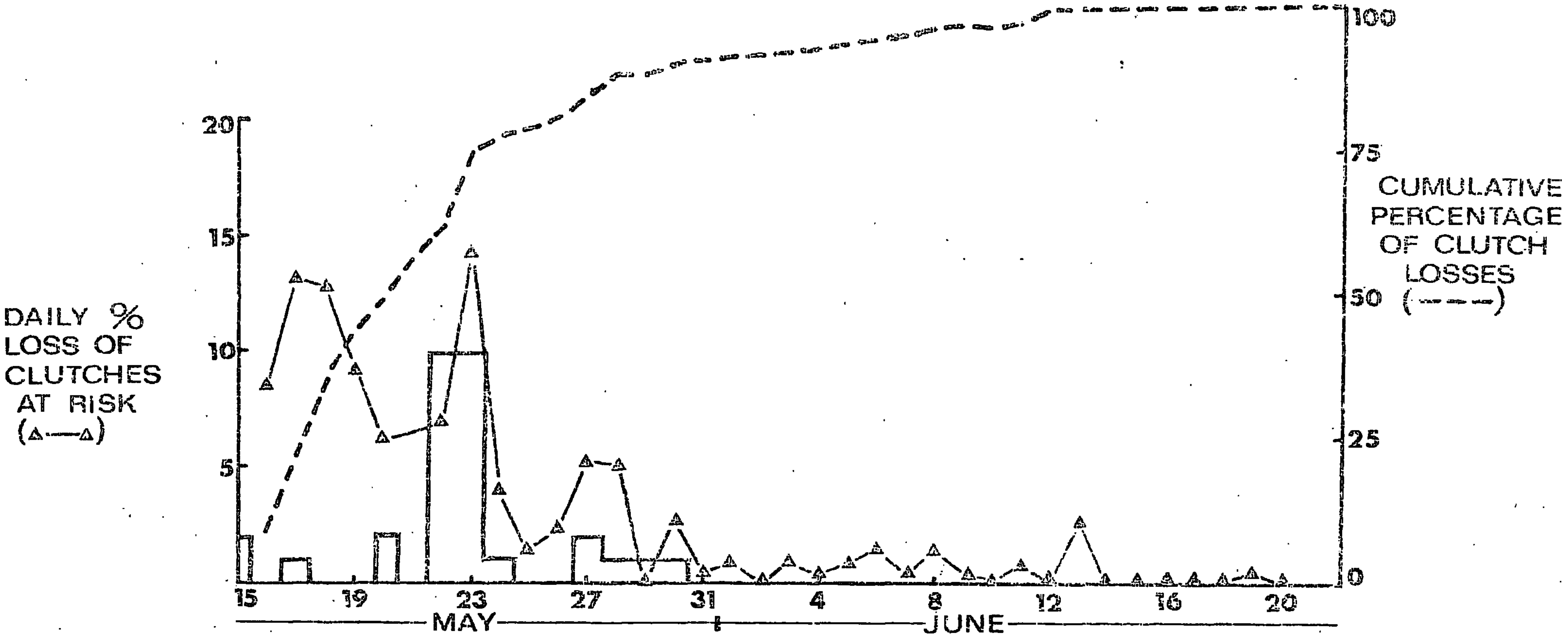
The pattern of egg-laying of Sandwich Terns from 1968-1970.

disturbance produced no evidence of desertion in the same portion of the laying span in 1970. Also, similar levels of colony disturbance (less than 20 minutes per subcolony per day) by other workers (N. P. Langham, A. J. M. Smith, pers. comm.) have produced insignificant desertion. It is usually only in the first few days before, and at the start of laying that Sandwich Terns are abnormally sensitive to disturbance and they may desert the colony altogether if disruption is excessive (Cullen 1960, Chestney 1970). In view of this hazard, no work was carried out in the colony until 13 May when the birds were firmly established and egg-laying was well under way (Figure 40). It seems most probable, therefore, that a factor (or factors) other than human disturbance was responsible for the desertion of eggs in 1968.

To examine the time sequence of losses more closely, the percentage loss of clutches at risk was plotted for each day. The number of clutches at risk on day '<u>n</u>' was the number surviving from the previous day (n - 1) plus new clutches found on day <u>n</u>. In the case of a two-egg clutch, the clutch was not scored as lost if only one egg was lost and if incubation of the other one was continued. However, such cases were rare since, as noted earlier, the great majority (88.2%) of clutches consisted of a single egg and both eggs were usually lost from two-egg clutches. 'Lost' in this context means deserted (cold), broken (usually after desertion) or disappeared altogether. The temporal distribution of these losses is plotted in Figure 41. It is clearly demonstrated that severe losses were incurred in a concentrated period between 15 May (and possibly earlier) and 30 May. Thus, by 23 May, 75% of all clutches had been laid and 75% of the losses had taken place. By 30 May the cumulative loss had risen to 90%. The clutches started thereafter, representing 17% of the total number laid, suffered insignificant losses by comparison—only 10% (of all the losses) in 20 days. The catastrophic egg loss in May coincides well with the mortality of Sandwich Terns on the Northumberland coast. The similarity between the patterns of clutch loss and mortality is particularly striking between 21 May and 30 May, with a peak appearing in both distributions around 22-23 May, and a halt in mortality and

Figure 41

Daily and cumulative percentage loss of clutches started (i. e. not necessarily completed) by Sandwich Terns in May-June 1968. The histogram shows the numbers of Sandwich Terns found dead on the Northumberland coast during the same period (N = 32, from Coulson 1968a).



dwindling egg loss after 30 May. To emphasise the improvement after 30 May, Table 34 shows that the total loss of clutches before this date was 55% compared with 37% after it, which represents a highly significant difference ($X^2 = 11.81$, 1 d. f., $p<0.001$).

Table 34

Differential clutch loss before and after 30 May.

	Clutches laid	Clutches lost	% lost
Up to 30 May	473	261	55
After 30 May	109	40	37

Hatching success

This is a measure of the number of eggs laid that subsequently hatch, expressed as a percentage. As a standard component of breeding success, it is a frequently estimated parameter and can be directly compared in this case with other studies on the Sandwich Tern. Table 35 lists the hatching success of this species on Coquet Island over the six years for which data are now available.

Table 35

Hatching success of the Sandwich Tern in different years.

	PERCENTAGE SUCCESS					
	1965[1]	1966[1]	1967[1]	1968	1969	1970
Clutch 1	41.6	72.0	-	33.2	22.5	56.1
Sample	219	722		497	195	335
Clutch 2	66.2	73.1	-	61.2	(13.6)	70.0
Sample	83	78		67	11	335
All clutches	53.9	72.2	81.9	39.1	21.7	65.4
Sample	302	800	1982	564	206	670

[1] Data from Langham (1968).

It has already been noted that the breeding performance of the Sandwich Tern in 1969 was as abnormal as in 1968 but for different reasons. After several "false starts" in which the terns intermittently occupied and abandoned various areas on the island, the birds (a) eventually started laying 2-3 weeks later than usual (Table 33) and even then they were (b) poorly synchronised and (c) in widely separated groups. Considering this combination of factors, two of which (b and c) have already been shown to be associated with depressed hatching success (Langham 1968), it is scarcely surprising that success was as low as 21.7% in 1969. Among the other 5 years in Table 35, however, 1968 is conspicuous by its below average hatching success and this cannot be attributed to any of the adverse factors attendant in 1969.

Table 36 shows the seasonal variation in hatching success during 1968. Just as in Table 34, May 30 serves as an arbitrary but realistic dividing line for the data which are subdivided into 4-day periods, with the exception of the earliest (May 8-14) and latest (June 4-14) clutches examined.

Table 36

Seasonal variations in hatching success, 1968.

	HATCHING SUCCESS (%)					
Laying period	N[1]	Clutch 1	N	Clutch 2	N	All clutches
May 8-14	173	24.9	33	53.0	206	32.6
15-18	139	18.7	15	53.3	154	24.9
19-22	62	33.9	11	77.3	73	45.2
23-26	26	50.0	0	-	26	50.0
27-30	20	55.0	2	(100.0)	22	62.5
31-3	38	65.8	3	(66.7)	41	65.9
June 4-14	39	66.7	3	(100.0)	42	71.1
May 8-30	420	27.1} ***	61	59.0	481	34.3} ***
May 31-June 14	77	66.2}	6	(83.3)	83	68.5}
Whole period	497	33.2	67	61.2	564	39.1

[1] Number of clutches.

*** = $p < 0.001$.

The main point to note is the striking trend in hatching success which rose steadily from 32.6% to 71.1% during the spread of laying. This upward trend is significant for 1-egg clutches (Kolmogorov-Smirnov one-sample test, $p<0.01$) and for 1-egg and 2-egg clutches combined. By contrast, hatching success in 1970 (Table 37) varied seasonally within relatively narrow limits, but tended to be higher in the earliest laid eggs.

Table 37

Seasonal variation in hatching success, 1970.

	HATCHING SUCCESS (%)					
Laying period	N	Clutch 1	N	Clutch 2	N	All clutches
May 16-18	5	(100.0)	18	80.6	23	85.4
19-22	35	68.6	84	69.6	119	69.5
23-26	148	49.3	152	69.4	300	62.8
27-30	109	60.6	69	65.9	178	63.6
May 31-June 4	38	52.6	12	87.5	50	66.3
Whole period	335	56.1	335	70.0	670	65.4

Fledging success

This parameter measures the proportion of hatched chicks that survive to fledge. In disturbed colonies, Sandwich Tern chicks disperse from the nest-site into thickly vegetated areas only a few days after hatching and are then difficult to locate. In estimating fledging success, a slight upward bias was introduced by assuming that those individuals not seen again after 5 days from hatching fledged successfully.

Fledging success was about the same in 1968 as in other years and was actually a little higher than usual (Table 38).

Table 38

Fledging success of the Sandwich Tern in different years.

		1968		1969		1970	
Brood size	Order of hatching	Fledging success	N	Fledging success	N	Fledging success	N
B 1	1	90.1	181	86.7	45	81.7	219
B 2	1	87.9 }89.4	33	(100.0)	2	90.0 }84.7	219
	2	90.9 }	33	(100.0)	2	79.5 }	219
All chicks		89.9	247	87.8	49	83.7	657

The red tide phenomenon did not, therefore, adversely influence overall fledging success in 1968 and this is not unexpected since the first chicks did not hatch till June 2, by which time Sandwich Terns appeared to be less susceptible to ill effects (e. g. Figure 41). The seasonal pattern of fledging success (Table 39) shows no regular trend such as was demonstrated for hatching success. However, proportionately fewer chicks fledged from the earliest hatched eggs (i. e., those eggs laid during May 8-14) and this was apparent for both single and two-chick broods. Thereafter, fledging success was uniformly high.

Table 39

Seasonal variation in fledging success (F. S.) in 1968.

The success for all chicks in 1970 is also shown.

Laying dates		May 8-14		M 15-18		M 19-22		M 23-26		M 27-30		M 31-Jun 3		J 4-14	
Brood size	Hatch order	F. S.	N	F.S.	N	F.S.	N	F.S.	N	F.S.	N	F.S.	N	F.S.	N
1	1	77.8	54	96.6	30	100.0	22	92.3	13	90.9	11	100.0	25	88.5	26
2	1	75.0	12	(83.3)	6	(100.0)	8	-	0	(100.0)	2	(100.0)	2	(100.0)	3
	2	83.3	12	(100.0)	6	(100.0)	8	-	0	(100.0)	2	(50.0)	2	(100.0)	3
All chicks (1968)		78.2	78	95.2	42	100.0	38	92.3	13	93.3	15	96.6	29	90.6	32
All chicks (1970)				92.3	34	81.6	141	87.3	284	82.9	157	73.2	41		

(b) <u>The other tern species</u>

Pattern of egg-laying

In 1968, the first eggs of Common and Arctic Terns were laid on 25 May and the first Roseate Tern clutch on 6 June. These dates represent average commencement times for breeding by these species on Coquet Island (Table 40).

Table 40

Annual dates when first eggs were laid by Common, Arctic and Roseate Terns.

	1968	1969	1970
Common Tern	25 May	2 June	25 May
Arctic Tern	25 May	28 May	25 May
Roseate Tern	6 June	5 June	31 May

After the onset of laying, the number of clutches started by Common Terns showed a rapid initial increase but this trend was not maintained and the typically regular build-up towards a unimodal peak did not occur (Figure 42a cf. egg-laying patterns in 1969 and 1970, Appendix 5). Instead, a plateau level of laying was established in the first week of June and only thereafter did the anticipated increase follow. A retarded laying peak of this kind has not been recorded on Coquet Island in the other five years of breeding data available for comparison. Whether this pattern was directly related to the red tide phenomenon is not known but it seems probable that the normal synchrony of Common Terns was unsettled in late May and early June. Notably, the atypical portion in the spread of laying (Figure 42a) coincides with the observed mortality of adult Common Terns (Figure 38). Additional support is lent to the possibility of a real disruption of synchrony by evidence from the nearby Farne Islands. In 1968, at the same time of year, the breeding season of the Arctic Tern was shown to be abnormally delayed and spread, with a protracted plateau rather than a distinct peak of egg-laying (J. M. Horobin in Coulson 1968a).

