Geographic distribution of breeding season recoveries of adult and immature *Larus marinus, L. argentatus* and *L. fuscus* ringed in Finland

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An analysis was made of 1533 ring recoveries reported during the breeding season for individuals of different ages of the Great Black-backed Gull *L. marinus,* Herring Gull *L. argentatus* and Lesser Black-backed Gull *L. fuscus.* Many adults of breeding age were recovered within 100 km of the natal site, 42.6 % to 76.4 % depending on the species and age-class (5 yr, 6—8 yr and +8 yr). The behaviour of the immature gulls (1 to 4 yr) appears to vary. In all three species, some of the 1—2 yr birds stay in the southern part of the yearly range. Others migrate northwards and recoveries of these birds were made along the route to the natal area, but also beyond it. The main difference between the age-classes lies in the extent to which the southern part of the yearly range is utilized: delayed migration is shown by 1—2 yr gulls. In the Herring Gull the areas utilized by immature birds in Finland outside the natal area coincide with those chosen by adults that have dispersed into new breeding areas. No clear connection could be demonstrated between the length of the migratory journey and the rate of return of immature birds.

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Introduction

Gulls of the genus *Larus* in the size-class of the Herring Gull *L. argentatus* have a prolonged pre-breeding life. Chabrzyk & Coulson (1976) found that in a British population of Herring Gulls, the mean age for the breeding debut was 5.25 years, though individuals have been found breeding at the age of 3 years (Coulson et al. 1982).

In the course of the year the mature birds move between the breeding and survival habitats (= non-breeding habitat, terminology of Alerstam & Högstedt 1982). Immature birds may spend the whole year in the survival habitat, which may differ completely from the breeding habitat and be geographically isolated from it. Immature Kittiwakes *Rissa tridactyla* have been found to occur in great numbers far from their natal colonies during the breeding season (Coulson 1966), and the same pattern applies to a variety of other seabirds. With increasing age, immature birds make preparatory visits to breeding colonies, to which they may later be recruited. Large *Larus* species are often considered to select their first breeding location in the area, or even colony, of origin (Southern 1977). Yet, at least in the Herring Gull there is good evidence that emigration from the natal area is a common reproductive tactic (Coulson et al. 1982, Duncan & Monaghan 1977).

In this paper we examine ring recoveries of Great Black-backed Gulls *L. marinus,* Herring Gulls and Lesser Black-backed Gulls *L. fuscus* in order to determine the whereabouts of immature birds in the breeding season, and to investigate site-fidelity in adults. The use of accidental ring recoveries makes it, however, impossible to distinguish natal- from breeding dispersal (*sensu* Greenwood 1980), and it is not certain that all adults were breeding when recovered. We have previously established that both the Great Black-backed and the Herring Gulls are short-range movers, while the Lesser Black-backed performs seasonal migrations to areas up to 7500 km distant from the breeding area (Kilpi & Saurola 1984).

Material and methods

The recoveries. The main part of this study is based on a total of 1533 recoveries of birds of various age-classes (Table 1). Some additional recoveries have been used, and these are specified each time. All birds have been ringed as chicks.

As a rule, two main categories of recoveries are used; (a) birds reported as *found,* and (b) birds reported as *found in fresh condition.* Category (a) comprises mostly accidental recoveries by the public, while category (b) includes mostly birds that have been shot, and some that have been trapped and caught in fishing gear. Major systematic trappings in Finland are excluded from this analysis. All recoveries of sick or decayed birds have been excluded, as have recoveries incompletely reported, or obtained under uncertain circumstances. Most birds were found in the years 1960—81. The recoveries of Herring Gulls prior to 1950 have been excluded, but in the two other species some older recoveries are included to increase the size of the samples. It is assumed that the movement patterns have not changed significantly during the recovery period.

Table 1. Distribution by species and age-classes of the recoveries used in the main analysis. A few additional recoveries were used in Fig. 13.

Species	Age (yr): 1	2	3	4	5	6–8	+8	Total Recoveries
Great Black-backed Gull	31	21	34	33	16	39	13	187
Herring Gull, Gulf of Finland	80	72	101	96	73	132	97	650
Herring Gull, Archipelago Sea	57	75	83	46	22	42	14	339
Lesser Black-backed Gull	27	59	68	65	44	68	26	357

Study populations and study period. The material for the Great and the Lesser Black-backed Gull is too small to warrant any division into sub-sets. All recoveries are thus treated as if they belonged to the same population. In practice, most have been ringed on the S and SW coast of Finland, with a small fraction originating from more northern areas, or the interior of the country (Lesser Black-backed only). The Herring Gull material has been divided between two populations, one from the Archipelago Sea (AS) and one from the Gulf of Finland (GF) (Fig. 1). A few recoveries of birds ringed at other localities have been treated separately. In adult Great Black-backed and Lesser Black-backed Gulls, the breeding season (= summer) is considered to span May, June and July. The Lesser Black-backed Gull lays its clutches from the second half of May onwards, and most chicks will have fledged by the end of July. The Great Black-backed Gull starts breeding earlier, but parental care usually continues into August, the broods staying close to the nesting islet (Kilpi, unpubl.). The Herring Gull starts breeding in late April—early May, and the colonies off the south coast of Finland are normally abandoned in July, after which there is a rapid shift to survival habitats (Kilpi & Saurola 1983). In this study, the breeding season for this species is considered to span May and June. Recoveries of immature birds for all three species are analysed for the period May—July.

