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# Dispersal patterns of Western Gulls (Larus occidentalis) from southeast Farallon Island

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DISPERSAL PATTERNS OF WESTERN GULLS (LARUS OCCIDENTALIS)

FROM SOUTHEAST FARALLON ISLAND

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ABSTRACT

DISPERSAL PATTERNS OF WESTERN GULLS FROM
SOUTHEAST FARALLON ISLAND

by Laurence B. Spear

During 1978-1981 I studied age- and sex-related dispersal and foraging patterns of Western Gulls (*Larus occidentalis*) that breed on Southeast Farallon Island, California. Most adults were sedentary and foraged primarily on oceanic food during all seasons except fall, when human refuse was of major importance. Fall was the only period when adults did not maintain breeding territories. During the breeding season many subadults moved north to areas where oceanic productivity is high. During fall/winter most moved south to the Gulf of the Farallons/San Francisco Bay Area. Dispersal patterns of first-year birds varied markedly between years, apparently as a result of annual differences in oceanic productivity. The consistency of movement patterns of other age classes resulted from an age-related increase in fidelity to foraging locations. Males were more sedentary than females, probably because they are responsible for securing and holding breeding territories.

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# INTRODUCTION

Studies of age- and sex-related foraging and dispersal patterns are essential for understanding population regulation in larids (Lack 1954, 1968). The required studies are of additional interest because of the trophic plasticity of gulls; individuals may be sedentary or mobile, specialized or diverse in their foraging habits. Larids have been the subject of many studies that have produced much information on movements of different age-classes (reviewed by Southern 1980, Kilpi and Saurola 1983, Coulson and Butterfield 1985), and on feeding ecology, particularly of adults during the breeding season (reviewed by Ingolfsson 1967, Spaans 1971, Mudge and Ferns 1982, Sibley and McCleery 1983). The possibility of sex-related differences has received little attention, however (but see Monaghan 1980, Pierotti 1981, Sibley and McCleery 1983),and feeding ecology of subadults is not well known because they tend to disperse widely from the natal area. Finally, data from band returns amass too slowly to provide information regarding possible interannual variation in movement, which could provide insight regarding ecological factors that affect age/sex groups. Although a systematic study of individually marked gulls of known-age and sex could increase knowledge of these subjects, certain conditions must exist for a study of this type to succeed. First, the population must be large and well represented by marked, known-age birds. Second, the marked birds must be of known sex. Finally, the entire range of the population must be accessible at all seasons.

Western Gulls (*Larus occidentalis*) breeding on Southeast Farallon Island (SEFI), 48 kilometers west of San Francisco, California, satisfy these requirements. This population contains approximately 25,000 breeding adults, or about 40% of the world's population of the species (reviewed by Spear et al. 1986). Each year since 1971 approximately 2,000 gull chicks (10-15% of the young produced annually on SEFI) have been banded with a metal U.S. Fish and Wildlife Service band on one leg and a polyvinyl- chloride (PVC) color band on the other. A different color or leg combination was used each year. These gulls can be sexed within 95% confidence limits by observing differences in body size (see Appendix). Finally, the population range includes the narrow coastal zone of California, Oregon and Washington (Sanger 1973, Coulter 1975, Harrington 1975), which is accessible in all but a few sections during all seasons.

# STUDY AREA AND METHODS

The study area included the California (CAL), Oregon (ORE) and Washington (WA) coasts (Figure 1). I divided this region into 13 zones. Each zone extended about 160 kilometers (not including perimeters of bays) except zone 1, which included 350 kilometers of coast, and zone 8, which encompassed an 80 kilometer radius (= foraging range of Western Gulls; Hunt et al. 1979) around SEFI and included 130 kilometers of coastline. I defined five coastal "regions" including WA, zone 1; ORE, zones 2-4; NO CAL, zones 5-7; CE CAL, zones 8-10, including the San Francisco Bay area (SFBA); and SO CAL, zones 11-13.

The California Current flows along the coast from southern Washington to Pt. Conception (Figure 1). It is one of the four most productive current systems in the world (Thompson 1981). The area of highest productivity lies from the Gulf of the Farallons to central Oregon (Chelton 1981, Parrish et al. 1981). Between Pt. Conception and the Tijuana River the current flows offshore, and coastal waters within this region are less productive than more northern waters (Bernal 1981, Brinton 1981, Chelton 1981). Three "oceanographic seasons" occur in the California Current; the upwelling season (April-August) is most productive, the oceanic season (September-November) is least productive, and the "Davidson