On Coquet Island, however, Arctic Terns displayed a pattern of egg-laying typical of other years (Figure 42b cf. egg-laying patterns in 1969 and 1970, Appendix 5) with numbers of clutches rapidly reaching a unimodal peak in the first week of June. Laying is slightly less sychronous than usual but not so much as to suggest any significant difference. It is worth noting that, excep-

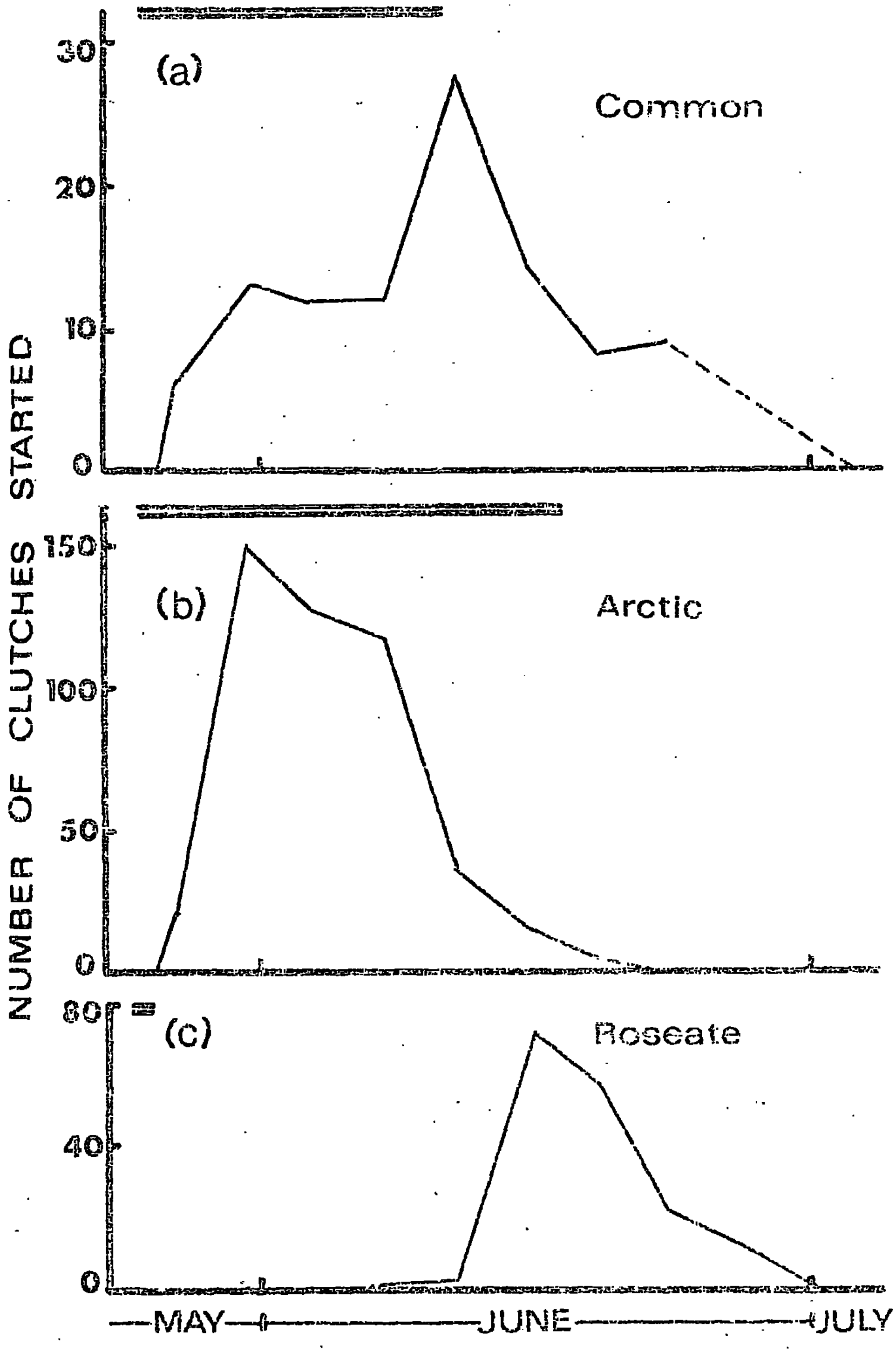


Figure 42

The pattern of egg-laying of Common, Arctic and Roseate Terns in 1968. The heavy double line (═══) indicates the time span between the finding of the first and last dead adult individual of each species.

ting the small number of terns that laid after June 19 which were not recorded, the mortality of Arctic Terns corresponds very closely in time with the spread of laying in this species. This is consistent with the fact, already mentioned, that the egg-laying process was causally implicated in the deaths of several individuals.

There were no discernible anomalies in the laying pattern of Roseate Terns which are always the latest species to start egg-laying on Coquet Island (Table 40). The peak of laying in 1968 was not reached till 15 June by which time the dinoflagellate bloom was probably over (Robinson 1968).

Hatching success and fledging success

The hatching success of each tern species for all eggs, irrespective of clutch size, is shown for 1968-70 in Table 41. In 1968, hatching success was the highest recorded over the three years. This was consistent for each of the three species, and was not affected by differences in clutch size (Appendix 6).

Table 41

Annual hatching success of Common, Arctic, and Roseate Tern eggs.

	1968		1969		1970	
	Success	N[1]	Success	N	Success	N
Common Tern	91.4	278	64.9	447	78.3	272
Arctic Tern	87.0	585	64.8	454	82.5	292
Roseate Tern	97.0	273	83.5	255	82.5	154

[1] Number of eggs.

A record (high) fledging success would probably have been recorded in 1968 but for the intervention of a severe storm between 15-17 July. For example, out of a total of 41 Roseate Tern chicks found dead throughout the whole breeding season, 32 (78%) of them died either during or shortly after this spell of bad weather. In spite of this set-back fledging success was still not exceptionally low in 1968 (Table 42 and Appendix 7). It can therefore be concluded that chick survival and hatching success were not impaired by any factor related to the dinoflagellate bloom.

Table 42

Annual fledging success of Common, Arctic, and Roseate Tern chicks.

	1968		1969		1970	
	Success	N[1]	Success	N	Success	N
Common Tern	85.1	308	95.2	290	84.0	213
Arctic Tern	92.7	399	89.7	292	74.5	235
Roseate Tern	83.9	254	94.4	213	85.8	127

[1] Number of chicks.

Discussion

By elimination of other possible factors, various abnormalities in the breeding performance of terns in 1968 can be unequivocally linked with the outbreak of paralytic shellfish poisoning in May and June of that year. Inspection of diet composition shows that the birds were feeding on sand-eels and sprats at the same time as vast numbers of dead sand-eels were being washed up on the Northumberland coast. The birds which died as a result of the transfer of toxin through the food chain were readily distinguishable by their characteristically prone, "cruciform" posture which resulted from violent vomiting and loss of motor coordination. It is likely that many terns suffered a sub-lethal dose of toxin and were not seriously debilitated. Evidence for this stems from regurgitated sand-eels which were disproportionately numerous compared with the actual number of birds found dead. Furthermore, one bird, a Sandwich Tern, showed symptoms of severe distress but recovered fully to breed successfully.

It is conceivable that sub-lethal effects acting within birds, coupled with the disquieting effects of incubating next to a neighbour suffering from general ataxia, combined to disrupt the continuity of incubation among Sandwich Terns. Unfortunately it was not possible to determine if distressed birds specifically elicited upflight behaviour from other birds or if these panics were a response to a more diffuse "nervousness" in the subcolonies. Whatever the precise cause, exceptionally widespread desertion of clutches took place and the abandoned eggs were quickly predated. Fickleness in breeding has often been casually attributed to Sandwich Terns but they do not readily abandon eggs after incubation has advanced a few days. The complementary frequency distributions of egg loss and mortality in this species (Figure 41) strongly suggest, therefore, that nest desertion was a repercussion of the effects of paralytic shellfish poisoning on the birds. Overall, about 60% of eggs was lost; this represents a 30% poorer hatching success than the average of other comparable years (from Table 35) and is a very low figure considering that an early start to the breeding season such as was made in 1968 is usually associated with good breeding productivity, providing adverse factors do not intervene. Only 1969 has so far yielded a poorer hatching record but this can be satisfactorily explained for reasons other than red tide.

Adult birds engaged in egg-laying were the most susceptible individuals and, with the possible exception of the earliest-hatched Sandwich Tern chicks, fledging success of young was not affected. Indeed chicks of all species showed good fledging success in 1968. In addition, the hatching success of Common, Arctic and Roseate Terns was unusually high. Apart from a less synchronised laying pattern than usual in Common Terns, the breeding performance of these three tern species did not show any abnormalities at all, even though adult mortality was comparable with that of Sandwich Terns. The question arises as to why Common and Arctic Terns in particular did not incur appreciable egg loss like the Sandwich Terns. Although Common and Arctic Terns show laying synchrony comparable with Sandwich Terns, they do not form aggregated, highly synchronised subcolonies like the latter. Instead, their inter-nest distance is much greater and they do not exhibit the marked sociality characteristic of Sandwich Terns. Consequently, while the loss of a few eggs in a subcolony of Sandwich Terns can lead to the unsettlement and disintegration of the entire group, this is much less likely in colonies of Common and Arctic Terns where mutual attachment is less well developed. In these terms, it is possible to see how major disruption could spread rapidly through a colony of Sandwich Terns but not through the more diffuse structure of Common or Arctic Tern colonies. This may explain the relative performances of these three species during the red tide phase in 1968; Roseate Terns, as has been pointed out, escaped harm by virtue of their traditionally late breeding season compared with the other terns. However, the situation is complicated by the fact that the breeding success of Sandwich Terns on the Farne Islands was apparently normal in 1968 (Coulson 1968a). It is difficult to explain the immunity of this breeding group which, considering its geographical location, was certainly as vulnerable as the Sandwich Terns on Coquet Island.

SECTION V

THE COMPOSITION OF TERN EGGS

Introduction

Egg quality has for a long time been the subject of intensive research by students of poultry husbandry but not till quite recently have similar investigations been widely extended to include natural avian populations. The colonial, ground-nesting habit of many seabird species renders them particularly suitable for easy access to large samples of eggs and has led to several detailed studies, mainly of a biometrical nature.

These have shown that, in a great many of the Laridae, the last egg in the clutch is usually smaller or narrower than preceding eggs. This phenomenon has been demonstrated in the Herring Gull Larus argentatus and Lesser Black-backed Gull Larus fuscus (Paludan 1951), Laughing Gull Larus atricilla (Preston and Preston 1953), Common Tern (Gemperle and Preston 1955), Black-headed Gull Larus ridibundus (Ytreberg 1956), Californian Gull Larus californicus (Behle and Goates 1957), Kittiwake Rissa tridactyla (Coulson 1963), Great Black-backed Gull Larus marinus (Harris 1964), Southern Black-backed Gull Larus dominicanus (Fordham 1964), Common Gull Larus canus (Barth 1967), and most recently in the Ring-billed Gull Larus delawarensis (Vermeer 1969).

In his study of the Herring Gull, Parsons (1971) has drawn attention to other differences in the terminal (third) egg of the clutch, showing that it contains relatively less lipid than the larger eggs preceding it in the laying sequence, and that it produces a chick which is less well endowed with lipid reserves than either of its siblings. This factor undoubtedly contributes to the relatively high mortality suffered by third chicks in the first few days after hatching (Parsons loc. cit.).

In view of the possibility that egg "quality" might contribute to post-hatching survival of tern chicks, it was decided to investigate further certain aspects of the physical attributes and nutritional composition of eggs laid by the tern species nesting on Coquet Island.

Field methods

During the peak laying period (early June) a random sample of nests—indicated by the presence of a single egg—was marked and successive eggs laid in the clutch were numbered with an indelible "Magic Marker" pen so that their position in the laying sequence was known. In the case of the Roseate Tern, the sample size was augmented by marking completed clutches and determining from the hatching order the sequence in which the eggs had originally been laid. This indirect method was necessary because clutches in this species were often not located before completion due to the cryptic siting of nests. Those eggs marked as they were laid served as a control group to establish that hatching order is a reliable indicator of laying order in two-egg clutches of Roseate Terns. The maximum length and breadth of each marked egg were measured to the nearest 0.1mm by means of vernier calipers.

In addition, 58 fresh eggs of Common Terns (7 clutches of single eggs, 9 of two eggs and 11 of three eggs) of known laying order were collected under licence from the Nature Conservancy for yolk and lipid analysis. Since the divisions between yolk and albumen breaks down during the early stages of incubation, removal of eggs as they are laid is a prerequisite for subsequent separation of the yolk. Eggs were therefore taken from the nests within 24 hours of being laid and were immediately replaced by eggs from neighbouring clutches to prevent desertion and so ensure completion of the clutch. After measuring the length and breadth of the removed eggs as described, they were preserved in a refrigerator for later analysis. The eggs were weighed after a short time in the refrigerator and, while some water loss may have occurred as a result of this procedure, this factor was not detrimental to the main objectives of the study.

Results

(i) Egg dimensions

Egg volumes (V) were calculated from the formula $V = 0.48 \times b^2 \times l$ where 'b' is the maximum breadth, 'l' the maximum length, and 0.48 is an adjusted correction factor which allows for the imperfect ellipsoid form of an egg. A similar factor has been used to determine volumes of Kittiwake eggs (Coulson 1963) and Herring Gull eggs (Parson 1971), and 0.48 is probably a good approximation for a comparative assessment of volume in tern eggs. The second parameter calculated was the shape index $(=\frac{100 \times b}{l})$ which is high when the egg is relatively short and broad, and low when the egg is relatively long and narrow. The index is independent of the size of the egg and can therefore be compared directly between species.

First and second eggs in clutches of two and three are hereafter called the *a* and the *b* egg respectively while the third egg in a clutch of three will be referred to as the *c* egg.

The dimensions, volumes and shape indices of eggs of the four tern species are shown in Table 43 and the statistical probabilities of significance are summarised in Table 44. Where the clutch consists of only one egg, that egg is invariably longer and greater in volume than any other egg (of whatever clutch size) in Common, Roseate and Sandwich Terns. These differences, though not significant, were consistent in both 1968 and 1969 and are reflected in a significantly lower shape index of single eggs in Common Terns in 1968 ($t = 2.68$, 34 d. f., $p<0.02$) and in Sandwich Terns in 1969 ($t = 2.08$, 173 d. f., $p<0.05$). Single-egg clutches of Arctic Terns, however, do not follow the trend shown by the other three species and tend to be intermediate in size between *a* and *b* eggs of two-egg clutches.

By laying single eggs that exceed in volume eggs in other clutch sizes, the Common Tern contrasts strongly with the Kittiwake (comparable in having up to three eggs in a clutch) which lays relatively small single eggs, closely resembling the terminal eggs of two-egg and three-egg clutches. Coulson and White (1961) and Coulson (1963) have shown that there is a high incidence of single-egg clutches among Kittiwakes laying for the first time and that these eggs are, on average, appreciably smaller than single eggs laid by birds in their second and subsequent breeding seasons. In Common Terns and other tern

Table 43

Mean dimensions, volume and shape index of tern eggs according to clutch size. Standard errors are shown.