The term immature is used for birds under the age of 5 yr (the year begins on 1 August) so that 4 yr birds are c. 48 months of age in summer. Immature individuals comprise birds in widely different plumages (see Grant 1982). Adults (+4 yr) are divided into three age-classes, 5 yr, 6—8 yr and +8 yr, and are considered to be breeding birds.

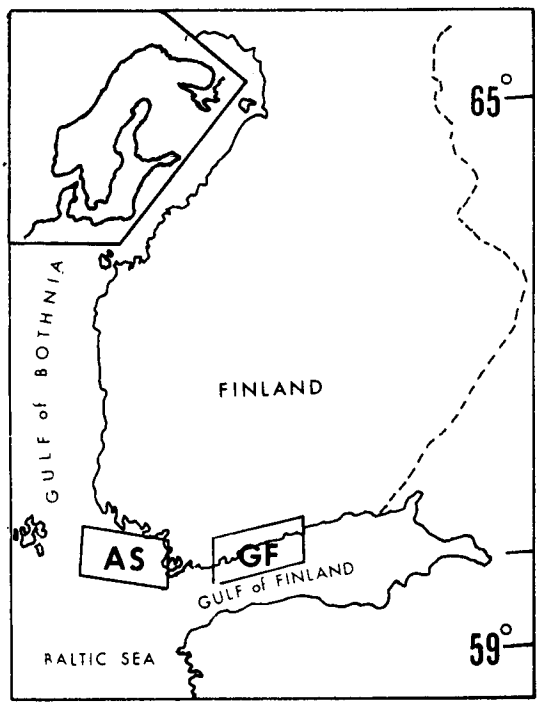

Fig. 1. The Finnish coast. The limits of the Archipelago Sea (AS) and Gulf of Finland (GF) study areas are shown.

Results

Distribution of immature birds during the breeding season. Birds that cannot breed (1 yr and 2 yr) or are unlikely to breed (3 yr and 4 yr) do not need to join a certain breeding colony by a fixed date. They may remain in the survival area used in winter, migrate to some areas lying on the route to the breeding area, or undertake full-length migration to or beyond the natal area.

Immature gulls of all three species were found in summer in the southern part of the yearly range. One 2 yr *fuscus* was shot south of the Equator in summer. Several recoveries of this species were made along the migratory route to the north, in the southern part of the range (Fig. 2). Older immature birds (3 and 4 yr) were recovered less frequently at great distances from the natal area in summer, than younger birds (Table 2, Fig. 3). In both *marinus* and *argentatus* the winter survival area includes most of the Baltic, since some birds do not leave the breeding area in winter (Kilpi & Saurola 1984). Recoveries of immature *marinus* have been made in the southern part of the yearly range in summer (Fig. 4), which indicates that some birds do not return to the breeding area. These are mostly 1 and 2 yr gulls (Table 2). The same pattern is found in *argentatus*; most of the birds recovered in the southern part of the Baltic were 1 yr old. When the proportions of birds encountered south of the breeding area (south of 59°N) are examined on

a month-by-month basis, it appears that younger immatures have a delayed migration (Fig. 5), though many eventually return to the breeding area during summer (Figs. 6 and 7).

Some immature gulls reach the natal area, here defined as the area within 100 km of the natal colony. A comparatively large fraction of the recovered immatures in summer were reported from this area (Figs. 8 and 9), older immature birds being more frequent there than younger ones. In May—June, 1 yr *marinus* form smaller proportions of the recoveries near the natal site than older gulls, but there is no significant difference between the age-groups (χ^2=6.2, df=3, n.s.). Significant differences between age-classes are found in *argentatus*, with larger proportions of older immatures found close to the natal site (AS, χ^2=9.3, df=3, P<0.05; GF, χ^2=21.9, df=3, P<0.001).

The recoveries of *fuscus* are more difficult to analyse, because of the uncertainty of the recoveries of 1 yr birds. These total 33 and nine of them were reported in May, five in or very near the natal colony. These 5 recoveries are reported as merely "found", and probably concern birds that died in or near the colony prior to migration in autumn. Later in summer a few recoveries of freshly found birds were made, two of them having been shot. If only the fresh recoveries are accepted, 2 out of 8 (25 %) were made close to the natal colony. If all the recoveries are accepted, 43.5 % come from the natal area in May—July. Even in this case there is a clear differences between the age-classes in occurrence near the natal site (χ^2=18.2, df=3, P<0.001). In view of the lack of field observations (Kilpi, unpubl.) of 1 yr *fuscus* in Finland, we are inclined to believe that the frequency in the latter case is much too high, but some 1 yr birds seem

Table 2. Percentages of summer recoveries made at considerable distances from the natal site in different age-classes of immature birds of three *Larus*-species. All the recoveries were made in the direction of the main winter occurrence.