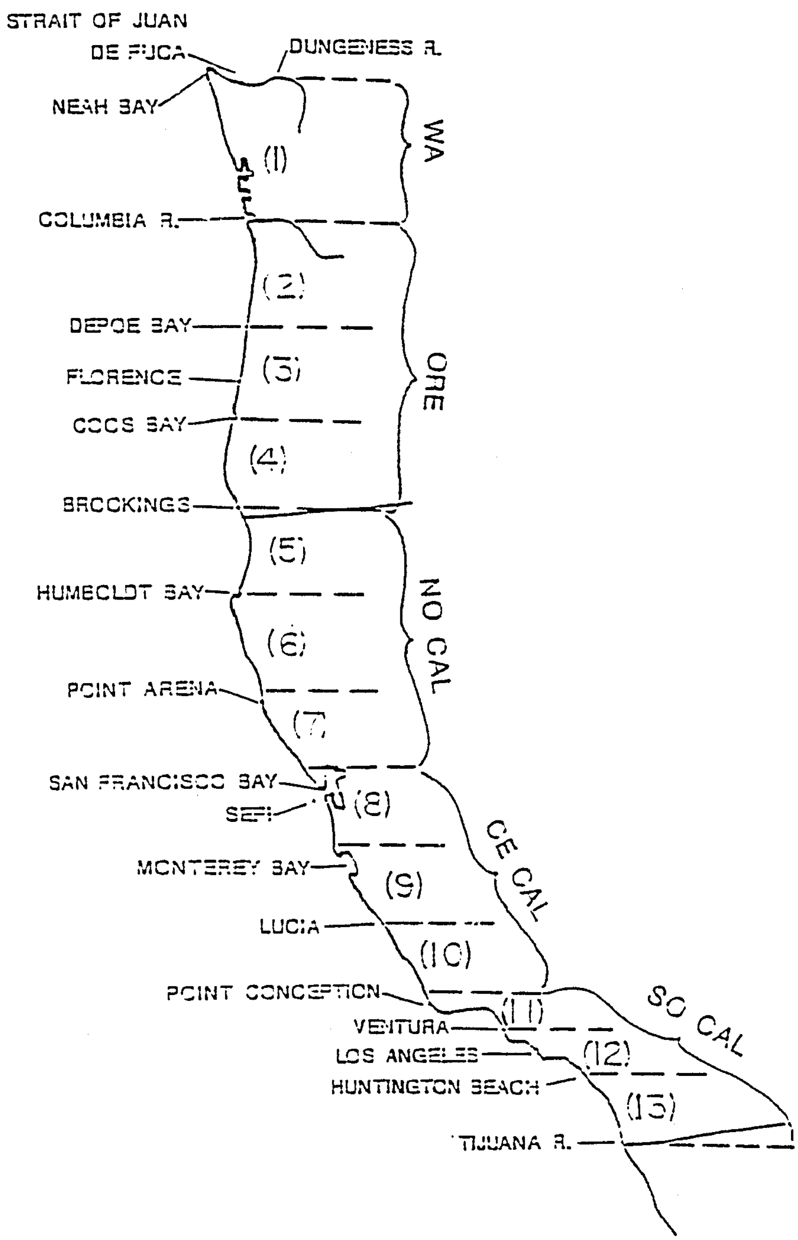


Figure 1. Study area and demarcation of zones and regions.

Current" season (December-March) is of low to moderate productivity (Bolin and Abbott 1963). Although timing of the three seasons is fairly predictable, marked interannual variation in plankton volume occurs (Bolin and Abbott 1963, Chelton 1981, Chelton et al. 1982, McLain and Thomas 1983).

The availability of human refuse and offal has affected gull population size and age structure for the past several decades (reviewed by Mudge and Ferns 1982). Therefore, between September 1979 and May 1981, I recorded the volume of refuse being deposited at each coastal dump between the Columbia and Tijuana rivers (Figure 1). SO CAL dumps received 49% of all refuse deposited, CE CAL dumps received 40%, NO CAL dumps received 5%, and ORE dumps received 6%. SFBA dumps (included in the CE CAL region) received 30% of all refuse deposited. The amount of garbage available was stable from September 1979 to July 1980 but declined by 18% between August 1980 and February 1981, when one SO CAL dump, two SFBA dumps, and one ORE dump were relocated inland. Relatively few gulls foraged at fish processors south of Monterey Bay. The volume of offal provided by commercial fisheries operating between Monterey and Neah bays increased by about 5% between 1978 and 1981 (Pac. Mar. Fish. Comm. Repts. 1979-1981,1983, CalCOFI Repts. 1980, 1982, 1983).

I defined the four calendar seasons as spring, April through June; summer, July through September; fall, October through December; and winter, January through March. Relative to oceanographic periods, spring and summer coincide with the productive upwelling season, fall and winter with the less productive oceanic and Davidson Current seasons. To study gull movements relative to oceanographic conditions, I set the birth date of SEFI Western Gulls at 1 April, although most eggs hatch in June (Coulter 1973). Western Gulls attain adult plumage in their fourth year; however, SEFI gulls average about five years of age when they first breed (Spear et al. 1987). Therefore, I considered fourth-year birds separately from older birds in most analyses.

In September 1978 I began monthly censuses of SEFI Western Gulls at 138 locations between the Columbia and Tijuana rivers (Figure 1). From July 1979 through May 1981 (excluding June 1980), 326 locations were censused monthly. Locations included all fishing ports, coastal dumps and accessible creek and river mouths. Western Gulls apparently prefer fresh water for drinking and bathing, and congregate at the latter locations (Spear, pers obs.). During spring/summer I also censused 49 sites on the outer coast of Washington, and from the Strait of Juan de Fuca to the Dungeness River. Each census included an age-class count of banded SEFI birds, a count of all large larids (=pink-legged gulls), and determination of the ratio between banded and nonbanded individuals. Censuses at a given location were usually conducted during the same time of day, and more important locations were censused when the most gulls were expected.