	Clutch size	N	a				b				c			
			Length	Breadth	Volume	S. I.	Length	Breadth	Volume	S. I.	Length	Breadth	Volume	S. I.
COMMON TERN	1	20	41.49 ±0.38	30.00 ±0.18	17.95 ±0.30	72.40 ±0.66								
	2	82	40.96 ±0.18	29.83 ±0.90	17.50 ±0.13	72.94 ±0.39	40.23 ±0.18	29.51 ±0.09	16.83 ±0.14	73.46 ±0.37				
	3	42	40.69 ±0.27	29.99 ±0.10	17.58 ±0.20	73.84 ±0.45	40.04 ±0.26	30.00 ±0.12	17.32 ±0.20	75.02 ±0.48	39.83 ±0.25	29.35 ±0.13	16.49 ±0.20	73.79 ±0.52
ARCTIC TERN	1	26	40.25 ±0.37	29.16 ±0.16	16.44 ±0.24	72.58 ±0.72								
	2	88	40.52 ±0.16	29.32 ±0.08	16.73 ±0.11	72.45 ±0.35	40.07 ±0.16	28.96 ±0.08	16.14 ±0.10	72.38 ±0.36				
	3	10	39.93 ±0.60	29.30 ±0.27	16.50 ±0.51	73.46 ±0.77	39.34 ±0.68	29.04 ±0.20	15.95 ±0.45	73.97 ±1.06	38.96 ±0.75	28.50 ±0.24	15.21 ±0.43	73.36 ±1.35
ROSEATE TERN	1	50	44.69 ±0.23	29.73 ±0.11	18.97 ±0.17	66.60 ±0.43								
	2	53	44.27 ±0.20	29.81 ±0.09	18.90 ±0.14	67.41 ±0.36	43.20 ±0.20	29.31 ±0.10	17.84 ±0.17	67.91 ±0.31				
SANDWICH TERN	1	54	52.28 ±0.29	35.73 ±0.14	32.06 ±0.30	68.45 ±0.47								
	2	15	51.71 ±0.43	35.51 ±0.36	31.99 ±0.66	69.40 ±0.64	49.37 ±0.48	34.78 ±0.27	28.73 ±0.65	70.50 ±0.51				

Table 44

The statistical significance of differences in dimensions, volume and shape index of tern eggs according to clutch size. Probabilities are shown where differences are significant; 'n. s.' means not significant.

Two-egg clutches

	N	a longer than b	a broader than b	a more volume than b	a lower S.I. than b
Common	82	<0.01	n.s.	<0.001	n.s.
Arctic	88	<0.05	<0.01	<0.001	n.s.
Roseate	53	<0.001	<0.001	<0.001	n.s.
Sandwich	15	<0.01	n.s.	<0.01	n.s.

Three-egg clutches

(i) Length

	N	a > b	b > c	a > c
Common	42	n.s.	n.s.	<0.05
Arctic	10	n.s.	n.s.	n.s.

(ii) Breadth

	N	a > b	b > c	a > c
Common	42	n.s.	<0.001	<0.001
Arctic	10	n.s.	n.s.	0.05

(iii) Volume

	N	a > b	b > c	a > c
Common	42	n.s.	<0.01	<0.001
Arctic	10	n.s.	n.s.	n.s.

(iv) Shape index

	N	a > b	b > c	a > c
Common	42	n.s.	n.s.	n.s.
Arctic	10	n.s.	n.s.	n.s.

species, eggs belonging to single-egg clutches do not conform to the Kittiwake's size pattern and may not, therefore, represent the early attempts of young or inexperienced birds. The measurements also confirm that most one-egg clutches are genuine and do not arise from the loss of the other eggs in typical clutches of two or three with which they do not correspond in size.

In all species, the a egg in a clutch of two exceeds the b egg in length, but only in the Arctic and Roseate Terns is the a egg also relatively broader (Table 44). The net result is that a eggs have a significantly larger volume than b eggs in all four species. There was no significant distinction, however, between shape indices of a and b eggs in clutches of two.

Three-egg clutches are rarely laid by Arctic Terns on Coquet Island but in 1970, the frequency of this clutch size was above average and enabled measurement of a small sample (10 clutches). In both Common and Arctic Terns, the a and b eggs in clutches of three were indistinguishable in every parameter measured (Table 44). On the other hand, the length, breadth and volume of the c egg of Common Terns were significantly smaller than those of the a egg, and the c egg was also significantly smaller in breadth and volume than the b egg. While the Arctic Tern's c egg was narrower than the a egg this difference was not sufficient to significantly reduce its volume relative to the a or b eggs in this species. The shape indices confirm the tendency in both Common and Arctic Terns for the b egg to be the most pyriform (short and broad) of the three eggs and the c egg to be the most elliptical (long and narrow). In Common Terns the b egg in a clutch of three is also shorter and broader than the b egg in a clutch of two, and has a significantly higher shape index ($t = 2.06$, 52 d. f., $p<0.05$ in 1968 and $t = 2.51$, 122 d. f., $p<0.02$ in 1969). Given a clutch of two and these probabilities of difference, it is possible to predict with considerable confidence whether or not a third egg will be added.

To summarise these findings, the maximum volume, at least in three of the species examined, was attained by eggs belonging to single-egg clutches although the differences were not significant; terminal eggs, whether in two or three-egg clutches, were smaller than preceding eggs and this difference is most consistently expressed throughout the four tern species as a volume difference (Table 45).

Table 45

Percentage difference between a and b egg volumes of two-egg clutches, and between a and c egg volumes of three-egg clutches.

Species	% VOLUME DIFFERENCE			
	N	$\frac{a-b}{a} \times 100$	N	$\frac{a-c}{a} \times 100$
Common	25	5.6	29	6.3
Arctic	88	6.3	10	7.8[1]
Roseate	53	5.6		
Sandwich	15	10.2		

[1] This difference was recorded in 1970 and is not significant; all other differences are significant and refer to 1968 data. These differences happened to be the maximum ones recorded between 1968-70 with the exception of the a-c difference for Common Terns which reached 10.4% in 1970 (N = 27).

(ii) Eggshell thickness

Shell thickness was examined in two species—Roseate and Common Terns. Representative samples of shells were measured using eggs of known laying sequence from clutches of all sizes normally laid by these terns. Roseate Terns habitually leave eggshells in, or near the nest-site and these were easily collected. However, both eggshells from clutches of two were not always found and the comparison of thickness therefore includes single eggs from clutches of two where only one shell of known hatching order was recovered from the nest. The data for Common Terns are based only on clutches from which all eggs were available for measurement.

Most fragments of shell consisted of the equatorial region or "waist" of eggs and, for the sake of uniformity, the polar ends of eggs were discarded and only waist fragments were measured. Tyler and Geake (1961) have stated that there is considerable variation in shell thickness from pole to pole of the hen's egg, but assume that "for comparative purposes, thickness measurements are not grossly in error...when measurements are taken at the waist." Any membrane still adhering to the dried shells was removed and five small pieces of shell (each c0.5cm long) were broken off from the equator of each eggshell. Two measurements of thickness were made on each piece, giving 10 individual values per egg. Each of the five pieces was inserted vertically in a block of plasticine which was mounted on a microscope stage. The focus was adjusted on to the proximate (upper) edge of the shell and the thickness at the two ends of the fragment measured to the nearest 15μ (0.015mm) on a micrometer eyepiece. The results are shown in Table 46.

Table 46

Mean shell thickness (μ) ± 1 standard error of Roseate and Common Tern eggs, according to clutch size.

	SHELL THICKNESS IN:											
	Clutch of 1		Clutch of 2				Clutch of 3					
	a	N	a	N	b	N	a	N	b	N	c	N
Roseate	154 ± 0.6	15	159 ± 1.4	21	148 ± 2.2	13						
Common	141 ± 4.7	11	143 ± 2.5	9	135 ± 3.5	9	143 ± 1.5	11	141 ± 1.5	11	138 ± 3.3	11

Roseate Tern eggshells ranged in thickness from 138μ -170μ. In two-egg clutches, b shells were significantly thinner than a shells (t = 4.28, 32 d. f., $p<0.001$) and the difference was still significant (t = 8.10, 4 d. f., $p<0.01$) when determined for those clutches where shells from both eggs were available for comparison. Eggshells from single clutches of Roseate Terns were intermediate relative to two-egg clutches, being significantly thinner than a shells in clutches of two (t = 2.98, 34 d. f., $p<0.01$) but significantly thicker than b shells (t = 2.43, 26 d. f., $p<0.05$).

Irrespective of clutch size, Roseate Tern eggshells were generally thicker than Common Tern eggshells which ranged from 102μ -163μ. Since complete clutches could be used for comparisons, Student's paired t-test was used for within-clutch tests of difference. These determinations showed that, in clutches of two eggs, b shells were significantly thinner than a shells ($t = 2.87$, 8 d. f., $p<0.05$); this relationship held for 78% of clutches examined. In clutches of three eggs, c shells were significantly thinner than a shells ($t = 2.55$, 10 d. f., $p<0.05$) in 73% of clutches measured. Other differences, whether within clutches of a particular size, or between clutches of different size, were not significant. In this respect, it is noteworthy that b shells in clutches of two were about equivalent in thickness to c shells in clutches of three. The results also suggest that in both terns the shell thickness of terminal eggs is more variable than in preceding eggs and that, in Common Terns, the greatest variability of all occurs in eggs from single-egg clutches (Table 46). The differences within clutches may indicate that when a and b eggs in clutches of two and three are formed the material available for shell deposition is available in excess so that a regulating mechanism can adjust thickness to quite precise standards whereas both a smaller and a more variable amount of material contributes to the terminal egg which varies in shell thickness accordingly. Measurements of Common Tern eggs were used to test the possibility of predicting shell thickness from either egg weight or egg volume and it was found that correlations with these measures were not significant.

(iii) Yolk and lipid content

Lipids are found in abundance in the egg yolk and, as an energy source and constituent of body cells, they are vital to the maintenance and development of the chick embryo. In the hen's egg, 99% of all the lipids are contained in the yolk (Romanoff and Romanoff 1949). The lipid remaining in the yolk sac after hatching is utilised by the growing chick during the first few days of post-embryonic life (Rol'nik 1968). Consequently, any variation in the size of the initial and residual (post-hatching) lipid reserve is of considerable interest. In the present study, it was possible to investigate only the first of these factors, namely the lipid store available to the embryo at the start of its development.

In all, 6 clutches of 1 egg, 9 clutches of 2 eggs, and 11 clutches of 3 eggs of the Common Tern were used in this analysis. Each egg was first hard-boiled and then opened up so that the solid yolk could be easily separated from the surrounding albumen. The yolks were then dried in a vacuum oven to constant weight and the lipid extracted with petroleum-ether using a modified Soxhlet technique (Odum 1960). The fat-free yolk residue was dried and the original lipid content found by subtracting weights.

There were no significant differences in the dry yolk weight between eggs within clutches of two or three. This relative uniformity in yolk size has been previously demonstrated in the Herring Gull (Parsons 1971) and in the domestic hen by Romanoff and Romanoff (1949) who first observed that the yolk constitutes an ever larger proportion of total egg weight as egg size decreases. The weight of lipid in the eggs of Common Terns shows significantly positive correlations ($p<0.001$) with both the dry weight of the yolk and the weight (wet) of the whole egg (Table 47), so that, as Moiseeva and Tolokonnikova (in Rol'nik 1968) showed for various breeds of poultry, and Parsons (1971) showed for the Herring Gull, the size of the Common Tern egg is a valuable indicator of the lipid reserves it contains.

Table 47

Relationship between weight of egg yolk and lipid in Common Terns. Values are derived from data for 1-egg, 2-egg and 3-egg clutches. Weights are in grams.

Regression							
x	y	N	Mean x	Mean y	Slope y on x	Corr. coeff.	p
Egg wt. (wet):	Yolk wt. (dry)	56	18.38	2.49	0.127	+0.63	<0.001
Yolk wt. (dry):	Yolk lipid	55[1]	2.48	1.50	0.864	+0.92	<0.001
Egg wt.:	Yolk lipid	55[1]	18.42	1.50	0.096	+0.51	<0.001

[1] These figures are less than 56 because one yolk was contaminated with H_2S and was not analysed for lipid content.

Soluble lipid comprised about 60% by weight of the dry yolk (Table 48) and in this respect the eggs of Common Terns closely resemble those of the Herring Gull (Parsons 1971) and probably other species whose chicks are nidifugous. The weight of lipid in eggs varied from 1.0–2.0g depending on egg size. Table 48 shows that of all eggs, <u>a</u> eggs in clutches of two contained the most lipid and <u>c</u> eggs in clutches of three the least; single-egg clutches were only moderately well provided with lipid reserves. There was no difference between <u>a</u> and <u>b</u> eggs in clutches of two (Student's paired t-test, t = 1.20, 16 d. f., $p>0.2$) but in clutches of three eggs the amount of lipid extracted from <u>c</u> eggs was significantly less than that from <u>a</u> eggs (t = 3.22, 20 d. f., $p<0.02$) in 90% of clutches examined. The <u>a</u> – <u>b</u> and <u>b</u> – <u>c</u> differences in clutches of three were not significant. Unlike the three-egg clutch of the Herring Gull where the <u>b</u> egg contains most yolk and lipid (by weight) (Parsons 1971), there is a steady gradation in amounts of yolk and lipid in three-egg clutches of Common Terns from the <u>a</u>, through the <u>b</u>, to the <u>c</u> egg.

Table 48

Relationship between mean weights (± 1 standard error) of egg, yolk and soluble lipid, according to clutch size.