Species	Age	At distance exceeding		Total recoveries
Great Black-backed Gull	1 yr	500 km	29.0 %	31
	2 yr		14.2 %	21
	3 yr		5.9 %	34
	4 yr		3.0 %	33
Herring Gull GF	1 yr		24.7 %	82
	2 yr		12.0 %	75
	3 yr		5.9 %	101
	4 yr		4.1 %	97
Herring Gull AS	1 yr		19.4 %	57
	2 yr		10.4 %	77
	3 yr		1.2 %	84
	4 yr		7.3 %	55
Lesser Black-backed Gull	1 yr	1000 km	15.0 %	20
	2 yr		20.3 %	59
	3 yr		5.9 %	68
	4 yr		0.0 %	63

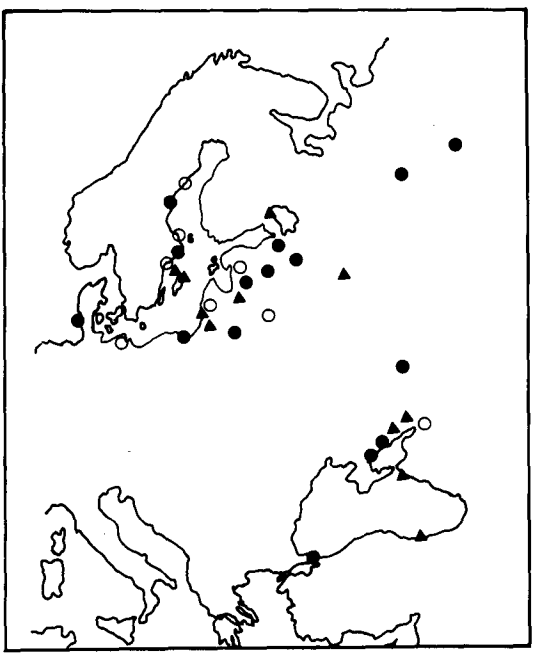

Fig. 2. European recoveries of immature Lesser Black-backed Gulls in May—July, excluding those made in Finland. Open dots = 1 yr, black dots = 2 yr and triangles = 3 yr.

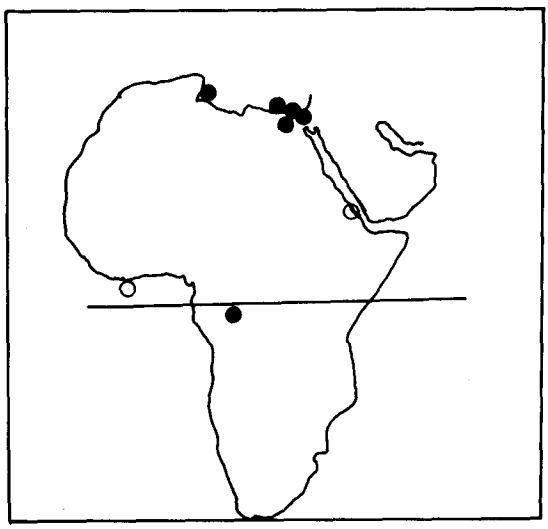

Fig. 3. African recoveries of immature Lesser Black-backed Gulls in May—July. Only birds found in fresh condition are plotted. Open dots = 1 yr, black dots = 2 yr.

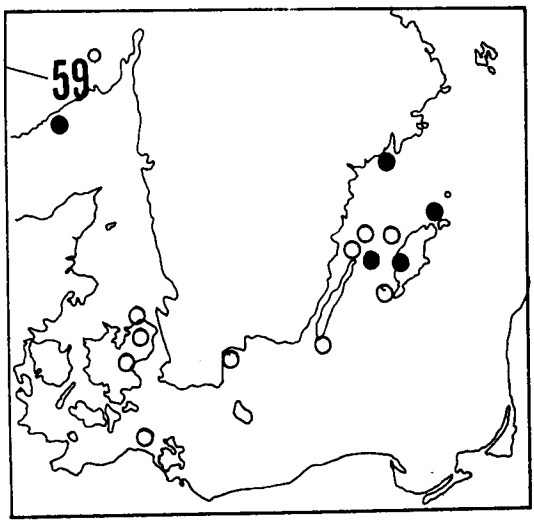

Fig. 4. Recoveries of immature Great Black-backed Gulls made south of 59°N in May—July. Open dots = 1 yr, black dots =2 yr.

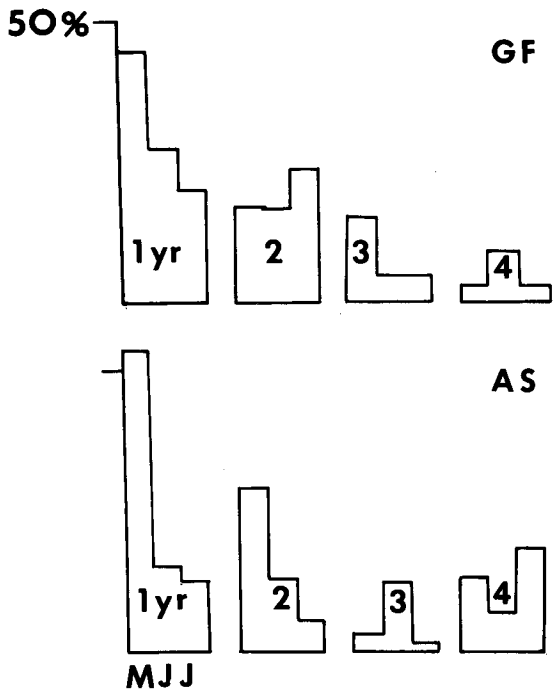

Fig. 5. Proportions of monthly (May—July = MJJ) recoveries made south of 59°N for immature Herring Gulls (1—4 yr) from AS and GF.

to return to the north. An additional difficulty in analysing *fuscus* recoveries is that some birds may have been misidentified by the ringer; we know of a few birds ringed as *fuscus* that were actually *argentatus*.

