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Pre-migration movements of coastal Finnish herring gulls (Larus argentatus) in autumn

Mikael Kilpi & Pertti Saurola

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The study presents autumnal movements of herring gulls, based on a total of 1633 ring recoveries of birds ringed mainly on the southern and southwestern coasts of Finland. Although strictly migratory in a conventional sense, these gulls exploit areas fairly close to the breeding area during August-October. Upon leaving the colonies, juvenile first year birds, to some extent disperse in various directions, but very few reach the main wintering area during early autumn. The recoveries centre around urban areas. Breeding adults seem to participate in this dispersal to a lesser extent. The analysis of postnesting dispersal in adults is hampered by birds that have dispersed prior to the autumn period, i.e. birds breeding far from their natal colony. Of a total of 325 recoveries of adults in May-June, some 20 % are reported from locations > 100 km from the natal colony.

It is suggested, on the basis of recoveries made on refuse dumps, that adults primarily exploit the nearest possible feeding sites upon leaving the colony. The use of dumps is considered to be important. Immature (2-3 rd year) birds that do not breed exploit a wide area in late summer and autumn. The areas exploited coincide with that used by dispersing first year gulls. Second year herring gulls, in particular, seem to shift to areas near the main wintering area much earlier than any other age-class. The pattern observed in 4-5th year birds resembles that of adults. There is thought to be spatial segregation between different age-classes during this period.

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1. Introduction

Members of the genus *Larus* commonly nest in dense colonies, and are as such ideal for mass ringing operations. Consequently, several studies dealing with the seasonal distribution of a variety of *Larus* species have been published (see Southern 1980). The herring gull has been studied intensively with the aid of ring recoveries (Drury & Nisbet 1972, Gross 1940, Moore 1976, Parsons & Duncan 1978 and references in these). Some of these studies have focused on describing the distributional dynamics of particular populations during the year (Drury & Nisbet 1972, Moore 1976), while others have treated special features such as post-fledging dispersal in juveniles (Burger 1981) or site fidelity in breeding adults (Duncan & Monaghan 1977).

The populations treated here breed on the Finnish coast. The gulls from these areas can, on good grounds, be considered migratory in the sense of Lack (1968a), since a majority of the birds spend their winter in an area essentially not overlapping with the breeding area (Kilpi & Saurola in press). In this paper we will concentrate on spatial and temporal distributions of different age-clases of herring gulls in autumn, during a period of time following the breeding season and preceding the major exodus to the survival area used in winter.

In studies spanning the entire year, juvenile herring gulls have been found to move considerably more than adults (Parsons & Duncan 1978). Moore (1976) proposed that this phenomenon, which he termed "differential migration", is highly adaptive since it reduces intraspecific competition for food. Immediately after the breeding season the herring gull population in any area will increase dramatically, which may lead to a situation where competition for food increases (see Lack 1968b). First year gulls are often considered socially inferior to older birds (Ulfstrand 1979), and dominance interactions may influence dispersal patterns by affecting resource utilization. Hypothetically it would seem a good alternative for adults to utilize the nearest suitable survival area immediately after breeding. Juveniles may, on the other hand, be excluded from these areas, and forced to move. Likewise it may be beneficial for non-breeding

immature birds to shift into other areas when there is a heavy influx of newly fledged juveniles and adults into the suitable survival areas near the colonies. We try here to find out whether there are actually any differences in dispersal patterns between the age-classes.

In the herring gull a proportion of the adults will breed in, or close to, the natal colony (Drury & Nisbet 1972). On the other hand it has been found that they may recruit into more distant areas as breeders (Coulson et al. 1982, Duncan & Monaghan 1977). This poses a problem in assessing the movements of breeding adults in autumn in relation to first year birds, the origin of which is indisputably determined. We will therefore also briefly examine the distribution of adults during the breeding season.

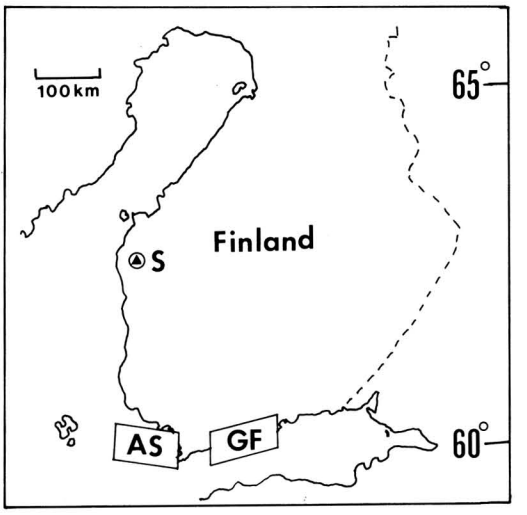

Fig. 1. Areas of origin of herring gulls treated in this study. Within both the AS and GF most birds have been ringed in a few main colonies. The S colony is the only sizeable colony in that area. See text in sect. 2.1

2. Material and methods

2.1 The studied cohorts

This analysis compares two populations of coastal breeding herring gulls (Fig. 1), one originating from the Gulf of Finland (GF), the other from the Archipelago Sea (AS). The GF is delimited by the longitudes 24°E and 26°E, the area being c. half a degree of latitude "high". Within this area the highest denities of breeding herring gulls along the Finnish coast are found (Kilpi et al. 1980). The total population within the Gulf of Finland exceeds 12 pairs (Kilpi et al. 1980), of which c. 9000 breed within the study area. Most of the ringing work was done in the late 1960s and early 1970s.