Clutch size	Egg	N	Mean egg wt. (wet)	Mean yolk wt. (dry)	Mean lipid wt. (dry)	Lipid wt. x 100 / yolk wt.	Lipid wt. x 100 / egg wt.
1	<u>a</u>	6	18.00±0.55	2.66±0.11	1.64±0.12	61.7	9.1
2	<u>a</u>	9	19.07±0.37	2.71±0.04	1.70±0.12	62.7	8.9
	<u>b</u>	9	18.53±0.39	2.65±0.05	1.66±0.05	62.6	9.0
3	<u>a</u>	11	18.56±0.58	2.65±0.08	1.62±0.07	61.1	8.7
	<u>b</u>	11	18.18±0.60	2.51±0.11	1.53±0.07	61.0	8.4
	<u>c</u>	11	17.52±0.43	2.47±0.09	1.49±0.02	60.3	8.5

Discussion

Studies on other larids (Herring Gull, Paludan 1951; Parsons 1971; Black-headed Gull, Weidmann 1956) have demonstrated the existence of an important adaptive mechanism which limits clutch size and so prevents the production of progressively smaller eggs that would give rise to runted chicks, assuming they hatched at all. The mechanism is triggered by the onset of incubation which leads to the cessation of egg-laying by inhibiting follicle growth. Thus follicles degenerate providing they have not reached a certain stage of maturity and this limits the number of eggs to be laid after the gull has started to brood. Parsons concluded from his experiments that the onset of incubation was also responsible for the relatively smaller size of the c egg and that the "switch-off" mechanism prevents ovulation if a follicle does not attain a minimum size. The Herring Gull's b egg in a clutch of two is then understandably about the same size as a c egg in a clutch of three since both would represent the minimum size compatible with successful ovulation.

A similar situation applies here in Common Terns where the b egg in a clutch of two is about equivalent in both volume and shell thickness to the c egg in a clutch of three. The diminution of shell thickness (Table 49) could, therefore, be another manifestation of this progressive switch-off mechanism, following the onset of incubation. It is to be expected that any inhibition of the egg-laying cycle would be particularly noticeable in the last step in the formation of the terminal egg, namely shell deposition. Moreover, it is reasonable that in clutches of two and three the shell of the terminal egg would

Table 49

Summary of variation, other than in size, among eggs of Roseate and Common Terns. Percentage differences in shell thickness and lipid content between eggs are calculated as in Table 3.

	Clutch of 2	Clutch of 3		
	a > b	a > b	b > c	a > c
Roseate Tern				
Shell thickness	6.9 (***)	-	-	-
Common Tern				
Shell thickness	5.6 (*)	1.4 (n.s.)	2.1 (n.s.)	3.5 (*)
Lipid content	2.4 (n.s.)	5.6 (n.s.)	2.6 (n.s.)	8.0 (*)

*** = $p<0.001$, * = $p<0.05$, n.s. = not significant.

be more variable in thickness than the shells of eggs formed earlier in the laying sequence (Table 46) if the rate of disengagement from the process of shell deposition varied between individuals. An apparent inconsistency in Table 46 lies in the fact that, of all eggs examined, shell thickness is least variable in eggs from clutches of one belonging to Roseate Terns and yet most variable in single eggs of Common Terns. However, a large proportion of Roseate Terns lay single eggs whereas this clutch size is atypical for Common Terns and may therefore be subject to unusual variation in the duration of shell deposition. Nor is this so unlikely when one considers that, for a species that normally lays two or three eggs, a single egg, being both the first and last egg in the clutch, may present special problems of fine adjustment for a switch-off mechanism. Berg (1945) has suggested that the thinner shells of successive eggs in the laying sequence of the domestic fowl may represent decreasing periods spent in the uterus and correspondingly less time available for shell deposition. While the switch-off explanation would seem to fit the facts better, Berg's idea cannot be refuted at present and underlines the need for further investigations.

Of more likely significance to the chick than shell thinning is the diminution of fat reserves in successive eggs of a clutch. As shown above, the c egg in a clutch of three begins with a deficit of 8% in lipids compared with the a egg. Such considerable inroads are made into the total fat store during embryonic development that an initial variation of this magnitude (8%) may be of ultimate significance to the chick's chances of survival. In the domestic hen, about 40% of the total yolk is still available to the chick at the time of hatching (Romanoff and Romanoff 1949, Romanoff 1960). A similar 60% depletion in lipid reserves during embryonic development applies equally to all eggs of the Herring Gull's clutch of three (calculated from figures in Parsons 1970, 1971). In the Adélie Penguin, the yolk available at hatching has been shown to be a useful reserve if the "off duty" bird is prevented from bringing food to the chick until some time after hatching (Reid and Bailey 1966).

If, as not infrequently happens, conditions are inimical to regular feeding when tern chicks hatch, the size of the fat reserves inherited at hatching could tip the balance between survival or death from starvation and exposure. Data presented in this study (Appendix 7) and by Langham (1968) show that in Common Terns, c chicks suffer appreciably higher mortality than a or b chicks from broods of three and Langham has shown that when the c chick succumbs it is usually from starvation in the first few days after hatching following failure to elicit an appropriate feeding response from the parents. It seems likely, therefore, that, as Parsons (1971) found for the Herring Gull, the Common Tern c chick must start life a more vulnerable chick than its siblings for having had relatively poorer fat reserves right from the outset of its development. Moreover, as a result of asynchronous hatching, the third chick to hatch is probably already in a difficult position to compete physically with two older and larger siblings.

FINAL
DISCUSSION

1. Terns as predators

Predation is a fundamental process in the transfer of energy through an ecosystem and so is central to an understanding of community processes. The earliest studies considered predation in relation to trophic structure and sought to answer the fundamental question of whether predators regulate the numbers of their prey, and vice versa. Since then, the emphasis has shifted to the intricate relationships within any one predator-prey system and particular interest has centred on the adaptedness of the predator to its environment. Not surprisingly, most of these studies have gravitated towards terrestrial animals, and particularly to birds, which offer outstanding advantages as subjects for field research. As a result of this work, there is now a considerable body of evidence to show that birds tend to optimise their energetic efficiency by choice of food sources and associated exploitation techniques (Orians 1961, Verbeek 1964, Verner 1965, Emlen 1966, 1968, Root 1967, Royama 1970, Gill 1971, Wolf and Hainsworth 1971). By contrast, the foraging strategies of seabirds have not been widely explored from this viewpoint, although a few recent studies have been made (Ashmole and Ashmole 1967, Ashmole 1968, Pearson 1968, Bedard 1969a, b, Salt and Willard 1971).

A tern's prey species are probably patchily distributed, rather than "fine-grained" in the sense of MacArthur and Pianka (1966). Terns therefore have to devote a considerable proportion of their time to searching for food. The problem of locating food is aggravated by the submarine distribution of the prey animals, and a sophisticated air-to-water plunging technique has evolved to exploit this elusive resource. The success of this strategy depends not only on the tern's own skill, which is partly a function of experience, but very likely on variations in the depth and density of the prey, the quality of the intervening water surface, and the strength of the wind. The tern's niche therefore necessitates the development of peculiar skills and these inevitably commit the bird to a high degree of specialisation. However, the food supply is so variable in space and time that terns cannot afford to be too rigid in their behaviour. Tinbergen (1932, pp. 11-12) has said (trans.): "In many ways, gulls appear to be much more adaptable than terns. Gulls look for food in many ways, changing with the circumstances. Terns, on the other hand, show a strange psychic unadaptability. Their behaviour, especially when they are searching for food, is very conservative. We could call them, briefly, over-specialised plungers." In a comparative sense, this may be true, but it would be misleading to think of terns as unadaptable or over-specialised within their own niche. In the interests of self-preservation, the tern must possess a repertoire of behaviour sufficiently versatile to respond quickly to sudden changes in prey availability. In other words, we should expect to find a well-developed capacity for opportunism, just as we find in many other predators such as gastropods (Paine 1963), robberflies (Powell and Stage 1962), fish (Nilsson 1955, Brooks and Dodson 1965), and other species of birds (Gibb and Betts 1963, Mook 1963, Orians and Horn 1969). The subsequent discussion will therefore examine some of the ways in which terns optimise their efficiency by showing the requisite balance of specialisation and opportunism in their choice of food sources and associated behaviour.

(a) Foraging sites

Although the four species of terns showed some partitioning of the foraging area around Coquet Island, this dispersion was not always adhered to, and birds displayed considerable opportunism in their ability to profit from new feeding situations. When a tern discovers an abundant source of food, a switch is made from searching to persistent plunge-diving behaviour and this may serve as a signal to other terns in the vicinity. Normally, feeding individuals are widely spaced from one another but they probably monitor the activity of their neighbours. The opportunity for social facilitation in feeding to operate between distant birds must be enhanced by the terns' conspicuous white plumage (Armstrong 1946) although signal value may not be the major function of white colouration (Phillips 1962). As has been shown, an increase in fishing success is accompanied by a visible increase in diving rates. Thus, terns could compare their own success with that of their neighbours by watching the diving rates of these other birds. Indirect evidence for efficient "communication" of information between terns derives from the rapid assembly of mixed-species flocks over fish shoals. When these shoals appeared inshore, they attracted Arctic and Roseate Terns which are otherwise rarely seen in this zone. This reflects the commonly observed phenomenon that mobile predators are readily attracted to high concentrations of easily obtained food, even if it is in the areas or habitats not normally frequented by the predator (Elton 1942). While the density of prey animals in shoals explains why diving rates exceed those of solitary feeding individuals, it is not immediately obvious _why shoals should enhance the terns' fishing success_. The likeliest interpretation is that fish in the shoal are thrown into confusion by the attack from birds on all sides. Deelder (1951) found that Perch _Perca fluviatilis_ could not catch cyprinids alone but if they attacked en masse, a cyprinid might run into one perch while avoiding another. Sette (1950) proposed a similar advantage for shoal formation of Mackerel _Scomber scombrus_ when feeding on plankton. I am not suggesting that group-feeding in terns represented a concerted strategy such as has been implied for these predatory fish and for other fish-eating birds such as certain cormorants, pelicans and boobies (Serventy 1939, Cottam _et al._ 1942, Gunter 1958, Nelson 1968, Parkin _et al._ 1970), as well as for porpoises _Phocaena_ spp. (Fink 1959), Coyotes _Canis latrans_, Wolves _Canis lupus_ (Murie 1940, 1944) and various other mammalian carnivores. Rather, it seems that in this case, the plunge-diving attacks of many individuals in a confined space inevitably lead to the disorganisation of the shoal, with fortuitous consequences for the terns.

It is therefore unlikely that fish shoal together in order to mitigate the predatory attacks of terns. It is now widely believed that the behaviour of fish shoals may confuse fish predators and so reduce their hunting efficiency. The members of the shoal probably achieve this effect by interweaving (Neill 1970), by bunching and moving faster when alarmed (Hobson 1968), and simply by existing as a group of similarly sized individuals, thereby complicating and delaying the predator's choice (Berlyne 1957, Radakov 1958, Breder 1959). These behaviours are partially effective against fish predators (Neill 1970) which have probably been a significant selective factor in the evolution of shoaling behaviour. A fish shoal has little chance of completely eluding a mobile fish predator whereas it can often evade avian predators simply by moving deeper. For this reason, the depredations of fish stocks by terns and other seabirds is probably slight compared with the inroads made by predatory fish, and it seems unlikely that avian predation has been a major influence on the evolution of fish behaviour.

(b) Diet and foraging methods

As Root (1967) has observed, the avian predator's diet is largely influenced by the tendency to concentrate on those kinds of prey which the bird can find, capture, and ingest most efficiently. Consequently, some selection of prey is to be expected. There is now considerable evidence that such selection occurs, and preference for particular sizes of prey is particularly well documented. Predators known to attack prey within certain size limits include damselflies (Lawton 1970), mites (Burnett 1964), crabs (McDermott 1960), larval and adult fish (Jackson 1960, Shelbourne 1962, Brooks 1968) and various mammalian carnivores (Bourlière 1963). In birds, body size and bill characteristics undoubtedly play important roles in determining the size of prey attacked (Ashmole and Ashmole 1967, Ashmole 1968, Hespenheide 1971).

It has previously been observed that variations occur in the sizes of prey brought to the breeding colonies by different tern species in Northumberland (Pearson 1968, Langham 1968) but these differences in themselves do not provide adequate evidence for a selective process. However, the present study has revealed two further lines of evidence for size preferences. Firstly, Sandwich Terns tended to capture larger prey than Common Terns when the two species were feeding alongside one another. Although it has been argued that Sandwich Terns are capable of diving deeper than Common Terns, it is most unlikely that this would seriously affect the range of prey size available to each species, and the simplest explanation for the disparity is that at least one size preference, or else two different size preferences were being exercised. Secondly, parasitic Roseate Terns seemed to discriminate against attacking terns that carried very small and very large fish.

Given certain physical attributes that allow a tern to handle prey up to a certain size, what is the most efficient size for it to choose? In their study of Forster's Tern, Salt and Willard (1971) showed that handling time (defined by them as the time taken to swallow a fish) for a prey item increased as a function of prey length squared. Since the weight, of food content, of the prey increases as its length cubed, the most efficient strategy for this tern, and probably for all plunge-diving terns, is to attack fish as large as can be handled. Salt and Willard neglected to consider that securing a fish underwater also takes time; this, as I have shown, also increases slightly with the size of fish tackled, and ought to be added to handling time. Thorson (1960), studying marine bottom communities, and Root (1967) also concluded that, for a predator that can handle prey of various sizes, it is generally less efficient to hunt for small prey.

The emphasis on capturing the largest possible prey is a particularly important principle for a tern that hunts for fish in the open sea, since this usually involves making repeated long flights to and from the colony in the breeding season. A. J. M. Smith (pers. comm.) has records of marked Sandwich Terns, known to have chicks, that were seen foraging 35 miles from their breeding station at Forvie, Aberdeenshire. This may be an extreme case, but return foraging trips of 20 miles were not uncommon in this study. Given that flight is a very energy-demanding activity, there will be strong pressures for maximising the food load delivered to the chick at each feeding. Thus, it was found that Sandwich Terns distinguished between the size of fish consumed for self-maintenance and the size they transported back to the colony for the young. Though a Sandwich Tern probably tries to catch as many items of a suitable size as it can, some decision-making mechanism leads it to eat the smaller ones itself and keep the bigger ones for its young. Presumably the decision to eat or alternately to retain a fish takes place after capture and the variables affecting this decision present an intriguing problem. It would be interesting to know, for example, if the time taken to catch a fish, or distance from the colony, influences the size of fish brought back to the chick. Incidentally, this discriminative ability was not used earlier as evidence that terns select which sizes of prey they attack, since the decision to swallow on the spot or carry to the chick could be based on post-capture information, such as the weight of the prey when held in the bill.