Some of the birds performing a return migration reach areas that appear to be outside the "normal" range. Two *fuscus* for instance, were found at the latitudes of southern Finland, but at very easterly longitudes (Fig. 2). Some *fuscus* and *marinus* had continued beyond their natal area. Many *argentatus* migrate past their natal area in summer, and exploit areas around urban centres frequented by newly fledged 1 yr birds in autumn (Kilpi & Saurola 1983). These areas probably have very good food supplies, and also low populations

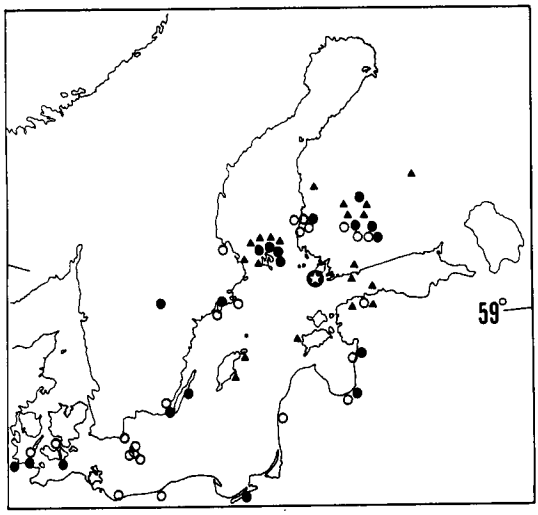

Fig. 6. Recoveries of immature Herring Gulls from GF (star) in May—June. All recoveries made 100 km from natal site plotted. Open dots = 1 yr, black dots = 2 yr and triangles = 3 yr.

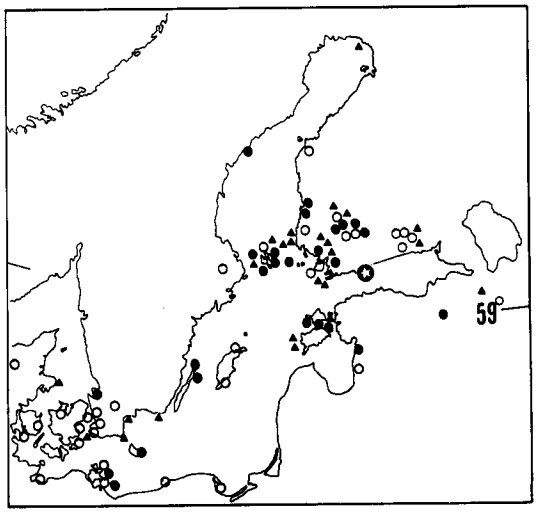

Fig. 7. Recoveries of immature Herring Gulls from AS (star) in May—June. All recoveries made 100 km from natal site plotted. Open dots = 1 yr, black dots = 2 yr, triangles = 3 yr.

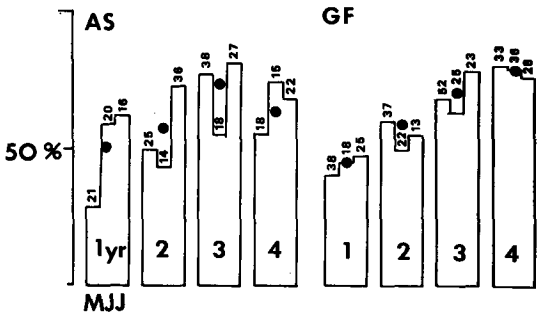

Fig. 8. Proportions of recoveries of immature (1—4 yr) Herring Gulls made within 100 km of the natal site in May—July. Total number of recoveries given for each month. Black dots show the proportion within 100 km for the whole period (M+J+J).

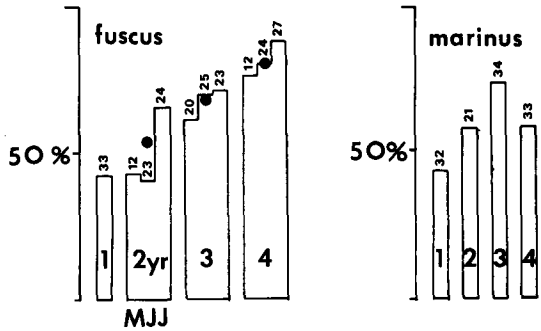

Fig. 9. Proportions of recoveries of immature (1—4 yr) Lesser Black-backed and Great Black-backed Gulls made within 100 km of the natal site in May—July. Total number of recoveries are given. Single bars and black dots show the proportion within 100 km of the natal site for the whole period (M+J+J).

of breeding birds. Immature birds of all age-classes are found in these areas. The proportion of immature recovered north of 59°N, but beyond the natal area, was about the same in all age-classes, ranging from 13 to 23 % of the total recoveries north of 59°N.

Return of birds of breeding age. Very few adults were recovered in the southern part of the yearly range in summer. Two (2.9 %, N=68) adult *marinus*, aged 6 and 7 yr, were found more than 500 km from their natal site, both in fresh condition. Four adult *argentatus* from GF (1.3 %, N=302) were recovered at similar distances. Two of these birds were 6 yr old, two 11 yr. No adults from AS were recovered at such distances. Only one 5 yr *fuscus* was recovered in fresh condition more than 1000 km from its natal site in summer (0.7 %, N=138).