The AS population is, for this study, deliminited by the longitudes 21°E and 23°E and the same latitudes as the GF area. Within the AS the colonies are more scattered, and the total population much lower, probably in the region of 5000 pairs (Bergman 1982, Kilpi unpubl.). Most of the ringing was done in the 1970s.

Both these populations have been growing at a fairly fast rate during the last decade. Depending on area, the population in the AS has grown 6-14 % per annum (Häkkinen 1980) and the GF population at c. 12 % p.a. in the 1970s (Kilpi unpubl.). These growth rates indicate that food is abundant during the breeding season.

For some additional comparisons we have used recoveries of birds ringed on Sanemossen bog near the coast (S) at c. 62°N. This small population comprised c. 500 pairs in 1971 (Lundberg 1977).

2.2 Breeding phenology

On the southern and southwestern coasts of Finland, adult herring gulls start occupying the colonies in the beginning of April. Laying normally starts in mid-April (v. Haartman et al. 1963-72, Kilpi unpubl.). According to Lundberg (1977) the gulls on Sanemossen lay in late April/early May. With an average incubation time of 27 days (Paludan 1951) and an averade fledging age of c. 50 days (Goethe 1956), most young will have fledged towards mid-July. In the southwestern archipelago the colonies are abandoned towards the end of July (own data).

In this study we have taken the starting date for independent life in juveniles to be August 1. It is not know whether they are actually independent of their parents by this date (see Burger 1980, 1981b for discussion on this topic). Consequently, the second year of life (2 yrs) starts a full year later, and so on. Chabrzyk & Coulson (1976) found that the mean age of first breeding in a British population of herring gulls was 5.25 years. On this basis we have assumed that birds in their sixth year (+5 yrs) are breeders.

2.3 The recovery material

In all we have used 1055 recoveries of first year birds, 364 recoveries of immature (2—5 yr) birds and 214 recoveries of adult birds. On the basis of these we examine the spatial distribution of recoveries in autumn i.e. August-October. A further 325 recoveries of adult herring gulls found in May-June are used to elucidate the distribution of the birds during the breeding season.

The recoveries used have accumalated between 1950 and 1981 the absolute majority being fairly recent. The GF material is on the whole somewhat older than the AS material, including many recoveries from the 1960s.

The analysis is based on two main categories of recoveries; (a) birds reported "found" and (b) birds reported "found in fresh condition", this meaning mostly shot birds. All recoveries concerning sick or decayed birds have been omitted. Birds recovered in unclear circumstances, with incomplete data, have been excluded. Birds known to have been trapped during Finnish herring gull control projects (Kilpi 1980) have been treated separately (see sect. 3.5).

3. Results

3.1 Post-fledging dispersal in first year herring gulls

Upon fledging, first year herring gulls rapidly move out of the colonies, and a substantial proportion of the birds disperse > 100 km from the natal site in various directions (Table 1, Fig. 2, 3, 4). The distances covered during the first months

Table 1. Proportions (%) of first year herring gulls staying within 100 km of the natal colony versus those dispersing further during August-October. Dispersed birds includes those found near the main winter survival area; see text.

Origin	August Stay	Disp.	N	September Stay	Disp.	N	November Stay	Disp.	N
GF	69.5	30.5	213	66.6	33.3	204	57.0	43.0	135
AS	42.4	57.6	210	47.3	52.7	129	41.9	58.1	86
S	43.4	65.5	32	40.0	60.0	35	36.4	63.6	11

of independent life are fairly limited. Off a grand total of 1049 recoveries from all three populations (GF+AS+S) in August -October, only 47 (4.5 %) have been reported at distance > 500 km from the natal colony in August-October. Of these recoveries, 35 concern birds found near the main winter survival area in the southern part of the Baltic, the maximum distance being 1044 km. In other directions (W-N-E) the maximum distance recorded is 930 km, with only 12 (1.1 %) recoveries at distances exceeding 500 km. The proportions of recoveries within 100 km zones during August-October, regardless of direction chosen, are shown in Fig. 2. It is noteworthy that infact a very small fraction of the juveniles have reached the winter survival area during these months.