The numbers of gulls inspected for bands varied with respect to the total present at different locations. To correct for this inconsistency I estimated total numbers of banded SEFI birds by multiplying the total number of large larids by the percentage of banded SEFI birds seen at respective locations. After censuses were completed I read band numbers with a 20-45x spotting scope. Of 5,580 individuals recorded, 43% were sexed by observing size differences (see Appendix) and 30% were sexed by observing courtship feeding and copulatory behavior on SEFI through 1986.

The number of banded SEFI birds censused was termed a "count," and the recording of a bird whose band was read is termed a "sighting." An individual sighted and then resighted during two contiguous seasonal periods was termed a "resightee," and "sedentary resightee" refers to a gull resighted within 80 km of the location where initially sighted.

I made daily censuses (weather permitting) of SEFI clubs during the first or second week of each month from March 1979 through June 1980, using the same method as for coastal censuses described above. The term "club" refers to a congregation of nonbreeding gulls near a colony

(Tinbergen 1953). Band-reading was also conducted at the clubs. To examine club attendance by different individuals I read bands at one important SEFI club several hours during evening (when largest numbers were present) 3 to 4 days each week from 14 April through 7 July 1979. Previous band-reading at several SEFI clubs had shown that individuals usually loafed at the same club site (Spear, pers obs.). It was possible to read the bands on the majority of birds each evening and thus monitor presence of individuals. Because all bands were not read each evening, I grouped data into 3-day periods.

To examine colony attendance by breeding adults I (and Farallon biologists and volunteers) made daily censuses (weather permitting) of a section of the SEFI colony from June 1979 through June 1981. To examine timing of dispersal and territory reoccupation by sexes of breeding adults, I determined departure and arrival dates of 180 banded gulls (91 males and 89 females that had bred in 1979) during censuses at known territories on the first or second week of each month from June 1979 through June 1980. The initial sample included 212 birds; gulls not seen during 1980 were excluded from the sample.

To examine seasonal movement I plotted initial sightings and resightings of individuals and calculated movement direction, percent of birds that were sedentary, and mean distance traveled by nonsedentary birds. Data from sightings on SEFI were included in the above analyses if either the initial sighting or the resighting occurred on the mainland.

At each loafing site I classified foraging habitat used by gulls according to four types: 1) dumps; 2) fishing ports; 3) oceanic habitat including beaches, rocky intertidal, estuaries, tideflats and offshore (including fishing and shipping operations); and 4) general habitat, including sites that appeared to represent oceanic habitat but which were less than 50 kilometers from dumps or fishing ports. The latter habitat was defined because band-reading demonstrated that gulls foraging at habitat types 1-3 sometimes loafed together if foraging locations were less than 50 kilometers apart. Loafing sites less than 50 kilometers from dumps or fishing ports were classified as representing oceanic habitat if band-reading showed that gulls using the sites did not forage at the dumps or ports.

All confidence limits are reported as the standard error (SE), and methods of statistical analyses are from Zar (1974). Unless otherwise stated, G tests were used.

# RESULTS

## Seasonal Abundance On The Coast

After the initial dispersal from SEFI in August, monthly counts of first-year birds on the coast varied insignificantly ($P > 0.05$, Figure 2). Differences in monthly counts varied significantly in each of the other four age classes ($P < 0.001$). In second- and third-year gulls this was due to higher counts during spring/summer than during fall/winter. The decrease in birds seen during the latter period was significantly greater ($P < 0.001$) than expected as a result of mortality and band loss (see Spear 1980, Spear et al. 1987). In fourth-year birds the difference in monthly counts was mainly due to higher counts during September and October, and lower counts during December through April. The pattern of variation in monthly counts of fifth- through tenth-year gulls was similar to that of fourth-year birds, except that the period of high counts extended from August through October. During the latter period counts averaged 3 times higher than during December through April. Of 734 known breeders (4 years or older, all had been sighted on SEFI breeding territories); 238 (32%) and 284 (39%) were sighted on the coast during August through October of 1979 and 1980, respectively. Resighting rates, as a function of the total sighted, indicated that 60-80% of the breeding population