The high proportion of the recoveries reported from areas within 100 km of the natal site (Fig. 10), indicates that a large part of the birds breed in their natal area. The proportion of recoveries made near the natal site did not differ between gulls of different ages in *marinus* or in *argentatus* from GF or AS (χ^2-tests, n.s.). In *fuscus*, 6—8 yr birds were found much less frequently near the natal site than 5 or/and +8 yr birds (χ^2=7.4, df=1, P<0.01 and χ^2=21.1, df=1, P<0.001, respectively). The proportion of 6—8 yr birds found near the natal site was high in May (72.7 %), but lower in June (25.0 %) and July (31.0 %). The difference between May and June is significant (χ^2=9.5, df=1, P<0.01). This does not appear to be an artefact; colonies off the southern coast of Finland often seem to have an excess of adult-plumaged birds early in the season (Kilpi, unpubl.). We suggest that *fuscus* starts breeding at a very late age. Why 5 yr birds were recovered so frequently near the natal site, is unclear.

Adults of all three species were recovered at localities > 100 km from the natal site (Table 3). The frequencies are so high that we suggest that either natal or breeding dispersal is a common reproductive strategy in all three species. The recoveries of adults more than 100 km from their natal sites are plotted in Figs. 11, 12, 13 and 14. In *marinus* recruitment to new breeding sites may occur over a large part of the Baltic. The areas used by dispersing adult *argentatus* partly coincide with areas used by immature birds found outside

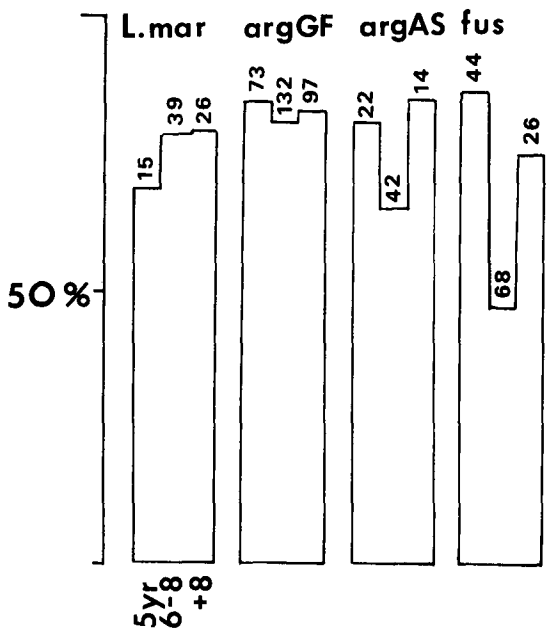

Fig. 10. Proportions of adults recovered within 100 km of the natal site in the breeding season according to age-class (5— +8 yr) for the three species. Total number of recoveries given.

Table 3. Percentages of recoveries made more than 100 km from the natal site for adults of different age-classes in three *Larus*-species. Totals for *L. marinus* and *fuscus* in May—July, and for *argentatus* in May—June. Compare with Fig. 11.

Species	Age	Dispersal > 100 km	N
Great Black-backed Gull	5 yr	31.3 %	15
	6–8 yr	21.1 %	39
	+8 yr	21.4 %	26
Herring Gull (GF)	5 yr	15.1 %	73
	6–8 yr	16.7 %	132
	+8 yr	15.9 %	97
Herring Gull (AS)	5 yr	22.7%	22
	6–8 yr	26.2 %	42
	+8 yr	35.7 %	14
Lesser Black-backed Gull	5 yr	13.6 %	44
	6–8 yr	57.4 %	68
	+8 yr	25.0 %	24

their natal area. Birds from the coast may recruite to areas in the interior of the country. It seems that adults seeking new breeding sites tend to choose areas with low breeding populations, but with good food supplies, since also immature birds gather in these areas. Some interchange of adults between GF and AS seems to occur. The recoveries of *fuscus* indicate that inland and coastal gulls may mix. Large-scale retrappings of breeding birds by ringers would shed further light on the origin of gulls settling in new areas and the extent of dispersal from natal or earlier breeding areas.

Discussion

Areas exploited by immature gulls. Immature birds of all three species use a wide variety of areas during the breeding season of adults. Their movements seem to vary more between age-classes than between species. Some birds migrate very late, or do not migrate at all, staying in the southern part of the yearly range. Most of these are 1 yr and 2 yr gulls in basically brown plumage (Grant 1982). Older immatures are more seldom encountered in the main winter survival area in summer, adults practically never.

A number of immatures start on a return migration in spring and summer, and some reach or pass the natal area. Young, 1 yr and 2 yr gulls again show the most extreme pattern. Compared with older immatures and adults, 1 yr and 2 yr *fuscus* and *argentatus* show a delayed return mig-

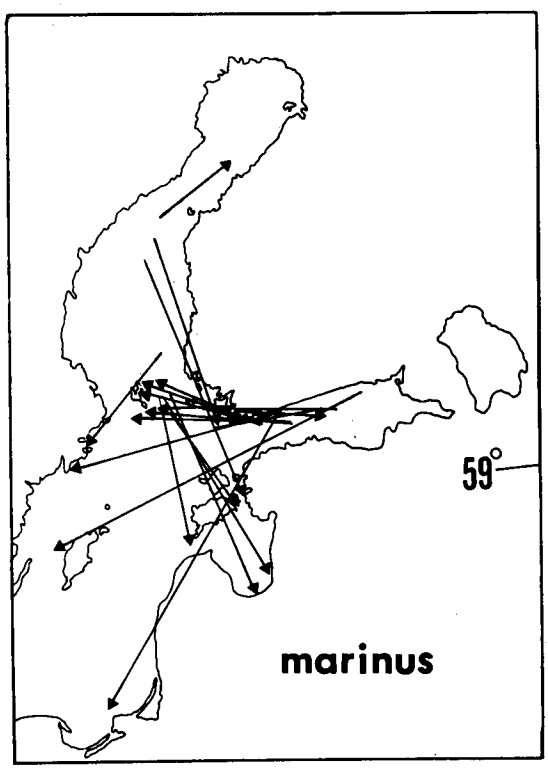

Fig. 11. Recoveries of adult Great Black-backed Gulls more than 100 km from the total natal site (base of arrow) in the breeding season.