For juveniles dispersing more than 100 km from their natal colony, certain preferred areas seem to exist (Fig. 3). Juvenile gulls from the GF use its coast extensively, with a substantial proportion of the birds found to the east of the area of origin. Very few GF juveniles are found within the breeding area of the AS population. Juveniles from AS move north along the coast up the Bay of Bothnia, and eastwards into the Gulf of Finland, reaching the GF breeding area. Juveniles from both GF and AS reach the interior of the country, the recoveries centring around urban areas in the lake district. Young herring gulls from S seem to move primarily along the coast within the Bay of Bothnia, many birds flying northwards. The recoveries again centre around urban areas.

Significant differences in proportions encountered within 100 km of the natal colony are evident when the populations are compared. Significantly more first year GF birds stay within the given 100 km zone than both AS and S birds in August and September (χ^2 = 31.5 and 12.3, df = 1, $p < 0.001$ in both comparisons with AS, χ^2= 11.2 and 9.3, df=1, $p < 0.001$ and 0.01 in comparison with S). In October the difference is insignificant in both cases (χ^2 = 4.8 and 1.7, df=1 n.s.). The differences between AS and S are insignificant (compare Table 1). These differences may be biased by locally varying recovery rates, mainly the intensity of shooting. The differences indicate that birds in areas where distances between suitable feeding sites are longer are forced to move further. The GF area is much more urbanized than both the AS and the S coast.

3.2 Post-breeding dispersal and fidelity to natal area in breeding adults

Many workers have concluded that adult gulls do not neceassarily breed in or near the natal colony (Drury & Nisbet 1972, Duncan & Monaghan 1977, Kilpi & Saurola in prep.). An adult bird found during the breeding season may quite safely be assumed to be breeding. The assumption is hampered by birds taking a year off (Coulson et al. 1982) or recovered en route on migration. Herring gulls make long foraging trips (Drury & Nisbet 1972), which can add to the confusion when assessing the breeding location of an adult. We have here assumed that an adult found > 100 km from its natal site during the breeding season may be considered unfaithful to its natal site when breeding. A substantial proportion of the breeding time recoveries are made > 100 km from the natal site (Table 2).

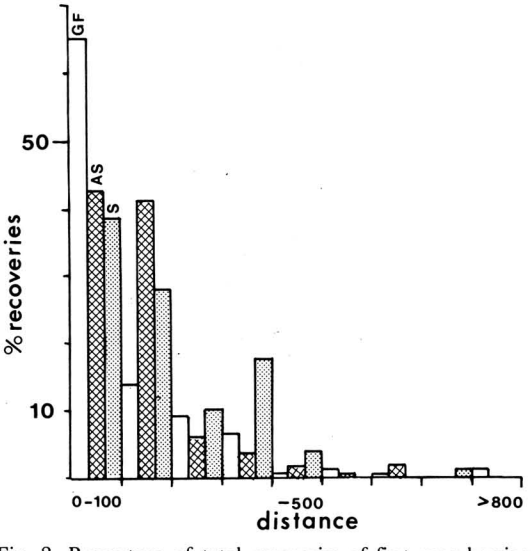

Fig. 2. Percentage of total recoveries of first year herring gulls within 100 km zones of the natal colony in August-October.

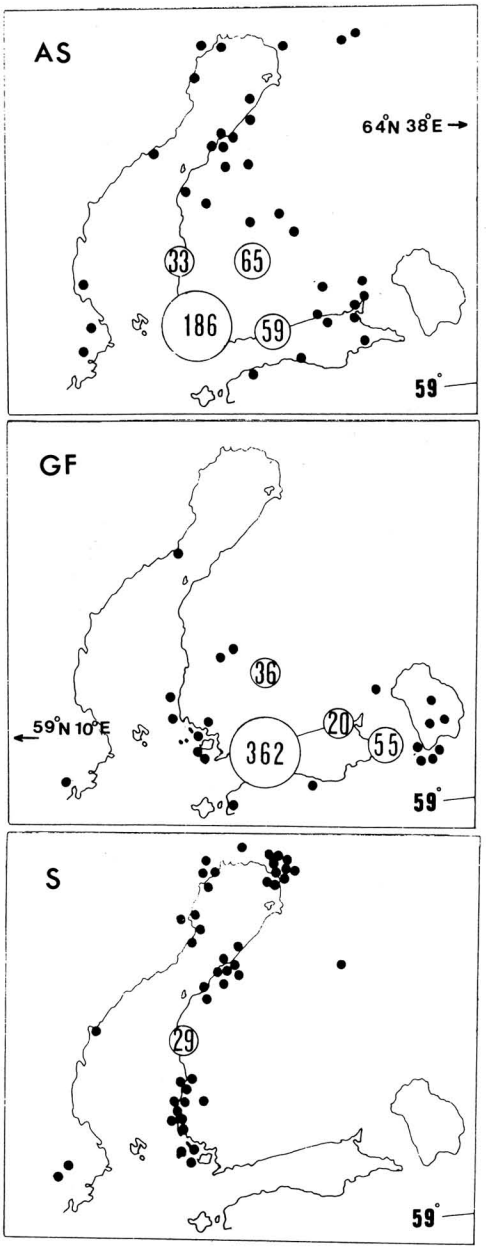

Fig. 3. Total number of recoveries of first year gulls from the three study populations north of 59°N in August-October. The number of recoveries within certain areas is denoted by circles also showing the number of recoveries. Individual recoveries plotted as black dots. One recovery of a bird from the AS recovered at the White Sea omitted from the map. A=GF, B=AS and C=S.