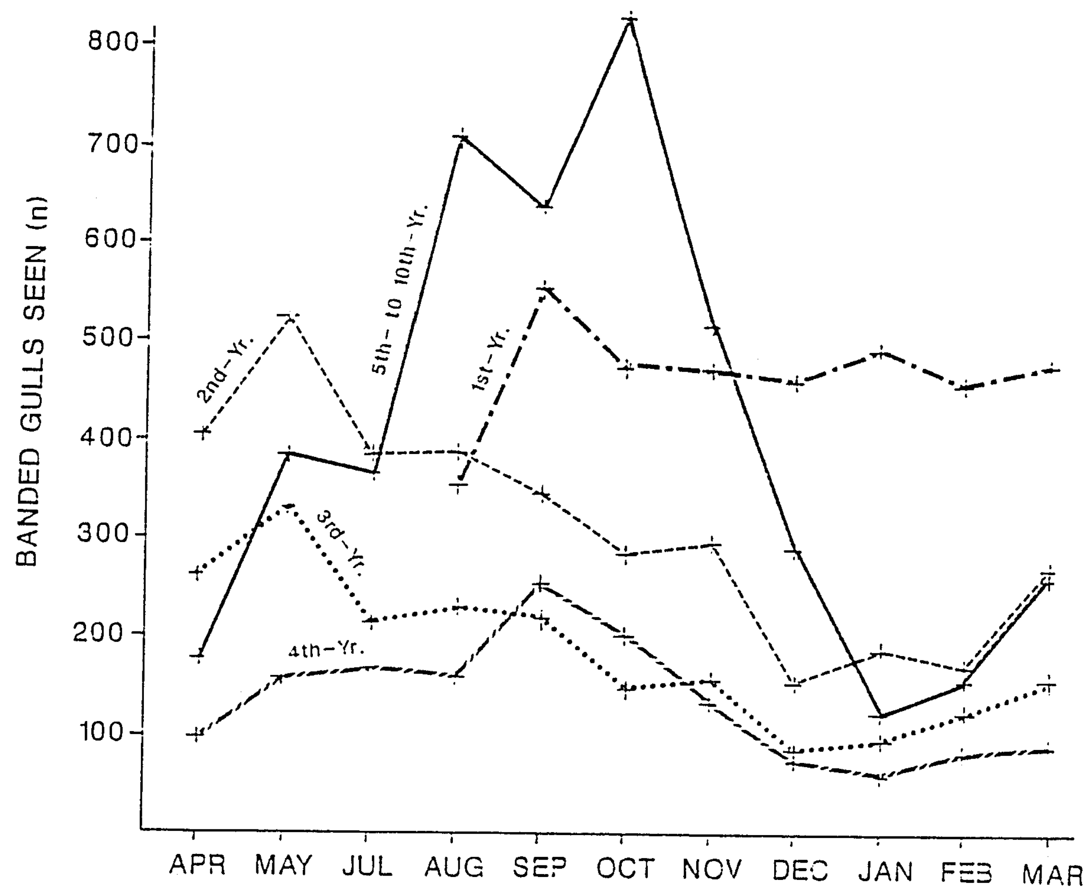


Figure 2. Monthly count of 5 age classes of banded Farallon Western Gulls censused on the coast (July 1979 to May 1981). Counts are given as the total for the two years. (No censuses were made during June.)

foraged on the coast each year during that period. In contrast, during December through April of 1980 and 1981, only 97 (13%) and 78 (11%), respectively, of the 734 breeders were sighted on the coast, and resighting rates indicated a maximum of 20% foraged on the coast.

Seasonal Distributions and Movements

Fledglings sighted on consecutive days when dispersing from SEFI averaged 81 ± 9.1 kilometers/day (range = 23-165 kilometers/day, n = 21). One fledgling traveled 139 kilometers/day for a 3-day period; another individual averaged 98 kilometers/day for 7 days. These are minimum rates because exact departure and arrival dates were not known.

All age classes were distributed significantly farther north during spring/summer than fall/winter ($P < 0.05$, Figure 3). A significantly lower proportion of first- and second-year birds were sedentary during spring/summer than fall/winter, but in this respect seasonal variation was insignificant among older birds (Table 1). Distances traveled by nonsedentary second- and third-year birds were significantly greater during spring/summer than fall/winter; however, seasonal difference in travel distances of first-year and fourth- through tenth-year birds was insignificant.