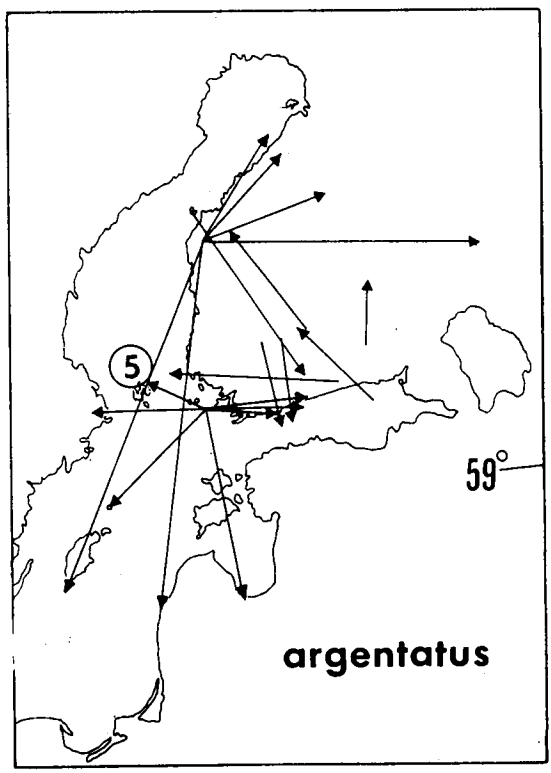

Fig. 12. Recoveries of adult Herring Gulls from AS and other localities made during the breeding season more than 100 km away from the natal site (base of arrow).

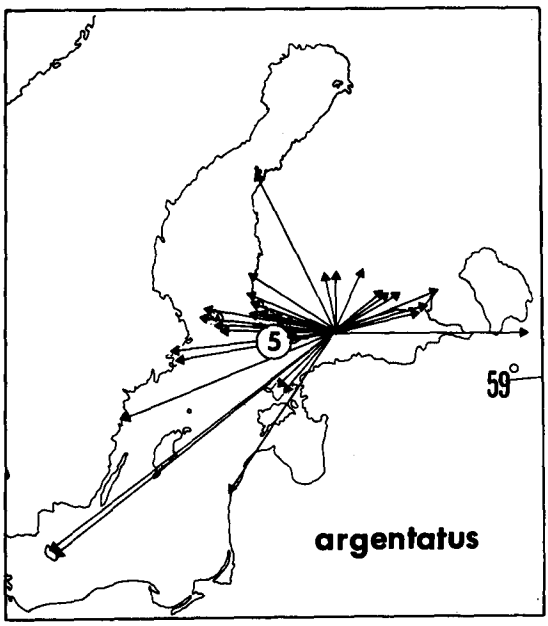

Fig. 13. Recoveries of adult Herring Gulls from GF made during the breeding season more than 100 km away from the natal site.

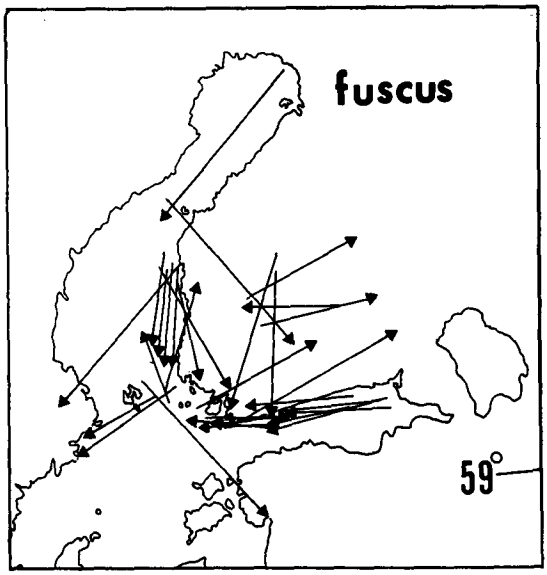

Fig. 14. Recoveries of adult Lesser Black-backed Gulls made during the breeding season more than 100 km from the natal site (base of arrow).

ration, tending to arrive in the breeding area when breeding is well underway in adults.

The data accumulated to date do not allow a detailed analysis of the dependence of return migration on the distance to be covered. Some immature *fuscus* reach their natal area, though the return flight is much longer than in the two other species (max. 7500 vs. 1000 km). However, the data indicate that immatures of *fuscus* complete the return migration less frequently than immature individuals of the other two species. Failure to return to the area of origin has been noted in several sea-birds, especially in long-range migrants (Ashmole 1971, Coulson 1966, Møller 1982). The two younger age-classes of large *Larus* species are physiologically unable to breed (see Coulson et al. 1982), and their distinctive brown plumage may be an adaptation to manifest this. Goethe (1956) reported that *argentatus* in brown plumage are driven away from breeding colonies, but little is known about interactions between immature and adult gulls in areas with dense breeding populations. Both in *argentatus* and *fuscus* immature individuals of all ages are found in the breeding colonies, and 1 yr and 2 yr *marinus* have been found on breeding islets of conspecifics (Kilpi, unpubl.).