The existence of adults not faithful to their area of origin when breeding makes the assessing of post-nesting movements difficult, since the

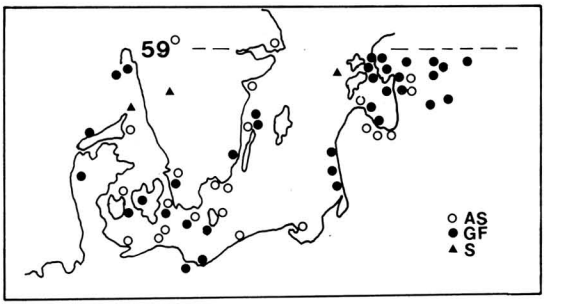

Fig. 4. Recoveries of first year herring gulls from the three study populations south of 59°N in August-October. These recoveries represent only a minor fraction of the total recoveries of this time period (less than 10 %); see text in sect. 3.1 and Fig. 7.

Table 2. Proportions of presumed breeding adults encountered > 100 km from their natal colony in May-June (breeding period) and August-October. The differences between the populations are insignifcant (χ^2 test).

Origin	May-June		August-October	
	%	*N*	%	*N*
GF	17.1	240	20.9	172
AS	22.8	57	32.3	31
S	28.6	28	36.4	11

recovery patterns can equally well be produced by birds moving longer distances, or birds dispersing short distances from more remote breeding sites. When the spatial distribution of May-June and August recoveries are plotted (Fig. 5), they appear almost indentical in the GF case. Thus it seems that GF adults do not disperse after breeding over larger areas. A number of recoveries of adults from AS to the east of the breeding area (Fig. 5) may indicate post-breeding dispersal.

Over the whole autumn period, slightly more first year birds are encountered at distance > 100 km from the natal site than adults (Table 3). The differences approach significance (χ^2=6.2 and 6,3, df=1, p< 0.025 for comparison between first year birds and adults from the GF and AS respectively). The adult values are biased by birds which have dispersed prior to the autumn season, hence this result indicates that first year birds tend to disperse more readily.

3.3 Where are immature birds found in autumn?

Of a total of 13 recoveries of first year herring gulls from the GF in July in their second summer, 10 (76.9 %) come from an area north of

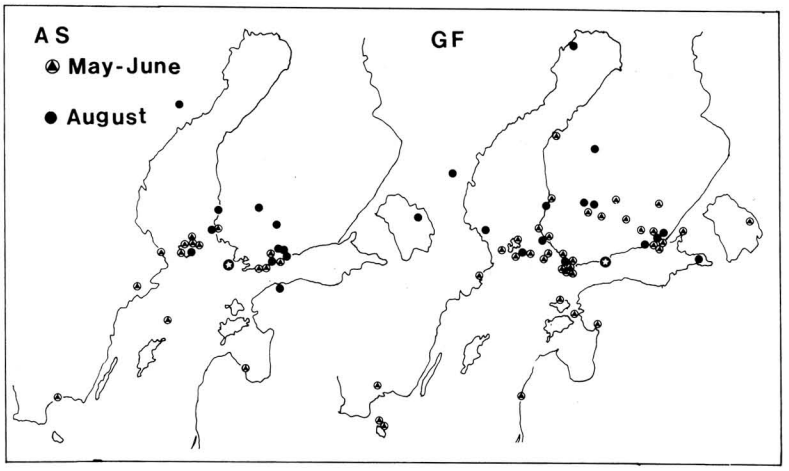

Fig. 5. Spatial arrangement of breeding period (May-June) and early post-nesting recoveries of adult herring gulls from the AS and GF in relation to natal colony (star). Only recoveries > 100 km from natal colony plotted.

Table 3. Proportions (%) of first year and adult herring gulls recovered > 100 km from their natal colony in August and August-october; see text.

Origin	August			August-October		
	Disp.	Migr.	*N*	Disp.	Migr.	*N*
GF						
1 yr	30.5	3.8	213	34.6	8.2	552
adult	18.6	0.5	118	24.6	4.5	172
AS						
1 yr	57.6	2.4	210	56.2	4.9	425
adult	40.9	—	22	32.5	2.5	40

59°N, i.e. the gross breeding area of the Finnish population. The corresponding value for AS gulls is 36 out of 38 recoveries (94.7 %). The material from S is too small for us to draw any conclusions. In conclusion, most juvenile birds return to the breeding area after the first winter. The return seems, however, very late. Other immature age-classes return earlier (Kilpi & Saurola in prep.).