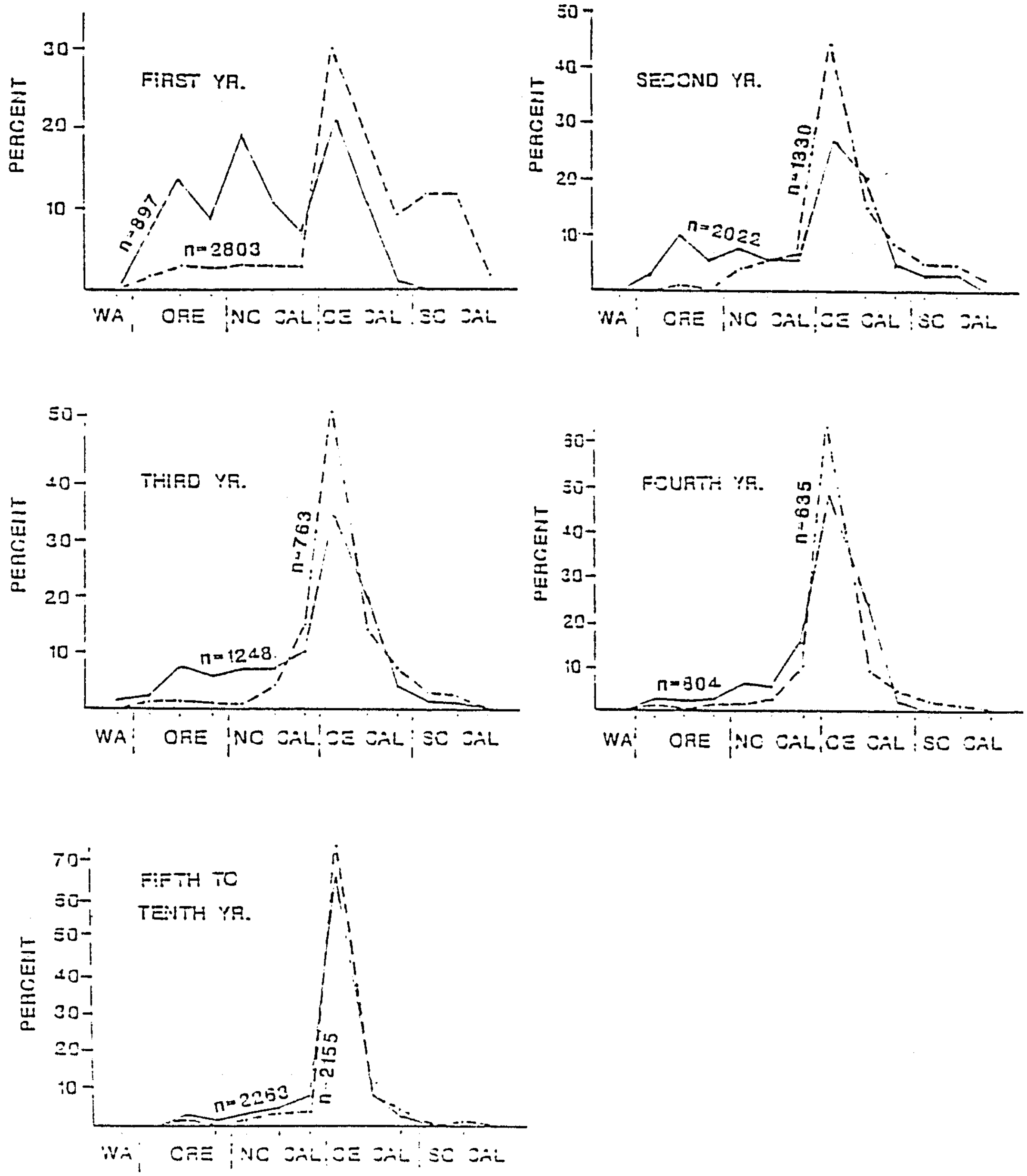


Figure 3. Seasonal distributions of 5 age classes of Farallon Western Gulls (1979-1981). Solid line = spring/summer, dashed line = fall/winter. See Figure 1 for location of zones (1-13) and regions.

Table 1. Movement of Farallon Western Gulls on the mainland coast with respect to season and age.

| Age-class and period | No. of resightees[a] (n) | Percentage moving north/south | Percentage sedentary[b] | Distance traveled by nonsedentary birds (X ± SE, in km) |
|---|---|---|---|---|
| First-year | | | | |
| Summer | 897 | 64/15 | 21 | 484 ± 9.7 |
| Autumn/winter | 501 | 10/43*** | 47 | 509 ± 26.6 NS |
| Second-year | | | | |
| Spring/summer | 381 | 39/05 | 56 | 594 ± 33.3 |
| Autumn/winter | 225 | 11/20 | 69 ** | 368 ± 29.8 ** |
| Third-year | | | | |
| Spring/summer | 160 | 26/07 | 66 | 447 ± 44.8 |
| Autumn/winter | 121 | 7/19 | 74 NS | 284 ± 34.5 * |
| Fourth-year | | | | |
| Spring/summer | 122 | 19/13 | 69 | 293 ± 31.9 |
| Autumn/winter | 127 | 12/13 | 75 NS | 265 ± 26.2 NS |
| Fifth-tenth Year | | | | |
| Spring/summer | 290 | 13/09 | 78 | 260 ± 18.4 |
| Autumn/winter | 285 | 8/10 | 82 NS | 270 ± 22.7 NS |

[a] All first-year gulls counted during summer were considered resightees. Initial sightings were in zone 8 (SEFI); gulls resighted in zone 8 were considered sedentary.

[b] Asterisks denote a significant difference between adjacent values. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = no significant difference ($P > 0.05$). Comparisons between means were by Mann-Whitney U-test.

Oceanic conditions during spring/summer 1978 were unusual (see Discussion). Therefore, I compared census results from September 1978 (immediately following post-breeding dispersal) with those of respective locations in September 1979 and 1980. Only the distributions of first-year birds differed significantly during the 3 years ($P < 0.001$, Figure 4). This was mostly due to a more southerly distribution in 1978 and a more northerly distribution in 1979.

Counts of third-year gulls were 40% lower than those of second-year birds (Table 2). The difference was greater than expected from band loss and mortality ($P < 0.001$), which are expected to cause a 25% decrease between the second and third year (Spear 1980, Spear et al. 1987). Between-year variation in counts of other age classes was not greater than expected ($P > 0.05$).

The average distance that SEFI gulls ranged from the island decreased significantly with increase in age in all age classes (Table 2). This resulted from the fact that the proportion of sedentary birds increased significantly with age between all age classes except third- and fourth-year birds and flight distances of nonsedentary birds decreased significantly from the second to the fourth year.

A significant preponderance of females was found in second- and third-year birds sighted on the coast (Table 3). Differences between the sexes of first-year birds were