The Fairy Tern Gygis alba, like the Sandwich Tern, also brings fish to the chick mostly in its bill and, in their study at Christmas Island, Ashmole and Ashmole (1967) showed that these fish are larger on average than those swallowed by adults. Measurements of fish in the latter category were obtained from regurgitated samples. Lind (1965) and Safriel (1967) observed that the Oystercatcher also discriminates prey size in this way, while Root (1967) and Royama (1970) came to the same conclusion for the Blue-gray Gnatcatcher and Great Tit Parus major respectively. A simple model developed by Royama suggested that once young Great Tits fledge and start following the parents, it may no longer be so efficient for the parents to feed them larger prey, since the energy costs of transportation are less. On fledging, young terns also follow their parents to the feeding grounds, and it seems probable that adults are then less likely to feed their offspring with prey items larger than they would normally eat themselves.

This feature of feeding behaviour suggests some other interesting points. Firstly, it raises the cautionary note that, for those species which carry a single item in the bill to feed chicks, determinations of prey size made at the nest-site could be based on a biased sample. It would therefore be misleading to deduce from such observations the overall size range of prey taken by the species. Secondly, species which swallow several prey for subsequent regurgitation to chicks should find it efficient to retain much smaller items for the young than species that can only carry one item at a time in the bill.

In support of this, Ashmole and Ashmole (1967, p. 48) found that adult and juvenile Black Noddies Anous tenuirostris frequently regurgitated fifty or more tiny fish. Terns in the present study sometimes compromised by carrying back up to five small sand-eels in the bill.

Regurgitation may seem to be always a more efficient strategy than ferrying back a single fish, however large. But while regurgitation is obviously adaptive for oceanic species that have to fly considerable distances in search of food, it has not evolved in birds like the Fairy Tern and the Sterna species studied here because these terns obtain most of their food close to the colony and need to provision their chicks at relatively frequent intervals. Furthermore, species that swallow prey for later regurgitation probably need to evolve a means of retarding digestion of their food load (Murphy 1936, p.660, Dorward 1962, Ashmole and Ashmole 1967).

By far the most frequent prey species of all four terns in the breeding season were sand-eels and sprats, presumably because they were available in large numbers. Other fish species occasionally fed to the chicks were Cod Gadus morrhua, Norway Pout G. esmarkii, Four-bearded Rockling Onos cimbrius and Herring Clupea harengus. These usually appeared in the diet in "runs", lasting a few days and so were probably taken opportunistically, as and when they became available. Other species only appeared in the diet at times of food shortage when few fish were being brought into the colony and chicks were losing weight. These species, such as flatfish (O. Heterostomata) and Common Shrimp Crangon vulgaris, may be harder for chicks to ingest and are therefore overlooked when more suitable prey species are available. Finally, there were those prey species, like the Fifteen-spined Stickleback Spinachia vulgaris and the poisonous Lesser Weaver Trachinus vipera which were only represented in the terns' diet by the occasional specimen, possibly because they were not only difficult, but also dangerous, for both adults and chicks to swallow. The fact that these fish were usually found uneaten and discarded beside nests tend to support this supposition. Discrimination against prey of this sort is a common feature of food choice in many predators (e. g. Bristowe 1941).

In Sierra Leone, Sandwich and Common Terns usually dived or dipped for fish but I also saw them contact-dipping for offal behind fishing boats and removing freshly dead fish from the shore. Terns have little opportunity to obtain food by these methods in temperate regions where various gulls dominate the coastal scavenging niche. In Sierra Leone, the Grey-headed Gull Larus cirrocephalus was present in small numbers but was not seen sharing in these scavenging activities. Amadon (1965) has suggested that the absence of gulls on tropical oceanic islands is caused by the low availability of appropriate food and a similar explanation might apply in Sierra Leone where other birds, such as Black Kites Milvus migrans and Palm-nut Eagles Gypohierax angolensis may predominate as coastal scavengers in winter (pers. obs.). Whatever the reasons for the absence of gulls, their scarcity allows terns to behave as facultative scavengers at sea; in Miller's (1967) terms, these terns therefore "include" part of the gulls' "fundamental niche". Here at least, the terns' capacity for adaptability is not in doubt. The main feature of the terns' foraging behaviour was that they possessed one or two basic methods which were highly adaptable. Thus, surface plunging is a maneouvre that can be finely adjusted to suit varying prey situations. The height of the dive is carefully regulated to allow for the depth of the prey below water and, if necessary, the tern can increase its impetus at entry by making acceleratory wingbeats during the aerial part of its plunge. The bird's hunting skill enables it to catch fish even when success seems least likely, notably when the water surface is ruffled. Indeed, it appears that the tern catches fish more successfully when the surface is broken than when it is smooth. This may be because these surface conditions interfere more with the ability of prey animals to see the tern than vice versa, so that the tern's advantage would be simply the result of a visual interaction. It is difficult to assess the extent to which terns might actually be adapted, e. g. perceptively, to deal with sea conditions of this kind, but the difficulty experienced by a human observer in emulating the tern's ability to detect submarine prey suggests that some special visual acuity has evolved in terns. Indeed, it would be surprising if the birds had not adapted in some way to the wind and sea conditions that characterise their feeding habitat. The nature of such adaptations in unknown and offers a challenging field for further research.

With regard to other feeding methods, it is worth noting that the plunge dive was evidently a preadaptation for the remarable attacking strategies of parasitic Roseate Terns. The other basic foraging manoeuvre, namely the "contact dip", also has wide applications and with minor adjustments, was used variously for picking up crustacea, fish and offal from the sea surface, and for retrieving dead fish from the shore. Contact dipping is also the first stage in the development of plunge diving by newly fledged terns.

In conclusion, there is little doubt that the Sterna species studied are flexible in regard to where they feed, which prey animals they feed on, and how they capture them. These catholic foraging habits are consistent with the spatial and temporal variations in the food supply. Given that some of the species are not averse to scavenging and robbing, and are successful in these sidelines, it is clear that terns are capable of expanding their niche when the opportunity arises. Similar demonstrations of versatility and opportunism in predators are widely documented but, inasmuch as the existence of most seabirds at sea is something of a mystery, these findings represent a special addition to the generalisation.

2. Foraging experience and deferred maturity

The age at which an animal breeds for the first time is, as Wynne-Edwards (1962, p. 565) described it, "a parameter that enters strongly into the vital statistics of every species." In many invertebrates this factor is negligible since the entire life cycle is very short. A now famous example concerns the fruit-fly Drosophila melanogaster which completes its life cycle—egg, larva, pupa, mature imago—in only two weeks under optimum conditions (Begg 1959, p.56). In vertebrates, there exists a great variety of life history patterns in which the pre-reproductive phase may last only a few weeks or up to many years (Table 50). In many poikilotherms, especially fish, and also in some of the

Table 50

Age of first breeding in a selection of vertebrates.
Unless otherwise stated the ages quoted refer to years.

CLASS & SPECIES	AGE	SOURCE
Actinopterygii		
Goby *Aphya pellucida*	1	Nikolsky (1963, pp. 159-160)
Sole *Microstomus kitt*	4-5*	Rae (1965, p. 56)
Sturgeon *Huso huso*	15-20	Nikolsky (1963, p. 160)
Amphibia		
Frog *Rana esculenta*	2	Smith (1951, p. 151)
Salamander *Desmognathus* sp.	4 5*	Organ (1961)
Frog *Rana p. pretiosa*	5-6*	Turner (1960)
Reptilia		
Lizard *Anolis carolensis*	1	Oliver (1955)
Snake *Vipera berus*	3-5	Bellairs (1969, p. 465)
Turtle *Terrapene carolina*	8-11**	" " "
Crocodile *Crocodilus niloticus*	20	Cott (1961)
Tuatara *Sphenodon punctatus*	20	Dawbin (1962)
Aves		
Finch *Taeniopygia castanotis*	3 months	Lack (1968, p. 176)
Tern *Sterna fuscata*	6	Robertson (1964)
Albatross *Diomedea epomorpha*	8-11	Richdale (1952)
Mammalia		
Mouse *Mus musculus*	7-10 weeks	Snell (1956, p. 59)
Gorilla *Gorilla gorilla*	6-7 ***	Schaller (1963, p. 96)
Elephant *Loxodonta africanus*	7	Perry (1953)
Whale *Physeter catodon*	9	Ohsumi *et al.* (1963)

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* Applies to females only; males breed one year earlier

** Applies to females only; males breed two-three years earlier.

*** Applies to females only; males breed three years later.

larger mammals, growth is slow and sexual maturity seems to coincide with the attainment of physical maturity. However, this is evidently not the case in most birds in which the necessity for efficient flight at an early age has selected for rapid physical development. Long periods of immaturity are especially common among seabirds and large birds of prey and are usually associated with high adult survival and low reproductive rates (Ashmole 1963, Amadon 1964). Deferred maturity, as the phenomenon is commonly called, has therefore been widely discussed in relation to population dynamics of birds, principally by Lack (1954, 1966), Wynne-Edwards (1962), Skutch (1953, 1967), Ashmole (1963), Fretwell (1969), and most recently by Nelson (1970), but its causation and function still remain a source of controversy.

Wynne-Edwards contended that delayed breeding has evolved as one means of regulating population size and he suggests that populations (especially those comprising individuals with a long life span) control their recruitment rate "by holding back a reserve of full-grown adolescents or virgin adults and admitting to breeding status only the number actually justified at the time by circumstances" (1962, p. 557). As regards seabirds, this regulation was believed to be achieved by conventional limitation of the number of breeding sites so that recruitment is just adequate to replace losses. Lack has contested this view and has argued instead that delayed maturity could have arisen only if breeding when very young imposed excessive strain on the birds and thereby increased their mortality rate. A major source of stress might arise from difficulty in finding enough food for self-maintenance and for rearing chicks. This led Ashmole (1963) and Amadon (1964) to suppose that young birds are inefficient at collecting food and might therefore be at a competitive disadvantage with older, more experienced individuals. Ashmole postulated that, where breeding is retarded for a long time, feeding efficiency must continue to improve for several years and that individuals will not breed until such time as they can successfully raise a chick without risk to themselves. Some evidence for slow learning of feeding skills derives from the long periods of post-natal care observed in species that have specialised hunting methods (Ashmole and Tovar S. 1968).

Ashmole formulated these ideas from a consideration of oceanic birds in the tropics where the food supply tends to be scarcer than in temperate waters and is usually patchily distributed. In opposition, Skutch (1967) found it "incredible that a bird whose skill in fishing increases so rapidly that it can feed itself after a few weeks at sea should thereafter improve so slowly that several additional years must elapse before it develops sufficient proficiency to nourish, with the help of its mate, the single nestling that most of these oceanic birds rear." Skutch was therefore forced to the conclusion that delayed maturity is another adaptation that helps adjust reproduction to mortality.

Skutch's argument is echoed by Nelson (1966b, 1970) who cannot believe that three and four year old Gannets Sula bassana do not breed because they are deficient in foraging experience. Fretwell (1969) tried to reconcile the apparent contradiction by suggesting that these young birds refrain from breeding because they would raise subdominant offspring that were likely to die before they reached breeding age. Thus deferred maturity would evolve in spite of the ability of young birds to rear chicks to fledging. However, Fretwell's assumption may be unnecessary, since Williams (1966) has emphasised that where adult mortality is low (as in many seabirds), then an individual's breeding production in any one season represents a relatively minor fraction of the potential output during its life span. It follows that the risk of breeding precociously need only be very slight in such species to tip the selective advantage in favour of postponing the attempt for another year.

Attempts to explain the causation of low reproductive rates have also been made through a comparative approach by considering the life histories of animals in different sorts of environments. This approach was pioneered largely by Skutch (1949) in his comparison of reproductive rates of birds in temperate and humid tropical regions. His general conclusions have found support in a recent theoretical model developed by Gadgil and Bossert (1970) who attribute late maturation (and other parameters of low reproductive rates) to stable environments where catastrophic mortality is rare and availability of resources is low. MacArthur and Wilson (1967) reached a similar conclusion; their "k strategists", which exhibit low reproductive effort, occupy the k~~f~~ind of environment predicted by Gadgil and Bossert's model.

Such predictions, however, are only as accurate as the field observations that give rise to them, and these are largely inadequate. This is especially true of marine ecosystems in which the distribution (both in space and time) and availability of food is little understood, as is the ability of birds to exploit it. At present, the post-fledging experience of the familiar Herring Gull is almost as much a mystery as the prodigious wanderings of immature albatrosses. In particular, the foraging success of birds—which is central to the Lack-Ashmole thesis—has received scant attention. Lambert (1943) investigated the "predation efficiency" of the Osprey <u>Pandion</u> <u>haliaetus</u> and suggested that the decline in fishing success from 96% in May to 86% in August might be partly due to the foraging efforts of inexperienced young birds in the latter part of the season. Unfortunately, this deduction was not tested by field observations. More recently, however, a few studies have been directed specifically at the rate of development of foraging efficiency in immature members of species which require a high degree of skill for obtaining food. Since most of this information was not available to earlier reviewers, its relationship to our knowledge of deferred maturity deserves consideration.

An improvement in fishing success with age has now been demonstrated in four species of fish-eating bird—a heron, a pelican, and two terns. The available results are summarised in Table 51. Fishing success is the percentage of "stabs" (in the case of the heron) or plunge dives that yielded a prey item. This parameter has been re-calculated for the Little Blue Heron from the original data which were published in different form.

Table 51

Change in fishing success (%) with age in various fish-eating birds.