In August, when the first year birds have begun their exodus from the breeding colonies, a number of immature birds are encountered near the natal area, while others use more distant areas (Table 4). Within the GF area a low proportion of both second year and third year herring gulls are found in August. Significantly higher proportions of 4-5th year gulls are found < 100 km of their natal colony in August ($\chi^2 = 14.0$ and 7.6, $df=1$, $p< 0.001$ and 0.01 for comparison between 4-5th year and second and third year birds, respectively). The proportion of 4-5th year gulls approaches that of adults (72.7 % and 81.4 %, respectively, of August recoveries) found < 100 km from the natal colony. The proportion of 4-5th year gulls within this zone decreases as atumn progresses (Table 4). The proportions of both second and third year herring gulls from the GF within 100 km of the natal colony are low in August, but there is a drastic increase in the encounters near the natal colony especially in second year gulls in September (Table 4). In third year birds the proportion > 100 km from the natal colony rises gradually. Second year gulls rapidly disappear from these areas in October, when a shift to more southern areas takes place in these birds (Fig. 7, 8).

Both 4-5th and third year gulls from the AS are encountered in a fashion close to that described for GF birds in August-October. The main difference is the high proportion of second year gulls found close (< 100 km) to the natal colony in

Table 4. Proportions (%) of second year to 4-5 yr herring gulls found < 100 km of their natal colony versus those outside this zone in autumn. Includes brids that are found close to the main winter survival area.

Cohort	August			September			October		
	Stay	Disp.	*N*	Stay	Disp.	*N*	Stay	Disp.	*N*
GF									
2 yr	29.0	71.0	31	63.0	37.0	27	28.0	72.0	25
3 yr	30.8	69.2	13	38.5	61.5	13	50.0	50.0	16
4-5 yr	72.7	27.3	44	62.1	37.9	29	56.5	43.5	23
AS									
2 yr	63.0	37.0	27	57.2	42.8	28	16.7	83.3	12
3 yr	44.4	55.6	9	40.0	60.0	10	57.1	7	7
4-5 yr	76.9	23.1	26	66.6	33.3	18	66.6	33.3	6

August. Again, the numbers of recoveries of this age-class within the 100 km zone decreases sharply in October. When the spatial distribution of recoveries of second and third year birds are plotted and compared with the distribution of first year birds in autumn (Fig. 6) it appears that the same areas outside the 100 km zone but north of 59°N are used. The distribution of recoveries of GF birds found > 100 km from the natal site in October (Fig. 9) illustrates that second year birds have shifted towards the south, while the majority of the recoveries concerning other ageclasses still come from northern areas (compare also Fig. 7). Second year herring gulls from both the GF and AS migrate considerably earlier than any other ageclass studied here. More than 80 % of the second year birds from the AS have migrated to the south in October, in contrast to 10 % of the first year birds. About 52 % of the second year birds from the GF are found south of 59°N in October, in contrast to 14 % of the first year birds. The number of adults encountered south of 59°N is still lower than the figures for juveniles. Older, 4-5th year herring gulls seem to migrate somewhat earlier than juvenile and adult gulls, but the few third year birds found do not conform with this pattern.

The use of northern areas > 100 km from the natal colony by immature birds decreases rapidly in autumn. In October nearly all immature birds have disappeared from the areas still exploited by both first year and adult gulls. Most second year birds have migrated to the south, while 4-5th year old gulls have gathered near their natal area.

3.4 Areas exploited in autumn

In autumn, coastal Finnish herring gulls partly exploit the same resources as those used by breeding birds in the breeding season, and partly move into areas where the breeding period exploitation is lower (the inland areas used). The recoveries plotted on a map show concentrations around urban centres, possibly partly due to greater changes in recovery, but also due to the exploitation of urban resources, such as dumps.

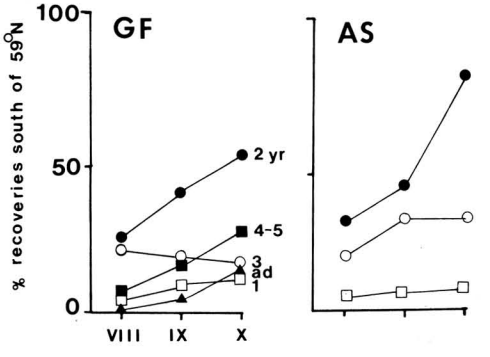

Fig. 7. The proportions of herring gulls of different ages that have "migrated". The proportion is expressed as the percentage fraction of the monthly total encountered south of 59°N. Note that it is very probable that due to varying probabilities of recovery, the precentage fraction does not show the actual proportion of birds "migrated". It is assumed that the probability of recovery does not vary between ages.