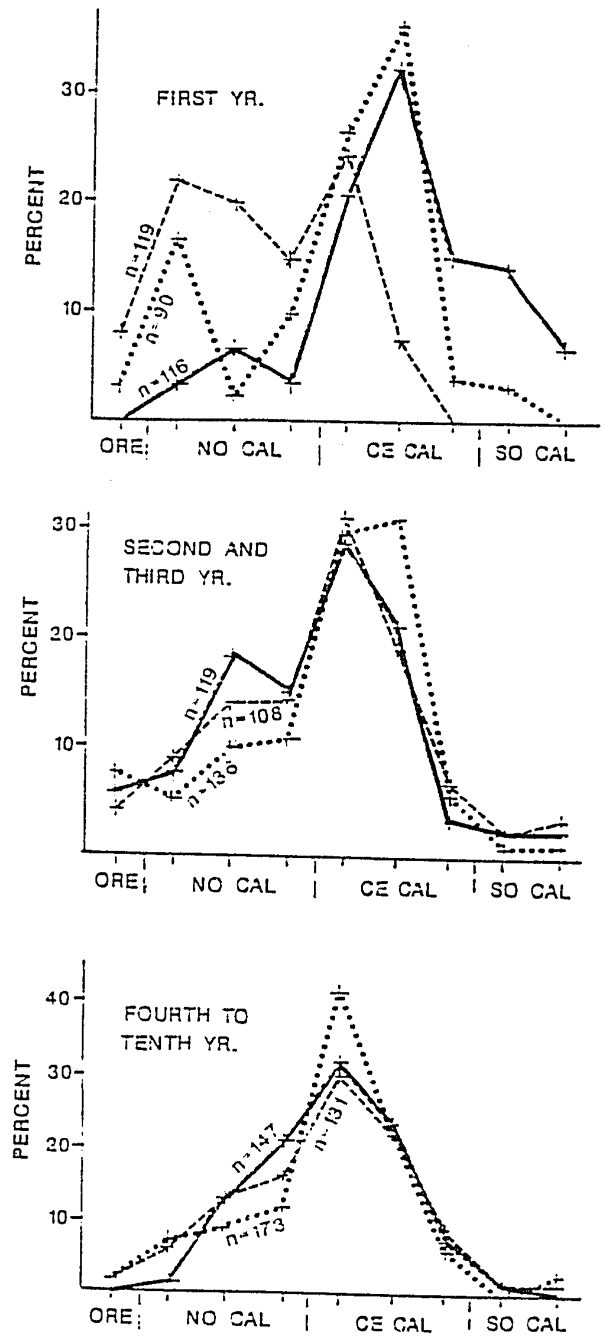


Figure 4. Distribution of 3 age classes of banded Farallon Western Gulls between Florence, Oregon, and Los Angeles, California (September 1978-1980). Solid line = 1978, dashed line = 1979, dotted line = 1980. See Figure 1 for location of zones (4-12) and regions.

Table 2. Movement patterns of Farallon Western Gulls by age-class.[a]

| Age class | Total censused (n) | Distance from SEFI (km) X ± SE | No. of resightees (n) | Sedentary birds (%) | Distance traveled by nonsedentary birds (km) X ± SE |
|---|---|---|---|---|---|
| 1st yr. | 3,700 | 333 ± 4.3 | 1,398 | 30 | 490 ± 10.4 |
| | | *** | | *** | NS |
| 2nd yr. | 3,352 | 286 ± 4.6 | 606 | 61 | 527 ± 24.6 |
| | | * | | * | * |
| 3rd yr. | 2,011 | 232 ± 5.3 | 281 | 69 | 387 ± 30.9 |
| | | *** | | NS | ** |
| 4th yr. | 1,439 | 156 ± 4.4 | 249 | 72 | 280 ± 21.2 |
| | | *** | | * | NS |
| 5th-10th yr | 4,417 | 123 ± 2.1 | 575 | 80 | 264 ± 17.6 |

[a] Asterisks denote a significant difference between adjacent values. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). NS = no significance difference ($P > 0.05$). Comparisons between means were by Mann-Whitney U tests.

Table 3. Movement patterns of Farallon Western Gulls by sex and age class.[a]

| Age class | No. of sightings (n) | | | Distance from SEFI ($\bar{X} \pm SE$, in km) | | |
|---|---|---|---|---|---|---|
| | Males | | Females | Males | | Females |
| First-year | 831 | NS | 792 | 319 ± 9.0 | NS | 331 ± 9.7 |
| Second-year | 758 | *** | 955 | 262 ± 8.9 | *** | 320 ± 9.4 |
| Third-year | 432 | ** | 573 | 196 ± 9.4 | *** | 299 ± 11.7 |
| Fourth-year | 261 | NS | 324 | 131 ± 8.5 | *** | 187 ± 10.9 |
| Fifth-tenth-year | 534 | NS | 524 | 113 ± 5.1 | ** | 150 ± 7.7 |

| Age class | No. of resightees (n) | | Sedentary birds (%) | | | Distance traveled by nonsedentary birds ($\bar{X} \pm SE$, in km) | | |
|---|---|---|---|---|---|---|---|---|
| | Males | Females | Males | | Females | Males | | Females |
| First-year | 316 | 304 | 37 | NS | 33 | 483 ± 23.7 | NS | 519 ± 25.4 |
| Second-year | 200 | 239 | 66 | ** | 52 | 438 ± 35.5 | ** | 593 ± 39.3 |
| Third-year | 101 | 131 | 75 | NS | 65 | 294 ± 40.0 | * | 463 ± 48.2 |
| Fourth-year | 95 | 99 | 82 | * | 69 | 216 ± 27.2 | NS | 325 ± 40.2 |
| Fifth-tenth-year | 235 | 209 | 84 | * | 74 | 227 ± 18.7 | * | 311 ± 26.3 |

[a] Asterisks denote a significant difference between adjacent values. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = no significant difference ($P > 0.05$). Comparison between means were by Mann-Whitney U-test.

insignificant with respect to movement distance from SEFI, proportion that were sedentary, and distance flown by non-sedentary birds. When compared to second- through tenth-year males, females of the respective age classes were distributed significantly farther from SEFI, were less sedentary (not significant in the third-year), and flew longer distances (not significant in the fourth year).