Species	Newly fledged	6-9 months	⩾ 18 months	⩾ 2 yrs	Normal age (yrs) at 1st breeding
Little Blue Heron[1]	64	69 - 71	75	-	1
Brown Pelican[2]	-	-	49	69	2
Sandwich Tern[3]	-	13	17	-	3-4

[1] Fishing success from Recher and Recher (1969). Breeding age from Palmer (1962, p. 432).

[2] Fishing success from Orians (1969). Breeding age from Palmer (1962, p.276).

[3] Fishing success from this study. Breeding age from Langham (1971).

It appears that Little Blue Herons may breed before they attain maximum feeding efficiency but this point was not discussed by the Rechers. Nevertheless, the delay in breeding is compatible with a process of improvement in foraging skills. In the case of the Brown Pelican, a plunge-diving species, hunting skills seem to take a long time to perfect and again, the data give good reason to believe that fishing success is an important determinant of delayed maturation in this species. A good case for correlating these phenomena is also made out for the Oystercatcher which does not breed till at least three years old, and more often not till four or five (Harris 1967). This species takes three years to become as proficient as adults at opening Edible Mussels *Mytilus edulis*, one of the main constituents of its diet (Norton-Griffiths 1968).

Among the terns, information is now available for two species. Willard (in Recher and Recher 1969) has found that two year old Caspian Terns in the Gulf of Mexico continue to miss prey more often than adults and in this species most birds probably start breeding at three years (Ludwig 1965). Willard (pers. comm.) observed that yearlings compensate for their lower fishing success by foraging longer and since this reduces the time available for courting activities, he believes that these birds may be effectively eliminated from the year's breeding population. Two year old birds also had to spend longer foraging than adults although the difference was not so striking as in yearlings. However, Willard considers the added impediment of regular food parasitism by Laughing Gulls sufficient to reduce the likelihood of successful breeding by two year olds.

In the present study, the fishing success of Sandwich Terns in their first winter had almost achieved parity with that of older birds, and on this basis alone, it is difficult to see why more Sandwich Terns do not breed at two years by which time the gap should have closed. From ringing recoveries (Langham 1971) it is known that when Sandwich Terns first fledge and migrate to the tropics, they remain there for over a year (first winter, second summer and second winter). The majority penetrate into northern waters in their third summer when they are two years old. These birds, in common with the situation found in many other seabirds, e.g. Kittiwake <u>Rissa</u> <u>tridactyla</u> (Coulson and White 1958) and Manx Shearwater <u>Puffinus</u> <u>puffinus</u> (Harris 1966), usually appear around the colonies rather late in the season (June-October) and rarely attempt to breed. I know of only one authenticated record of a Sandwich Tern nesting at this age (A.J.M. Smith, pers. comm.). Most birds postpone breeding till the following summer, or even till the one after that, i.e. they breed at three or four years old. It seems likely, therefore, that the non-breeding visits of immature birds to the summer quarters are largely exploratory and may enable terns to gain valuable experience of migration routes, feeding areas and breeding stations. For a long distance migrant, obliged to feed its young during migration, such knowledge may prove vital. Moreover, it is known from colour-ringing studies that Sandwich Terns do not necessarily return to their natal colony to breed for the first time, and it seems possible that immature birds are "monitoring" a number of potential breeding places in their preliminary visits to temperate waters. Similar behaviour has been recorded for other seabirds and also landbirds, notably the Rook <u>Corvus</u> <u>frugilegus</u> (Coombs 1960), Grey Heron <u>Ardea</u> <u>cinerea</u> (Lack 1954) and White Stork <u>Ciconia</u> <u>ciconia</u> (data of

Zink, discussed by Lack 1968). In many species which show this kind of dispersive behaviour, birds are known to occupy a nest-site in the year prior to first breeding, and although most terns do not do this, attendance at colonies in pre-breeding years may still be a necessary prelude to successful courtship and pairing. In short, the acquisition of various skills other than the ability to forage efficiently, might justify breeding of Sandwich Terns in their third or fourth year, and might also improve the chance of breeding being successful in subsequent years (cf. Ashmole 1963, Lack 1968, p. 282).

In the species discussed above, the improvement in fishing efficiency is not so rapid as Skutch was led to believe in 1967. Moreover, the prolonged parental care evident in many seabirds conflicts with Skutch's supposition that such birds can feed themselves "after a few weeks at sea". Royal Terns, Caspian Terns, Elegant Terns and Crested Terns Thalasseus bergii have all been seen feeding six month old young (Ashmole and Tovar S. 1968, Willard, pers. comm., Pyle and Small 1951, and Diamond 1971, respectively). Post-fledging dependence is also long in other groups of seabirds, e.g. at least three months in the Red-footed Booby Sula sula (Nelson 1969), three to four months and sometimes longer in the Ascension Island Frigate Bird Fregata aquila (Stonehouse 1963), and at least fourteen months in the Great Frigate Bird Fregata minor (Schreiber and Ashmole 1970).

As Ashmole (in Farner and King 1971, p. 261) has pointed out, the critical factor inhibiting younger birds from breeding may be the depletion of energy reserves it incurs. Thus, unless a bird's reserves, or ability to maintain them, exceed a critical minimum, it may be hazardous to embark on a breeding attempt. However, there is no critical evidence for this at the moment. Such measurements as have been made are concerned with body weight and have not distinguished between protein and fat levels. This distinction is important since, weight for weight, a reduction in muscle protein could represent a more serious state of debilitation than an equivalent reduction in fat alone. Carrick and Ingham (1967) have found that female Royal Penguins

Eudyptes chrysolophus schlegeli do not normally lay unless their weight is above a certain threshold when they first come ashore in spring, and Fisher (1967) advanced a similar argument for those adult and juvenile (5-7 year old) Laysan Albatrosses Diomedea immutabilis at Midway that fail to breed. It has been found that the weights of these non-breeders on arrival at the colony are far below even those of "starved" incubating birds. In the case of the Oystercatcher, Mercer's (1968) study strongly suggests that a minimum pre-breeding weight of about 600g is necessary if the female is to withstand the substantial weight losses during early incubation and chick-rearing. Data of P. J. Dare (quoted by Norton-Griffiths 1968) show that, compared with adult Oystercatchers, first-winter and older immature birds suffer a severe decline in body weight between November and March and are well below the body weights of adults when the breeding season begins. These differences are consistent with the inferior feeding efficiency of young birds and Norton-Griffiths (1968) concluded from this that, even if they were sexually mature, these young birds would be quite unable to maintain themselves, far less any young, if they tried to breed. While most authors have drawn attention to disparities in pre-breeding weights, it should be pointed out that a young bird might be quite capable of reaching an appropriate body condition for commencing breeding but quite incapable of meeting the additional maintenance requirements of breeding itself. In this latter case, any physiological mechanism that forestalls breeding will be difficult to detect.

Occasionally, when populations experience an unusually abundant food supply, some young individuals are found to breed at an earlier than average age. If as Lack has proposed, birds have evolved physiological regulating factors to prevent maturity being reached too early, these cases of precocious breeding indicate that the mechanism may be rather flexible. It is suggested that intraspecific competition for food is reduced under favourable conditions, permitting young birds to acquire the food resources necessary for egg-formation, incubation and chick-rearing without risk to their own survival (Ashmole 1963, Lack 1966). Unfortunately, there are very few studies in which precocious breeding can be confidently linked with a plentiful food supply, but one example sometimes cited (Wynne-Edwards 1962, p. 566, Lack 1968, p. 148) concerns the Pomarine Skua Skua pomarinus. Between 1951 and 1953 near Barrow, Alaska, investigation was made to determine the effects of a dramatic population increase of the Brown Lemming Lemmus sibiricus on the breeding biology of various avian predators (Pitelka, Tomich and Treichel 1955). In 1952, Lemmings were only moderately numerous and the nesting population of Pomarine Skuas was "sparse", consisting "largely if not entirely of adult birds," two or more years old. In 1953, however, the Lemmings reached peak abundance and this was associated with a very high nesting density of S. pomarinus which included a small percentage of sub-adult birds, probably no more than one year old. It is tempting to infer from this situation that the normal constraints on young skuas were relaxed in 1953 but a much longer study would be necessary to substantiate this. At present, there are insufficient records to demonstrate that the breeding of birds in sub-adult plumage is exceptional in this species. Moreover, any relaxation of pressure on food-finding in 1953 was not reflected in hatching success which was lower than in the previous year. Indeed, the influx of avian predators in 1953 casts doubt on whether the food supply available to each individual was much greater than in 1952.

However, there is another example in which a significant difference in the age structure of two breeding populations of the same species is not in doubt. At South Georgia, where Elephant Seals Mirounga leonina have been heavily culled, male and female individuals grow faster and have shorter periods of immaturity than at Macquarie and Heard Islands where the populations are unexploited and stable (Carrick, Csordas and Ingham 1962, discussed by Ashmole 1963 and Lack 1966). The earlier breeding of the females at South Georgia is attributed to reduced competition for food in the vicinity of the island so that subordinate (mainly young) individuals can store enough blubber to make a landfall with the amount required to sustain them through the breeding fast. In theory, it would be an interesting experiment to switch the culling pressure from South Georgia to Macquarie and examine the subsequent growth and onset of maturity in these two populations. Finally, it may be added that the deferment of maturity in fish is also variable. Here, the attainment of an appropriate body size is probably a much more proximate factor than it is in most birds. Given an improvement in food supply, the growth rate of many fish species can accelerate markedly and the onset of maturity is advanced accordingly (Smyly 1957, Nikolsky 1963, p. 159,226).

In this discussion, I have deliberately confined myself to attributes of pre-breeding biology. The lower success of young birds breeding for the first time, such as that found by Coulson and White (1958) for the Kittiwake, may denote lack of experience in a variety of behaviours which are only questionably implicated in the original reason for breeding being deferred. It is not yet possible to arrive at a confident conclusion on the significance of delayed maturity but, in the absence of any evidence to the contrary, the facts appear to favour the views of Lack and Ashmole that prolonged deferment has evolved by natural selection in those species in which forfeiture of a few breeding attempts when inexperienced is preferable to jeopardising a potentially long breeding life.

The foregoing discussion does not alter this basic hypothesis but it does enable a few features of the problem to be put in perspective. From the little data available, it seems increasingly likely that foraging efficiency may be a significant facet of experience in some seabirds and it certainly deserves more consideration than some authors have hitherto attributed to it. The apparent difficulty in explaining very long periods of deferred maturity in terms of inexperience may be a consequence of an over-simplified view of the factors involved. As Gadgil and Bossert (1970) have emphasised, "natural selection would tend to an adjustment of the reproductive effort at every age such that the overall fitness of the life history would be maximised ". The adjustment will be mediated through a subtle interaction of selective pressures and it would be invidious to single out any one without considerable knowledge of the ecology of the species concerned. For example, during the outbreak of paralytic shellfish poisoning in Northumberland in 1968 (Coulson *et al.* 1968a), deferred maturity of the Shag *Phalacrocorax aristotelis* evidently prevented the deaths of a substantial cohort of immature birds which were largely dispersed outside the area most severely affected. Events of this kind, sporadic as they are, will contribute to the "profit" and "cost" of breeding at any particular age. The role played by the establishment of the pair bond prior to breeding for the first time also remains to be elucidated. The identification of relevant factors may be impossible to achieve for most pelagic seabirds, but the studies described above suggest that a great deal could be done with the more accessible species.

SUMMARY

1. Introduction

The study was concerned with the ecology of four, closely related species of maritime terns. The main aim was to examine the ways in which these terns differed in their methods of utilising available food resources and to identify factors that influenced their foraging success. The four species were studied at Coquet Island, Northumberland where they co-exist in the breeding season. Further observations were made on two of the species in Sierra Leone, West Africa during their wintering period. The study areas are described.

2. Interspecific variation in foraging methods

Feeding dispersion in the breeding season and the methods used to obtain food are described. Localised concentrations of easily accessible prey attracted feeding flocks of all four species and were characterised by convergent feeding methods. At other times, distinct spatial and behavioural differences in foraging were evident. Arctic and Roseate Terns usually foraged offshore whereas Sandwich Terns were most frequent inshore. Common Terns were probably the most ubiquitous, using both inshore and offshore areas. Significant differences were found in the heights of plunge dives and subsequent immersion times of the different species and it is suggested that this may result in some interspecific differentiation of feeding layers in the sea surface. The larger the fish tackled, the greater was the submergence time of plunge diving Sandwich Terns. Apart from plunge diving, all species used the contact - dipping technique to skim small prey items off the surface and this method was exploited principally by Common and Arctic Terns when fish were apparently in short supply. Sandwich Terns preferred to catch larger fish than the other species and this may explain why contact-dipping was generally a less conspicuous feature of their foraging repertoire. Sandwich Terns also tended to take larger prey than Common Terns in their winter quarters. These interspecific differences in

feeding habits should alleviate competition for food and facilitate coexistence, especially in the breeding season.

3. Robbing behaviour of Roseate Terns

Apart from sea fishing, Roseate Terns robbed other terns of their food at Coquet Island. The elaborate robbing manoeuvres are described. The interaction was examined to determine whether these parasitic terns responded to variations in the abundance and nature of the food supply available to them through the host population of terns. There were seasonal changes in the species of host most commonly attacked, corresponding with the different breeding times of the terns. There was also a diurnal rhythm of robbing intensity dictated by the diurnal pattern of feeding activity in the hosts. Thus, the number of terns actively parasitic was directly proportional to the numbers of available hosts. The numbers of robbing attacks increased at a rate which declined as the density of hosts increased; this effect is attributed to limitations on attack rate imposed by handling time. Robbing success was directly proportional to host density which suggests that the parasitic terns benefited from the apparent confusion that attends dense air traffic. Small fish were more often robbed from hosts than large fish which might be better protected by their owners. However, parasites tended to select the commonest size of fish for attack, showing a lower preference for challenging hosts which carried very small or very large fish. Never more than five Roseate Terns were actively parasitic at any one time, suggesting that the behaviour is confined to a few, specialist individuals. This is contrasted with the widespread occurrence of less elaborate robbing behaviour displayed by Common Terns in the colony at times of food shortage.