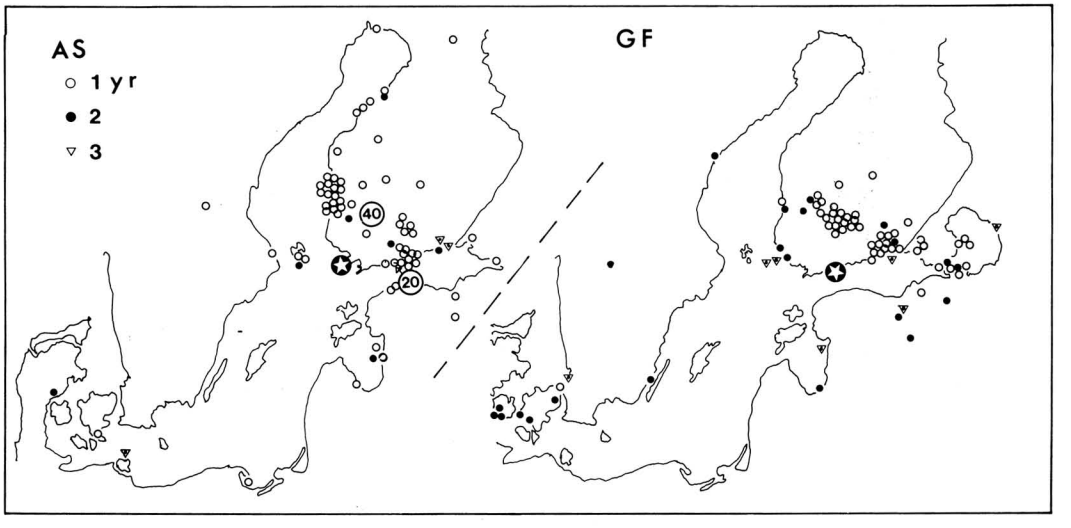

Fig. 6. Spatial arrangemnt of recoveries of three ageclasses of herring gulls from the AS and GF in August in relation to natal colony (star). Only recoveries > 100 km from natal colony plotted.

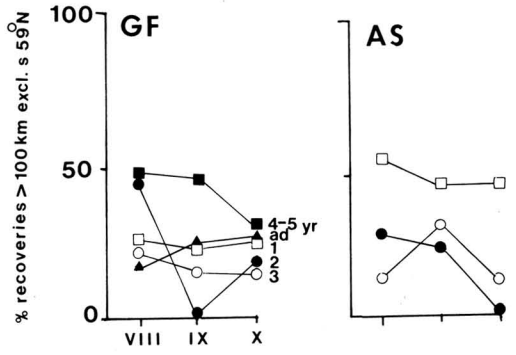

Fig. 8. Exploitation of areas > 100 km from the natal colony in late summer (includes only recoveries north of 59°N) and early autumn in herring gulls of different ages. Compare with Fig. 7.

3.5 Exploitation of dumps

The success and increase in the herring gull population during the 20th century has been linked to increasing amounts of cultural waste (garbage and fish offal) provided by man (Burger 1977, Harris 1970). Ample, dependable food resources such as dumps may be of particular importance for juveniles in autumn, and for all age-classes in winter (Drury & Smith 1968). Monaghan (1978) has reported extensive use of dumps by adult herring gulls in particular in winter, but she concluded that on the British coast, dumps did not constitute the only or even the major source of food. In SW Sweden high numbers of herring gulls fed on dumps in winter, but they also favoured the original feeding habitat such as the littoral zone in the archipelago whenever the water level permitted its exploitation (Kihlman & Larsson 1975). In Finland no regular tidal fluctuations occur, and the water level tends to be higher in autumn than in summer. It seems likely that, due to this, herring gulls in Finland use dumps extensively. In 1979 one of us (MK) counted the numbers of herring gulls present on the largest dump in the GF area (Helsinki dump). On each occasion the dump was observed thoughout the day, and the highest number present was recorded. Up to 2000 first year birds were seen on single occasions ($\bar{x}$ = 676, SD = 492, 17 counts between August 1 and October 5), but the number of fledglings had been greatly reduced in the archipelago through egg manipulation that season (Kilpi 1980). The maximum loss of one year old birds within the GF was estimated at c. 12 000 (Kilpi 1980). Gulls of other age-classes were present in large numbers. Adult-plumage birds reached a peak on August 21 with 6000 individuals present ($\bar{x}$ = 3590, SD = 1130, 18 counts), representing roughly a third of the breeding population within a radius of c. 30 km of the dump (see map in Kilpi et al. 1980). All age-classes indentifiable in the field (Grant 1982) were recorded feeding on the dump. In 1979, 108 previously ringed adults and 55 first year gulls were caught with the aid of a trap. Most of these birds originated from colonies close to the dump (Fig. 10). Only 4.0 % of the adults caught had originally been ringed in colonies > 100 km distant from the dump, whereas 20.0 % of the juveniles originated from these distances. Häkkinen &Nummelin (1980) trapped herring