Great Black-backed and Herring Gulls encounter resident conspecifics of all ages throughout the yearly range. Lesser Black-backed Gulls staying in the southern part of the yearly range occur together with several species of gulls of medium or large size (Sooty and White-eyed Gulls *L. hemprichii* and *L. leucopthalmus,* Herring and Audouins Gull *L. audouinii* and Great Black-headed Gull *L. ichtyaetys*). In the interior of Africa where Lesser Black-backed Gulls from Finland occur, the only resident gull species is the small Grey-headed Gull *L. cirrocephalus* (Dementiev et al. 1969, Grant 1982). The degree of resource competition, if any, between resident species and immature gulls not returning to northern areas is not known for any of the species studied here. Immature gulls returning to the breeding area, may benefit from being able to familiarize themselves with existing breeding colonies (Baker 1978), and will also have an opportunity to find good feeding areas.

Our data show that the tactics used by immature individuals vary a good deal, and this variation will be beneficial if conditions in any part of the total survival area deteriorate rapidly. The use of accidental ring recoveries prevented us from detecting another possible type of migratory behaviour: movement backwards or forewards within a large area. The observed distribution of recoveries could also be brought about by such movements (see Baker 1978 for discussion on exploratory migration).

Breeding site selection. Young gulls recruite to breeding colonies (or in the particular case of *marinus* in Finland, select vacant sites between solitary pairs), on the basis of information gathered during pre-breeding seasons. In highly colonial gulls such as *argentatus* and *fuscus,* dense

colonies attract recruits (Chabrzyk & Coulson 1976, Götmark 1982). Chabrzyk & Coulson (1976) suggested that high-density colonies are the most attractive, though territories are more easily established in less dense colonies (see also Coulson et al. 1982). The fact that concentrations of both colonial species exist along the coast of the Gulf of Finland (see map in Kilpi et al. 1980) supports the hypothesis that dense colonies are attractive. The presence of a colony may not, however, be the only cue used, and the presence of good feeding sites may be an important factor. Some of the immature gulls studied here were found in areas with current low densities of breeding birds. In *argentatus*, these areas are exploited in autumn as well by large number of birds (Kilpi & Saurola 1983). This high degree of exploitation does indicate good sources of food. Adult *argentatus* that have emigrated from our study populations have been recovered in these areas, and the population of breeders in these areas has been growing fairly rapidly. We suggest a very strong connection between good conditions for immatures and a rapid growing breeding population.

Emigration. According to the criteria of McNicholl (1975), all three species studied here breed in very stable habitats, in contrast to, for instance, gulls breeding in marshes (e.g. Franklin's Gull *L. pipixcan*, Burger 1974). In view of the stability of the breeding habitat, the birds should tend to use the same area and the same colony for several years in succession. Although we cannot separate natal and breeding dispersal, most adults in all three species seem to breed in their natal colony or natal area. Another factor involved besides the stability of the breeding habitats, is the stability of the feeding habitat around the colonies. Feeding conditions probably vary in time, and the variation may be so great that emigration becomes more beneficial than site fidelity. The tendency to seek new breeding areas may well be an innate trait. Several other factors, such as frequency of disturbance by predators, may decrease the advantage of site fidelity. To the human eye at least, suitable islands for all species seem to occur in abundance along the Finnish coast. In many cases no compelling reason for emigration is apparent, since suitable islands are left unexploited. Yet, a fairly large fraction of the adults of all species (20—25 %) seem to have emigrated to more distant areas.

Implications for range extension. The tendency to emigrate has in several instances been shown to be beneficial. In the North American Herring Gull, Nisbet (1978) has reported lowered breeding success and a cessation of population growth in traditional areas, while Burger (1977) found good breeding success in a marginal, newly invaded area. Birds with long pre-breeding lives and extensive movements during this phase, have ample opportunity to gather information on the conditions in large areas, and their suitability for survival and breeding. Viksne (1968) postulated a connection between juvenile movements and range expansion in the Black-headed Gull *L. ridibundus*. A similar connection seems to exist in the Herring Gull, a highly successful species that has invaded extensive areas in the 20th century (Harris 1970, Burger 1977). It remains to be ascertained whether immature gulls that exploit areas outside the current breeding centres are responsible for the establishment of new breeding colonies. It is interesting to note that emigration and extensive movements in juveniles occur not only in prosperous and increasing populations, but also in declining populations, such as those of the Lesser Black-backed in Finland. All populations must have been successful at some phase of their history, and the maintenance of emigration as a reproductive tactic may be due to genetic factors.

Selostus: **Suomessa rengastettujen aikuisten ja esi-aikuisten meri-, harmaa- ja selkälokkien levinneisyys pesimäaikaan**

Kirjoituksessa tarkastellaan 1533 poikasrengaslöydön perusteella eri-ikäisten meri-, harmaa- ja selkälokkien levinneisyyttä pesimäaikaan (touko—heinäkuu). Aikuisia (pesiviksi oletettuja) lintuja tavataan melko laajalla alueella, joskin suurin osa löytyy alle 100 km säteellä synnyinpaikaltaan ikäluokasta ja lajista riippuen (42 % — 76 %, kuvat 10—14). Esiaikuisia tavataan laajemmalla alueella, etenkin 2-kv ja 3-kv lintuja pitkin kesää talvehtimisalueen eteläosia myöten. Suurin osa meri- ja harmaalokeista näyttää kesän mittaan palaavan Suomen rannikolle, joskin myöhemmin kuin aikuiset (kuvat 4—7). Selkälokkeja (2-kv ja 3-kv) on ammuttu päiväntasaajan tienoilla, vaikka ilmeisesti jopa 2-kv lintuja tavataan Itämeren piirissä kesällä (kuvat 2—3). Osa 2-kv selkälokeista näyttää palaavan Pohjolaan, mutta hyvin myöhään, ja luultavasti varsin suuri osa muuttaa vain osan matkaa. Koska harmaalokkeja on rengastettu selkälokkeina, on vaikea täysin varmistaa vuoden ikäisten selkälokkien paluuta Suomeen.