4. Feeding rhythms

Both a diurnal and a tidal rhythm were involved in determining the rate at which terns arrived at the colony with food. The peaks of feeding activity at dawn and towards dusk corresponded with the pattern known for other species of birds. More birds arrived at the colony with food at low tide than at high tide although this tendency was more striking in the inshore-frequenting Common and Sandwich Terns than the offshore feeding Arctic and Roseate Terns. The tidal pattern correlated with a higher rate of fish capture at low tide than at high tide in the shallow, littoral zone. At low water, fish may be more readily visible and more vulnerable to capture in the shallow backwaters that are formed by the receding tide.

5. Effects of age and prey abundance on feeding

Studies in Sierra Leone indicated that experience is an important factor in the development of feeding skills in the Sandwich Tern. A comparison between first-winter birds (estimated to be between 7 and 9 months old) and older individuals showed that a significantly smaller proportion of plunge dives by the first-winter birds yielded prey. There were no major differences between the two age classes in diving rates or in size of fish captured, but the older terns tended to dive from greater heights. Immediately after fledging, Sandwich Terns make shallow dives, have a negligible fishing success, and are strongly dependent on their parents for food. It is therefore suggested that young terns gradually gain the judgement necessary to dive profitably from increasing heights and so learn to exploit prey in a greater range of water depth as they get older.

It was also shown that, by driving shoals of fish to the surface, predatory fish enhanced the fishing success of both age groups on certain days. In the breeding season too, terns feeding in flocks over shoals had a higher rate of prey capture than terns hunting solitarily.

6. Effect of windspeed and sea conditions on feeding

Sandwich Terns and Common Terns had a higher capture rate when there was some wind and the sea was ruffled compared with days when there was little wind and the sea was calm. The higher capture rates were produced by a combination of better success and faster diving rates. In the case of the Sandwich Tern, it seemed that both higher windspeeds and greater surface disturbance, considered separately, were enhancing factors, and some possible interpretations of these relationships are suggested. Since excessive winds and rough seas undoubtedly impair the ability of terns to obtain food, it is proposed that these environmental factors increase to levels that optimise fishing ability, after which their effects are depressive.

7. Environmental factors and chick growth

A step-down multiple regression analysis was carried out to determine if the factors found to affect the fishing success of the adults also influenced the growth rate of Sandwich, Common and Roseate Tern chicks. Both the amount of variation in growth rates explained, and the contributory variables, were very different between species and between years. Part of this heterogeneity is attributed to changes in the availability of food which could not be evaluated. The most important variable tested was windspeed. This factor had a strongly linear depressive effect on the weight increase of Roseate Tern chicks in 1968, a 10 knot wind causing a 67% reduction in growth rate. In the same year, the weight increase of Common Terns was positively correlated with windspeeds up to 7 knots but stronger winds had a negative effect. Windspeed had a negligible effect on the growth rate of Sandwich Tern chicks. In addition to wind, rainfall and sea conditions had measurable effects on the weight increase of Common Tern chicks. Other variables measured were of minor significance. These results are discussed in relation to the feeding ecology of each species.

8. Paralytic shellfish poisoning and breeding biology

In 1968, the marine food chain on the Northumberland coast was seriously affected by an outbreak of paralytic shellfish poisoning caused by a bloom of dinoflagellates. This caused widespread mortality of fish but there was no evidence of a food shortage at Coquet Island. The effects of this phenomenon on the breeding of the terns were examined. Symptoms of poisoning and abnormal mortality of adult terns on Coquet Island are described. Evidence is presented for exceptional disruption of the incubation stage in Sandwich Terns, leading to widespread desertion and predation of eggs. About 60% of all eggs laid by this species was lost, representing a 30% poorer hatching success than in other comparable years. Egg-laying in Common Terns was less synchronised than usual but the breeding success of this species, and of Arctic and Roseate Terns, was unaffected. The conspicuous disruption of incubation in the Sandwich Tern compared with the other species is explained partly in terms of different nesting behaviour.

9. Composition of eggs

Terminal eggs in the laying sequence, whether in two or three-egg clutches, had a smaller volume than preceding eggs, and also had thinner shells in the two species (Common and Roseate Terns) examined for this parameter. Analysis of the contents of Common Tern eggs gave the following results : There were no significant differences in dry yolk weight within clutches of two or three. However, the lipid content of the yolk was highly correlated with the weights of the yolk and the whole egg. Consequently, the size of the egg is a valuable indicator of the lipid reserves it contains. Soluble lipid comprised about 60% by weight of the dry yolk. Successive eggs in a clutch of three showed a steady reduction in lipid content such that the c egg contained, on average, 8% less lipid than the a egg. The differences in overall dimensions, shell thickness and lipid content within clutches are regarded as evidence for the existence of a "switch-off" mechanism in ovulation, following the onset of incubation. The smaller lipid reserves of the c egg may contribute to the fact that c chicks usually have a higher mortality than a and b chicks in broods of three.

10. Discussion

The efficiency of terns as predators is considered in the light of the foraging strategies demonstrated, and these are compared with other predator-prey systems. Despite their specialised feeding niche, it is argued that the terns possess the degree of versatility and opportunism necessary to exploit a food supply that varies considerably in space and time. This aspect is explored with reference to their ability to locate, capture and ingest prey. An efficient utilisation of food resources demands an ability to select prey of a suitable size and kind, both for self-maintenance and for raising young. The observation that adult Sandwich Terns tended to eat smaller prey than they fed to their young is discussed as an example of adaptive behaviour. A comparison is drawn between birds that feed chicks single items from the bill and those that regurgitate food for the young. The capacity for skilful robbing behaviour and for scavenging in the tropics when gulls are scarce is taken as evidence that Sterna species can extend opportunism beyond the confines of conventional fishing techniques.

In the second part of the discussion, the phenomenon of deferred maturity in birds and other vertebrates is reviewed and special attention is drawn to recent additions in our knowledge concerning the slow acquisition of feeding skills. Current theories on the causation and function of delayed maturity are outlined. The hypothesis that young birds are inefficient at obtaining food, and so are unable to breed without incurring risk to themselves, was lacking in critical evidence at the time of its formulation. Since then, some authors have argued that foraging experience is unlikely to play a significant role. However, the protracted development of fishing expertise in the Sandwich Tern indicated in this study, together with similar findings in other recent studies, suggests that inexperience at obtaining food is a relevant factor in deferring breeding age in some birds. There is some evidence for a link between such inexperience and the inability to accrue sufficient body reserves for surviving a breeding attempt, and this deserves further study. Supporting evidence from cases of precocious breeding is examined. In conclusion, the measure of experience that a young bird needs to acquire has sometimes been underestimated. The available facts appear to favour the view of Lack and Ashmole that prolonged deferment of breeding has evolved by natural selection in those species in which forfeiture of a few breeding attempts when inexperienced is preferable to jeopardising a potentially long breeding life.

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Appendix 1

Known history of tern colonies on Coquet Island

The earliest available faunistic accounts collated by Marples (1934) indicate that large numbers of Sandwich Terns and Arctic Terns, plus a few pairs of Common Terns and Roseate Terns were breeding on Coquet Island around 1830–31. In 1834, the present lighthouse was constructed and the keepers sent to man it brought their families and domestic stock. Once settled, the lighthouse keepers cultivated two small plots at the north end of the island and this development may have been a critical factor in the subsequent decline of the tern colonies. By 1874, Sandwich, Common and Arctic Terns at least had probably abandoned the island as a breeding station (Hancock 1874). Thereafter, the continuing absence of terns was recorded occasionally (1882, 1912 in Marples, op. cit.) and it seems that another 76 years elapsed before any tern species again succeeded in breeding on Coquet Island. The opportunities for breeding successfully in the intervening period were undoubtedly reduced further by the popularity of the island as a weekend picnic site for boat parties from the nearby town of Amble.

In 1958, two pairs of Common Terns were found to be breeding on the island (J. C. Coulson, pers. comm.) and in subsequent years, the other three tern species have also recolonised Coquet. It is interesting to note that the current robbing behaviour of Roseate Terns on Coquet Island is identical to that first observed on the Farne Islands in 1949 (Watt 1951) and since this kind of robbing behaviour has not been found so far on any other mixed tern colony in Britain (R. Smith, G. L. Sandeman, M. J. Everett, G. Waterston, C. Douglas Deane, pers. comm.) it is probable that some of the first Roseate Terns to colonise Coquet Island originated from the Farnes population. This possibility also holds for the origin of the other tern species, especially Sandwich Terns, some of which are known to alternate between the two breeding stations in different years. In recent years, Sandwich Terns ringed as pulli at most of the British and Irish breeding stations have been seen on Coquet Island (Langham 1968, pers. obs.).

After 1958, the size of the Coquet tern population increased rapidly and, since 1965, total breeding numbers (all species) have fluctuated between 2,000 and 3,500 pairs. Numbers of terns and Black-headed Gulls nesting annually are tabulated for 1965-70 in Table A1.

Table A1

The numbers[1] of terns and Black-headed Gulls breeding on Coquet Island.

The data for 1965-1967 (inc.) are from Langham (1968).

	1965	1966	1967	1968	1969	1970
Sandwich Tern	313	797	c1750	593	206	708
Roseate Tern	85	179	102	203	229	144
Common Tern	c1200	c1000	1212	c1200	c1200	c1200
Arctic Tern	c500	c500	560	c600	c700	c800
Black-headed Gull	10	57	68	80	105	c20

[1] Number of pairs.

Note: 1968-1970 estimates for Common Terns are correct to the nearest 100 pairs while estimates for Arctic Terns are correct to about 50 pairs.

The Sandwich Tern has fluctuated widely in numbers over recent years (range 206-1,750 pairs) which is probably due in part to the readiness with which birds will opt to settle instead on Brownsman in the Farnes group if better conditions should prevail there at the critical stage in early May. Roseate Terns have shown a steady increase in numbers between 1965 and 1969 and the low count in 1970 was certainly biased downwards by the unusually rich vegetation in which a proportion of nests must have remained undetected. Common Terns appear to have maintained a stable population size but Arctic Terns have shown a regular increase since 1966. The breeding population of Black-headed Gulls expanded annually up to 1969 but in 1970, the boulder beaches (which normally are a major nesting area) were abandoned and rather few nests were found on the plateau.

Appendix 2

Food of terns in Sierra Leone and Ghana

Since very little is known about the diets of Palearctic terns in their winter quarters, a brief account is given below of the stomach contents of 21 terns of various species collected in Sierra Leone and Ghana (separated by 1,000km = 625 miles) in Jan and Feb 1970. I am grateful to A. J. M. Smith and N. P. Langham for providing the stomachs of birds collected in Ghana. Most of the fish were identified with the aid of type specimens kept at the F. A. O. Fisheries Laboratory in Freetown, Sierra Leone. Dr. Alwyne Wheeler of the British Museum kindly undertook to identify the Carangidae and the Ephippidae. In addition to fish, a number of insects and their remains were found in the stomachs of 4 Black Terns examined. The findings are summarised in Table A2. Where fish were badly decomposed and identity was not absolutely certain, the prefix (*) is appended. (In these cases, an examination of body scales was made to help identification). The number (s) in brackets after each fish or insect type denote how many were found in each of the stomachs in which it occurred. Thus, Sardinella (6,1,1) means that 3 stomachs contained sardines and that there were 6 sardines in one stomach and 1 sardine in each of the other 2.

As far as Royal Terns were concerned, only one individual (an adult female shot at Kwesmi on 23 Feb) was responsible for the diverse range of stomach contents from Ghana; these amounted to 7 fish and included no less than 3 species of the deep-bodied Family Carangidae. The most frequently recorded species, however, was Brachydeuterus auritus although there is a possibility that some of these were actually a closely related member of the Pomadasyidae, namely Pomadasys jubelini. Brachydeuterus is a very abundant pelagic fish on the West African coast, ranging from Senegambia to Angola. Shoals of Sardines Sardinella eba and Anchovies Engraulis guineensis are also abundant in shallow, coastal waters, and were often seen being caught by Sandwich, Common and Black Terns in Sierra Leone although too few specimens were collected to reinforce this by examination of stomach contents.

In general, the largest tern species took the largest fish. Measurements of the volume of stomach contents and the lengths of the fish comprising them

(Table A3 and A4) showed that volume and length could be ranked in the same order as the body sizes of the terns concerned. The lack of adequate samples precludes statistical analysis of these data.

Table A2

Tern	SIERRA LEONE	No. of birds	GHANA	No. of birds
Royal	*Sardinella eba* (Clupeidae) (6,1,1) *Brachydeuterus auritus* (Pomadasydiae) (1) Mullet species (Mugilidae) (1)	4	*Vomer setapinnis* (Carangidae) (3) (*) *Chloroscombrus crysurus* (Carangidae) (2) (*) *Trachinotus* sp. (Carangidae) (1) (*) *Chaetodipterus goreensis* (Ephippidae) (1)	1
Sandwich	*Sardinella eba* (1) *Brachydeuterus auritus* (1, 1) Mullet species (1)	3		0
Common		0	*Engraulis guineensis* (Engraulidae) (4,6) Mullet species (1)	3
Whiskered		0	(*) *Brachydeuterus auritus* (1, 1)	2
Black	Pisces: *Sardinella eba* (1, 1) Insecta: Unidentified remains (1)	2	Pisces: (*) *Brachydeuterus auritus* (3, 1) *Engraulis guineensis* (5, 2) Insecta: Formicidae (Ants) (13, 1, 1) Gerridae (Pond skaters) (5, 1, 1)	6

Table A3

Lengths of food items from the different tern species

Tern species	Mean length (cm)	Range (cm)	No. of fish	No. of terns
Royal	6.7	3.3 - 18.5	15	5
Sandwich	7.1	3.0 - 10.0	4	3
Common	c5.0	-	10	2
Whiskered	c5.0	-	1	1
Black	4.4	2.5 - 5.5	11	4

Table A4

Volumes of stomach contents from the different tern species

Tern species	Mean volume (ml)	Range (ml)	No. of fish	No. of terns
Royal	27.0	14.0 - 42.0	14	3
Sandwich	8.0	3.0 - 13.0	3	2
Common	5.3	1.0 - 9.0	11	3
Whiskered	3.0	2.0 - 4.0	2	2
Black	2.4	0.3 - 6.0	c12	6

Appendix 3

Calculation of daily tide scores

Daily tide ratings were calculated as follows. The maximum score (6) was given to the hour immediately preceding and the one immediately following low tide, and the score was then reduced by 1 for every hour away from low tide. Thus, in a 12-hour cycle, the hour before and the hour after high water are assigned a score of 1. A fishing day is assumed to last from 4.00-21.00 hours in mid-summer. Each of the intervening 17 hours can then be allocated a score ranging from 1 to 6 depending on the tide stage with which it coincides (this latter information is available in tide tables). Some days will obviously have more "low tide hours", and therefore a higher aggregate score, than others. All possible combinations of diurnal and tidal hours are shown below in Table A5. On this basis, the index of low tide hours in a day can be 51, 53, 57, 62, 66, or 68. i. e., there is a 33% difference between the maximum and minimum number of low tide hours, using this scale. To simplify data preparation, these indices (51, 53 etc.) were scored 1-6 in ascending order of magnitude. Any day can then be assigned a score between 1 and 6 if the times of high and low tides are known.