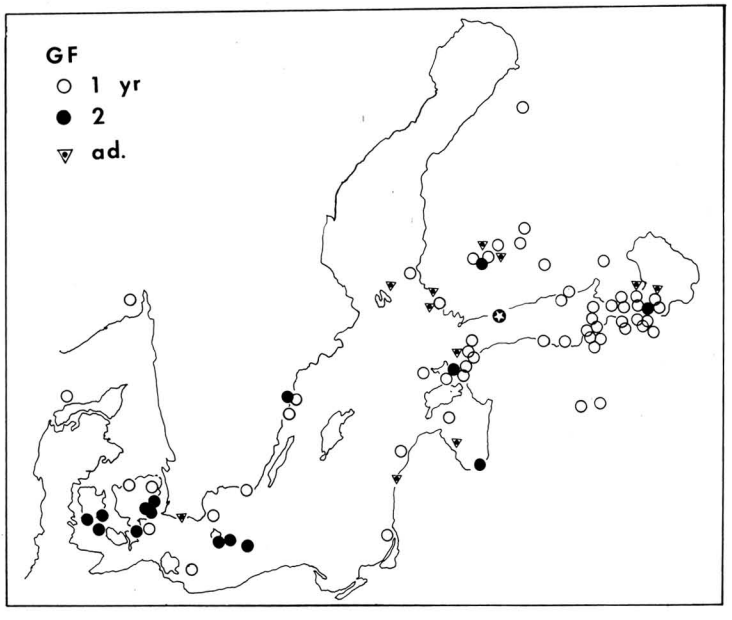

Fig. 9. Spatial distribution of recoveries > 100 km from natal colony in October for herring gulls from GF.

gulls on a dump in the AS area, and also found that most gulls caught originated from within c. 40–60 km of the dump. They found equally low proportions of gulls from more distant (> 100 km) areas. Though the data is biased by local variations in ringing efforts, it does indicate that in late summer and early autumn the primary users of a particular dump are local breeding birds. The data also indicates that juveniles move more readily than adults.

4. Discussion

4.1 Dispersal from the colonies by juvenile and adult herring gulls

Burger (1980, 1981) has argued that adult herring gulls may feed and care for their chicks for up to at least six weeks after the young have fledged. In this case, this would imply that most, if not all, juvenile birds will accompany their parents to suitable survival habitats in early autumn. These survival habitats may or may not include the breeding colony. Prolonged parental care would be favoured by an ample food supply, in which case the parents may feed large young without stress (Bruger 1981). If, on the other hand, there is a shortage of food, this may lead to rapid dispersal in juveniles and possibly also adults (Lack 1968 b).

No precise data on the timing of break-up of the families has been collected on the Finnish coast. Flocks of purely juvenile birds can be seen already in early August, and juveniles both fed independently and sometimes formed roosting flocks away from the adults on the Helsinki dump in August and September 1979 (Kilpi unpubl.). It has been established in several species of *Larus* gulls that young birds are inferior in foraging (Burger & Gochfeld 1982) and that they also are socially inferior to adults (Ulfstrand 1979). Several causative factors apparently operate with respect to post-fledging dispersal in juvenile birds.

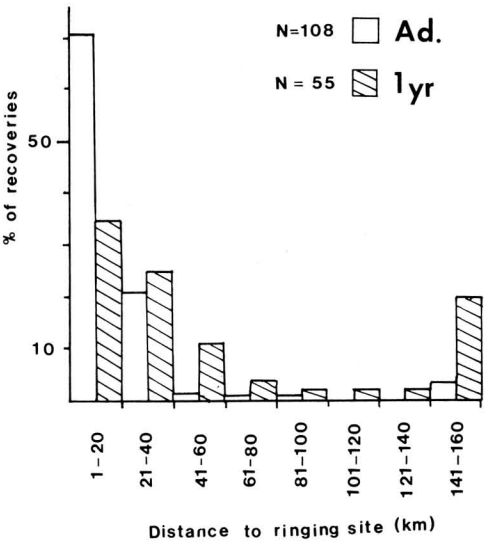

Fig. 10. Distance from ringing-site to recapture site for adult and first year herring gulls caught at the Helsinki dump in August–October 1979. The main breeding colonies lie some 20–30 km from the dump (Kilpi et al. 1980). Most of the trapped birds have been ringed in these colonies. The colonies 141–160 km from the dump site are the main breeding colonies in the AS area.

We suggest on the basis of our data that adult herring gulls in autumn only travel short distances to suitable feeding grounds. On the Finnish coast such sites are usually dumps, where birds congregate in large feeding flocks. The extent of the dispersal is primarily affected by the location of these dumps.

If adults tend to prefer feeding sites close to the main breeding colonies, this may well lead to a situation where juveniles are excluded from these resources, and thus forced to disperse over wider areas. No behavioural data verifying the exclusion of young from dumps by adults are available for this study.

Table 5. Proportions (%) of different age-classes in three samples of herring gulls caught on dumps. The unringed birds on the Helsinki dump have been aged according to plumage characteristics (Coulson et al. 1982, Grant 1982).