Esiaikuisia lokkeja tavataan kesällä paitsi lähellä synnyinsijojaan (alle 100 km, kuvat 8—9) myös muualla Suomessa, harmaalokkeja esim. sisämaassa alueilta, joille viime aikoina on syntynyt kasvavia pesimäkantoja.

Rengaslöydöt eivät valaise kysymystä miksi nuori, pesimätön lintu muuttaa pohjoiseen kesällä. Aikuisten lintujen emigraatio ja nuorten liikkeiden yhteys jää epäselväksi. Sekä nuorten lokkien muuttokäyttäytymisen että pesimäpaikkauskollisuuden vaihtelun uskotaan olevan adaptiivista: vaikka suuret lokit elävät suhteellisen vakaissa ympäristöissä, muuttaminen "jonnekin muualle" saattaa olla edullista liiallisen populaatiotiheyden aiheuttamien seuraamusten välttämiseksi.

References

Alerstam, T. & Högstedt, G. 1982: Bird migration and reproduction in relation to habitats for survival and breeding. — Ornis Scand. 13:25—37.

Ashmole, N. P. 1971: Sea bird ecology and the marine environment. — *In:* Farner, D. S. & King, J. R. (eds.): Avian Biology, Vol. 1:223—286. Academic Press, New York.

Baker, R. R. 1978: The evolutionary ecology of animal migration. — Hodder and Stoughton, London.

Bergman, G. 1982: Population dynamics, colony formation and competition in Larus argentatus, fuscus and marinus in the archipelago of Finland. — Ann. Zool. Fennici 19:143—164.

Burger, J. 1974: Breeding adaptations of Franklin's Gull (Larus pipixcan) to a marsh habitat. — Anim. Behav. 22:521—567.

Burger, J. 1977: Nesting behaviour of Herring Gulls: invasion into Spartina salt marsh areas of New Jersey. — Condor 79:162—169.

Chabrzyk, G. & Coulson, J. C. 1976: Survival and recruitment in the Herring Gull Larus argentatus. — J. Anim. Ecol. 45:187—203.

Coulson, J. C. 1966: The movements of the Kittiwake. — Bird Study: 13:107—115.

Coulson, J. C., Duncan, N. & Thomas, C. 1982: Changes in the breeding biology of the Herring Gull Larus argentatus induced by reduction in the size and density of the colony. — J. Anim. Ecol. 51:739—756.

Dementiev, G. P., Gladkov, N. A. & Spangenberg, E. P. 1969: Birds of the Soviet Union, Vol. 3. — Israel Program for Scientific Translations, Jerusalem.

Duncan, W. N. M. & Monaghan, P. 1977: Infidelity to the natal colony by breeding Herring Gulls. — Ringing and Migration 1:166—172.

Fredriksson, S. 1979: Skrattmåsen Larus ridibundus i Sverige. — Vår Fågelvärld 18:173—200.

Goethe, F. 1956: Die Silbermöwe. — Neue Brehm Bücherei 182, Wittenberg.

Grant, P. J. 1982: Gulls: a guide to identification. — Poyser, Berkhamsted.

Greenwood, P. J. 1980: Mating systems, philopatry and dispersal in birds and mammals. — Anim. Behav. 28:1140—1162.

Götmark, F. 1982: Coloniality in five Larus gulls: a comparative study. — Ornis Scand. 13:211—224.

Harris, M. P. 1970: Rates and causes of increases of some British gull populations. — Bird Study 17: 325—335.

Kilpi, M., Puntti, H. & Toivonen, T. 1980: Numbers of gulls breeding on the northern coast of the Gulf of Finland. — Ornis Fennica 57:153—160.

Kilpi, M. & Saurola, P. 1983: Autumnal, pre-migration movements of coastal Finnish Herring Gulls Larus argentatus. — Ann. Zool. Fennici 20:245—254.

Kilpi, M. & Saurola, P. 1984: Migration and wintering strategies of juvenile and adult Larus marinus, argentatus and fuscus from Finland. — Ornis Fennica 61 (in press).

Langham, N. P. E. 1971: Seasonal movements of British Terns in the Atlantic Ocean. — Bird Study 18:155—175.

McNicholl, M. K. 1975: Larid site tenacity and group adherence in relation to habitat. — Auk 92:98—104.

Møller, A. P. 1982: The migration of European Sandwich Terns Sterna sandvicensis II. — Vogelwarte 31:149—168.

Nisbet, I. C. T. 1978: Recent changes in gull populations in the western North Atlantic. — Ibis 120:129—130.

Southern, W. E. 1977: Colony selection and colony site tenacity in Ring-billed Gulls at a stable colony. — Auk 94:469—478.

Viksne, J. A. 1977: The role of post-nesting dispersal of the Black-headed Gull Larus ridibundus for its breeding distribution. — *In:* Michelsons, H. A. & Viksne, J. A. (eds.): Ecology of waterfowl of Latvia. Riga.

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