Table A5

Time (hrs.) from low tide

			E B B ——→					F L O O D				
Time of day	-6	-5	-4	-3	-2	-1	+1	+2	+3	+4	+5	+6
4.00												
	1	2	3	4	5	6	6	5	4	3	2	1
5.00												
	2	3	4	5	6	6	5	4	3	2	1	1
6.00												
	3	4	5	6	6	5	4	3	2	1	1	2
7.00												
	4	5	6	6	5	4	3	2	1	1	2	3
8.00												
	5	6	6	5	4	3	2	1	1	2	3	4
9.00												
	6	6	5	4	3	2	1	1	2	3	4	5
10.00												
	6	5	4	3	2	1	1	2	3	4	5	6
11.00												
	5	4	3	2	1	1	2	3	4	5	6	6
12.00												
	4	3	2	1	1	2	3	4	5	6	6	5
13.00												
	3	2	1	1	2	3	4	5	6	6	5	4
14.00												
	2	1	1	2	3	4	5	6	6	5	4	3
15.00												
	1	1	2	3	4	5	6	6	5	4	3	2
16.00												
	1	2	3	4	5	6	6	5	4	3	2	1
17.00												
	2	3	4	5	6	6	5	4	3	2	1	1
18.00												
	3	4	5	6	6	5	4	3	2	1	1	2
19.00												
	4	5	6	6	5	4	3	2	1	1	2	3
20.00												
	5	6	6	5	4	3	2	1	1	2	3	4
21.00												
"Low tide hours"	57	62	66	68	68	66	62	57	53	51	51	53
Low-tide hour rankings	3	4	5	6	6	5	4	3	2	1	1	2

Appendix 4

Calculation of growth correction factors

Table A6 provides an example of how correction factors were calculated in the preliminary growth study. The growth rate of all tern chicks is characteristically faster in the middle portion of development so that chicks at this stage show a relatively large daily weight change compared with younger or older individuals. Thus in 1968 the weight increment (12.5g on average) of a Sandwich Tern chick between 8 and 10 days exceeded the overall mean growth increment (8.8g) by 3.7g. This excess weight was therefore subtracted from the observed daily weight increments of 8-10 day old Sandwich Tern chicks. Similarly, appropriate correction factors were added to or subtracted from the increments of all chicks as shown in column 3 of the Table. In this way, the age bias in growth rate can be eliminated and any residual daily changes in weight should reflect extraneous factors.

Table A6

Weight changes and calculated correction factors for Sandwich Tern chicks in broods of one (1968).

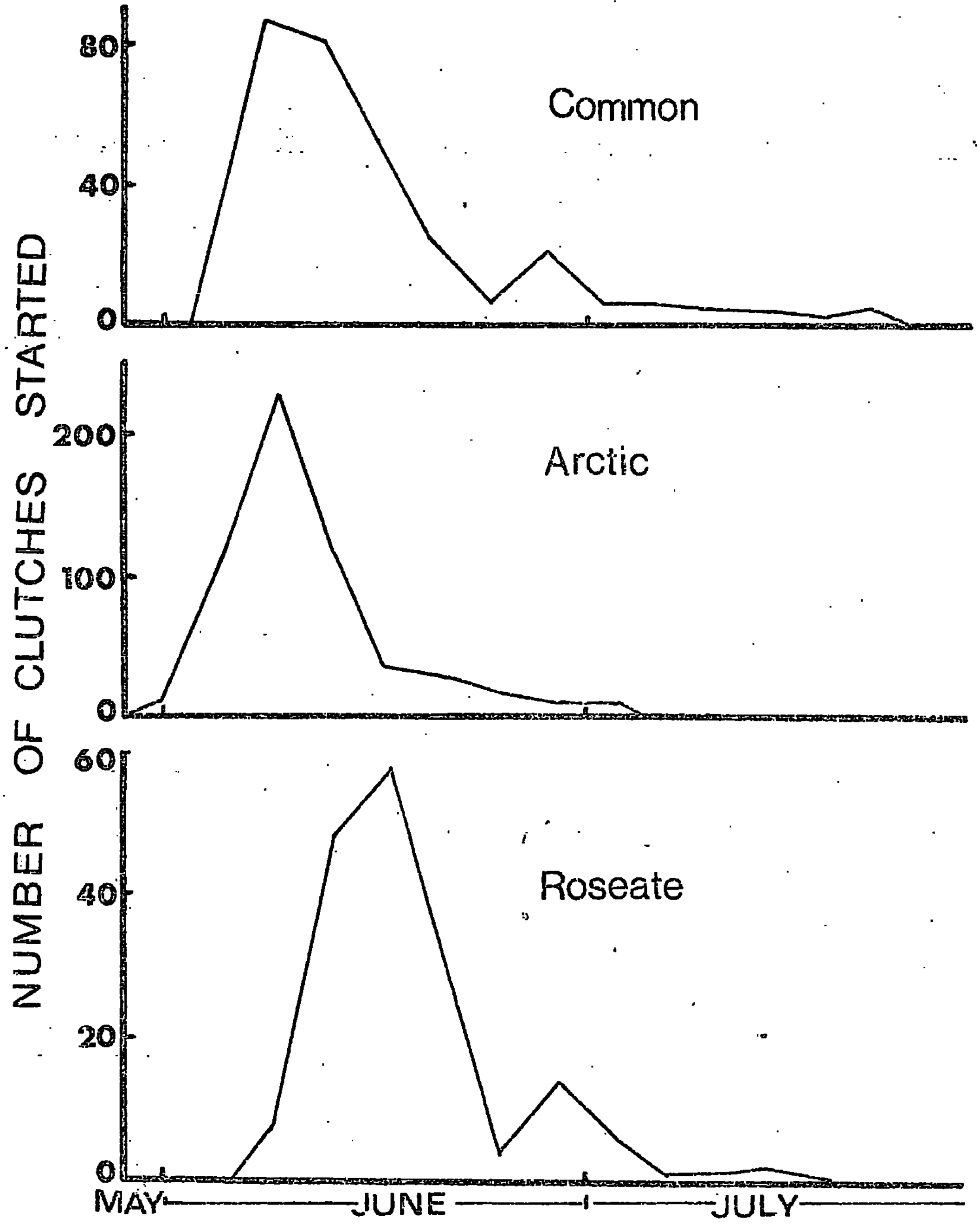
Age[1] (days)	Mean wt.[2] increase (g)	Correction factor (g)
0 - 2	7.5	+ 1.3
2 - 4	8.5	+ 0.3
4 - 6	10.5	- 1.7
6 - 8	8.3	+ 0.5
8 - 10	12.5	- 3.7
10 - 12	12.0	- 3.4
12 - 14	8.7	+ 0.1
14 - 16	5.7	+ 3.1
16 - 18	7.3	+ 1.5
18 - 20	6.9	+ 1.9
Overall mean =	8.8	

[1] Day of hatching is day '0'.

[2] Derived from mean growth curve of all single chicks.

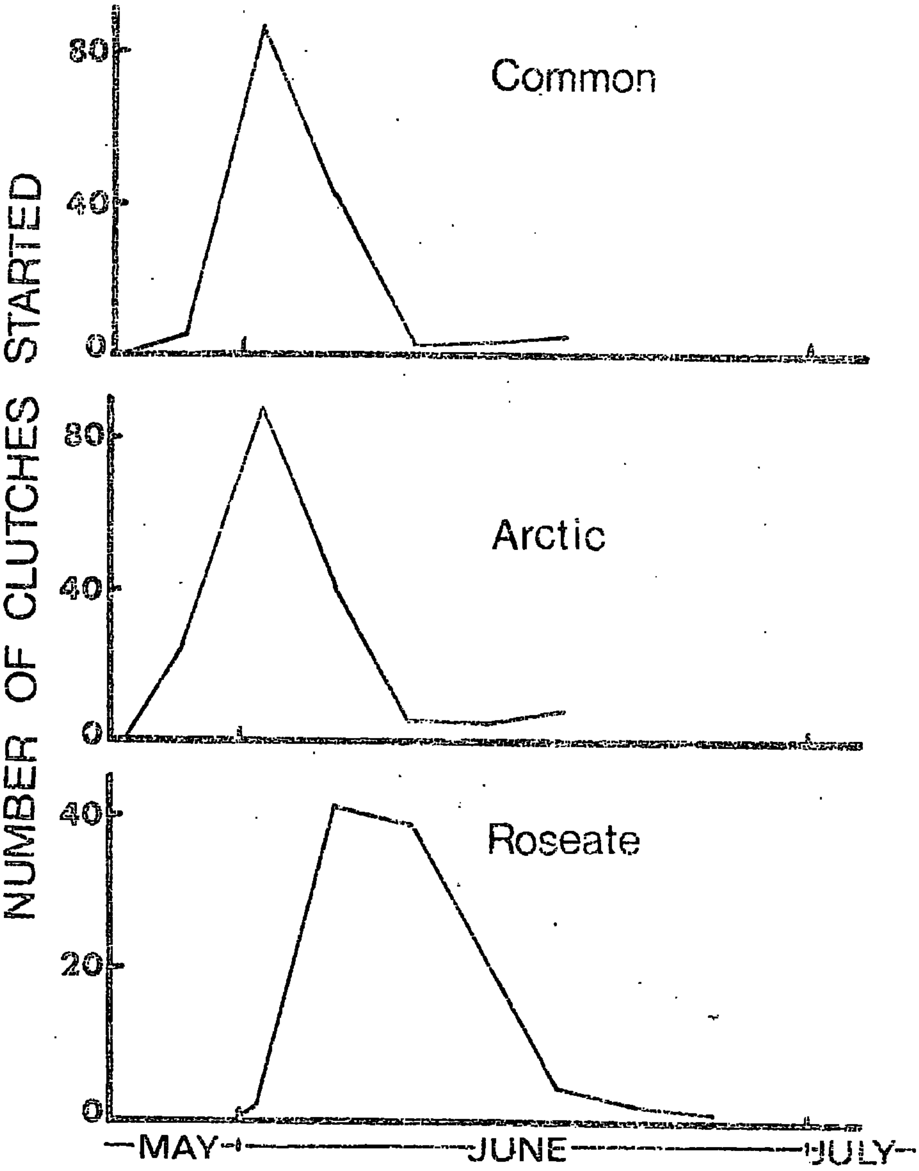
Appendix 5 a

Seasonal pattern of egg-laying by Common, Arctic and Roseate Terns in 1969.



Appendix 5b

Seasonal pattern of egg-laying by Common, Arctic and Roseate terns in [illegible].



Appendix 6

Annual hatching success for different clutch sizes

(a) Common Tern

Clutch size	1968	N[1]	1969	N	1970	N
1	66.7	18	28.6	42	31.3	16
2	92.3	52	59.7	108	68.3	41
3	93.6	52	78.8	63	86.2	58
Overall	91.4	122	64.9	213	78.3	115

[1] Number of clutches.

(b) Arctic Tern

Clutch size	1968	N	1969	N	1970	N
1	67.8	90	40.7	86	23.1	13
2	90.5	243	71.0	181	88.2	123
3	(75.0)	3	(66.7)	2	63.6	11
Overall	87.0	336	64.8	269	82.5	147

(c) Roseate Tern

Clutch size	1968	N	1969	N	1970	N
1	84.1	63	69.7	99	90.2	51
2	95.7	105	93.0	78	81.0	50
3	(100.0)	1	-	0	(0.0)	1
Overall	97.0	169	83.5	177	82.5	102

Appendix 7

Annual fledging success with hatching order and brood size

(a) Common Tern

Brood size	Hatching order	1968			1969			1970		
		Success		N[1]	Success		N	Success		N
1	1	95.2		23	100.0		21	100.0		12
2	1	93.3	90.0	75	98.5	96.3	67	89.7	87.2	39
	2	86.7		75	94.0		67	84.6		39
3	1	82.2	77.8	45	93.3	93.3	45	90.2	80.5	41
	2	84.4		45	95.6		45	78.0		41
	3	66.7		45	91.1		45	73.2		41
Overall success		85.1		308	95.2		290	84.0		213

[1] Number of chicks.

(b) Arctic Tern

Brood size	Hatching order	1968			1969			1970		
		Success		N	Success		N	Success		N
1	1	94.0		67	96.3		54	80.0		15
2	1	92.8	92.2	166	94.1	88.2	119	90.0	74.1	110
	2	91.6		166	82.4		119	58.2		110
Overall success		92.7		399	89.7		292	74.5		235

(c) Roseate Tern

Brood size	Hatching order	1968			1969			1970		
		Success		N	Success		N	Success		N
1	1	87.9		58	97.3		73	88.1		59
2	1	91.8	82.7	98	95.7	92.9	70	91.2	83.8	34
	2	73.5		98	90.0		70	76.5		34
Overall success		83.9		254	94.4		213	85.8		127