	Combined Turku dump sample 1978–79, all ringed birds		Helsinki dump sample 1979 unringed birds		Helsinki dump sample 1979 ringed birds
Age	August	September	August	September	August+September
2 yr	5.0	14.3	4.4	9.3	none
3 yr	5.0	14.3	3.0	6.5	2.0
4 yr	13.5	6.3	25.9	18.6	4.9
5 yr	14.9	12.7			9.0
>5 yr	61.7	52.4	66.6	65.6	84.1
Total *N*	141	63	405	183	101

Yet another possibility is that dispersing juveniles follow dispersing adults. Since adult recoveries in autumn are largely lacking from several areas much exploited by juveniles, we suggest that juveniles in fact disperse more readily, and autumn dispersal is age-dependent. The data suggests that juveniles in areas where human densities are lower (AS and S) disperse more readily than GF juveniles which live close to large urban centres. The extent of dispersal is affected by the location of food resources.

It is also possible that juvenile dispersal in autumn has in some circumstances had survival value, and dispersive tendencies may be part of a generatically controlled programme for migrational behaviour. The fact that juveniles in their first autumn do not moult, and thus have a complete plumage, enables the adoption of a more mobile strategy.

Adults, on the other hand, moult in autumn. A complete moult in the herring gull takes 4 months, it increases the energy demands of the bird, and loss of flight feathers hampers flying (Harris 1971, Verbeek 1977). Most adults caught on the Helsinki dump in 1979 were in a state of heavy moult. At least hypothetically. a more sedentary strategy would seem advantageous during this stage.

It has previously been argued for "non-migratory" populations of herring gulls (Moore 1976, Parsons & Duncan 1978, Southern 1980) that juveniles tend to move over larger areas than adults. Finnish herring gulls in autumn are essentially "non-migratory" and seem to conform to the same pattern.

4.2 Movements of immature birds

Of the immature age-classes, the second year birds exhibit a movement pattern in autumn which is very different from both juvenile and adult movements during the same period. Older immature birds bear a greater resemblance to adult birds in their movements. In late summer second and third year birds exploit areas outside the main breeding area of the populations from which they originate. Second year birds move out of these areas as soon as the influx of dispersive juveniles takes place, and they move still further towards the wintering grounds considerably earlier than any other age-class. Second and possibly also third year birds may be excluded by adults from the favoured dumps in autumn, but the exclusion may also operate during the breeding season, and the occurrence of immature birds in certain areas in early autumn may be a consequence of this. Parsons & Duncan (1978) found that second year birds tended to cover even longer distances than juveniles. In this study, the 4–5th year birds, which have a basically adult plumage, seem to behave like adult birds in autumn.

Immature birds, at least second and third year birds, seem to moult earlier than adults in autumn. (Harris 1971, Kilpi unpubl.). In consequence they have a renewed complete wing earlier and may be more mobile.

4.3 Spatial segregation

There seems to be a reasonably clear segregation of different cohorts of herring gulls in autumn. The main tactics used by most adults is exploitation of food resources close to the breeding colony. Juvenile gulls use this area to some extent, while a proportion of the birds disperse further, possibly due to exclusion by adults. Second year birds in basically brown plumage (see Grant 1982) exploit areas outside that used preferentially by adults, upon which they shift to the wintering area when the influx of dispersing young starts. Third year birds and especially 4–5th year birds use the same areas as adults.

4.4 Emigration in adults

We have assumed that adults found during the breeding season were actually breeding birds in that location. Whether we are dealing here with natal or breeding dispersal (see Greenwood 1980) is not known. The areas into which the apparent emigration takes the adults coincide with areas of current colonisation (i.e. the interior of the country) and also with the areas exploited by immature birds during the breeding season (Kilpi & Saurola in prep.). Suitable survival habitats located by immature birds may lead to the establishment of a breeding population in that area.

4.5 Dispersal versus migration

There is no sharp distinction between migration and dispersal in the non-breeding season. Essentially, both are habitat shifts (see also Alerstam & Högstedt 1982). A young Finnish herring gull starts its life by dispersing in autumn, then migrates to its winter quarters, migrates back, and then disperses into suitable survival habitats. The migration is only obligatory because of the lack of opportunities for survival on the Finnish coast in winter.

Burger (1981) recently summarized the movement patterns of different herring gull populations, finding two main types: long distance and

short distance. We do not question the distinction as such, but wish to point out that she based this distinction upon the location of the birds in winter. This blurs the adaptive significance of dispersal such as we have treated it here. During autumn, Finnish herring gulls are short-distance dispersers, during winter they are long-distance dispersers. In autumn the dispersal seems to produce spatial segregation between age-classes. As far as we know (Kilpi & Saurola in press) these herring gulls winter within the same area. Hence, habitat shifts induced by pronounced seasonality should not be confused with resource partitioning within an area where theoretically all birds can survive.

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