## Colony Attendance By Breeding Adults

Colony attendance by breeding adults peaked at the commencement of egg laying in April (Figure 5). During August and September, colony attendance declined sharply as adults dispersed. Less than 1% of the expected maximum attended territories between late September and early November. In November and December colony attendance increased to 50% of the maximum. The mean post-breeding dispersal dates of breeding males from SEFI (22 August ± 2.2 days, n = 91) differed significantly from those of breeding females (11 August ± 2.1 days, n = 89; $P < 0.01$, by Mann-Whitney U-test), as did dates of breeding territory reoccupation (males: 5 December ± 2.9 days, n = 91, and females: 30 December ± 3.2 days, n = 89, $P < 0.001$).

## Club Attendance at SEFI

Few breeding Farallon gulls occupy SEFI clubs (Spear et al. 1987). Club counts averaged significantly higher in

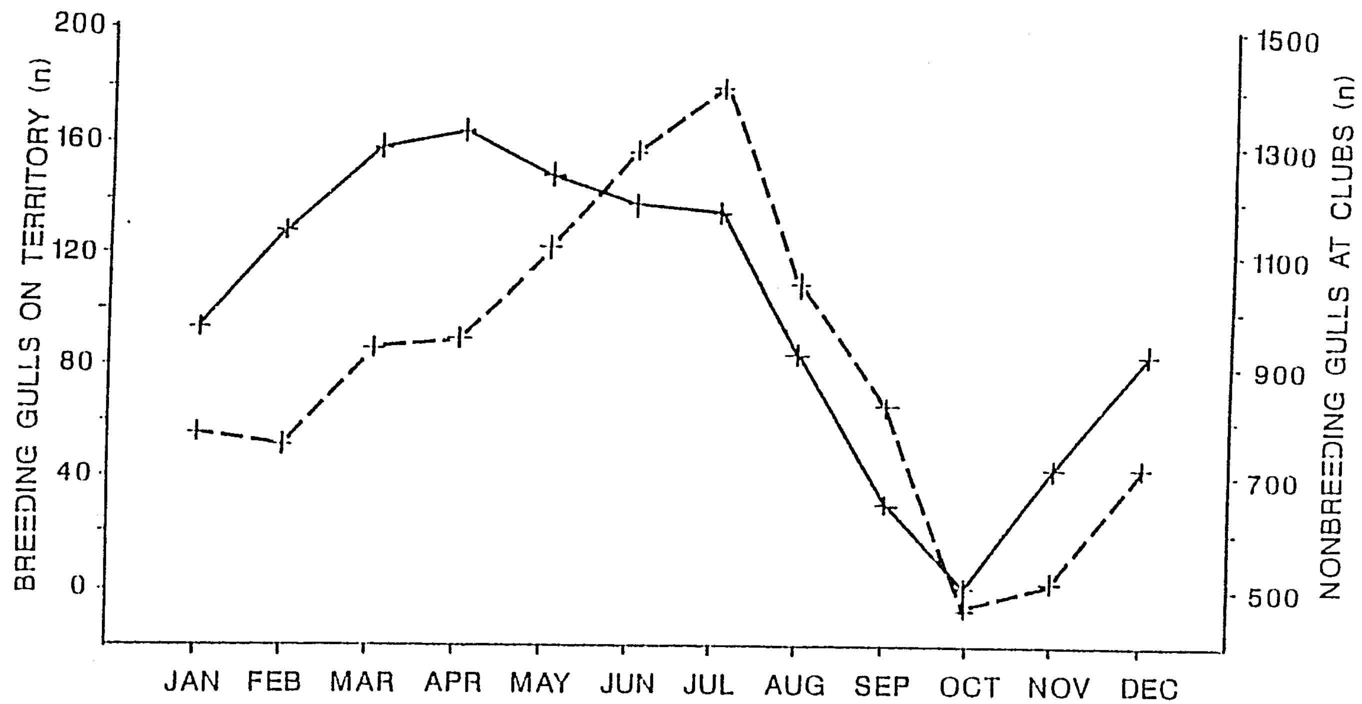


Figure 5. Colony attendance (= mean count; 679 censuses were made) by breeding adult Farallon Western Gulls during 1979-1981 (solid line) and club attendance (= mean count; 100 censuses were made) by nonbreeders during 1979-1980 (dashed line).

spring/summer (1,102 ± 34.3, $n = 52$) than fall/winter (689 ± 39.8, $n = 48$; $t = 3.15$, $df = 98$, $P < 0.01$). This was due to a significant increase in numbers of fourth- through tenth-year birds ($P < 0.001$, Figure 6), notwithstanding the significantly lower counts of second- and third-year birds (grouped; $P < 0.01$). Numbers of nonbreeding adults peaked in July, 3 months after peak colony attendance of breeders (Figure 5). Late arrival by nonbreeding adults at the natal colony also has been found in Herring Gulls (*L. argentatus*; Coulson and Butterfield 1986). Sex ratios (M/F) among first-, second-, third-, fourth- and fifth- through tenth- year birds occupying club sites were 0.70 ($n = 34$), 1.16 ($n = 268$), 0.71 ($n = 361$), 0.58 ($n = 136$) and 0.39 ($n = 151$), respectively. The bias towards females was significant in third- through tenth-year birds ($P < 0.05$). Bias towards either sex was not significant in first- and second-year birds ($P > 0.05$).

Individuals at a SEFI club frequently alternated between several days present and then several days absent (Table 4). As a function of length-of-stay, the number of sightings during two or more successive 3-day periods increased significantly between the second and third year in males, and between the third and fourth year in females. Duration between visits decreased significantly between the third and fourth year in both sexes. Duration between visits was significantly shorter for third-year males than

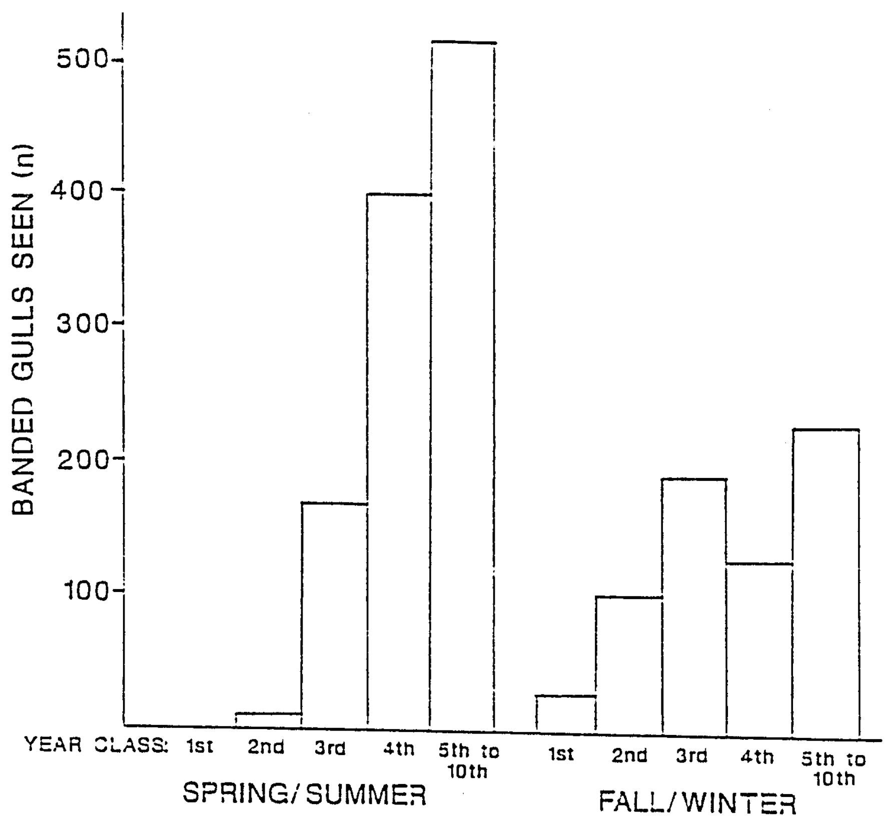


Figure 6. Age-class composition of banded Western Gulls in clubs at SEFI (1979-1980). Numbers of "banded gulls seen" are given as the mean for all censuses made during each seasonal period. Fifty-two censuses were made during spring/summer and 48 during fall/winter.

Table 4. Periodicity of club attendance by Farallon Western Gulls during spring/summer 1979.

| Age class | Gulls Sighted (n) | Total Sightings (n) | Sightings Made During 2 or More Successive 3-day Periods[a] n (%) | Duration Between Sightings Not Made During 2 or More Successive 3-day Periods[b] ($\bar{X} \pm$ SE days) |
|---|---|---|---|---|
| Second-year | | | | |
| Males | 39 | 54 | 9 (17)$^{x}$ | – |
| Females | 33 | 40 | 5 (13)$^{x}$ | – |
| Third-year | | | | |
| Males | 42 | 116 | 57 (49)$^{y,z}$ | $23 \pm 1.4^{g}$ |
| Females | 59 | 120 | 37 (31)$^{x,y}$ | $38 \pm 2.0^{f}$ |
| Fourth-year | | | | |
| Males | 26 | 77 | 49 (63)$^{z}$ | $16 \pm 2.2^{h}$ |
| Females | 36 | 94 | 56 (60)$^{z}$ | $20 \pm 1.9^{g,h}$ |

[a] Values that share a common superscript ($^{x, y, z}$) are not significantly different (G test, $P > 0.05$).

[b] Values that share a common superscript ($^{f, g, h}$) are not significantly different (ANOVA, $P > 0.05$).

third-year females; however, this parameter did not vary significantly between sexes of fourth-year birds.

## Foraging Site Fidelity

Gulls less than three years old often remained at the same foraging location for the duration of a spring/summer or fall/winter period. During spring/summer the percent of first-, second- and third-year birds sighted at the same location during two or more monthly censuses was 32% (n = 897), 42% (n = 840) and 57% (n = 417), respectively. (Values of n include the total sighted at least once). During fall/winter, values for respective age-classes were 44% (n = 1,037), 56% (n = 604) and 47% (n = 292).

Interannual fidelity to foraging sites increased significantly with age through the winter of the third year ($P < 0.05$, Table 5). After their third winter, gulls did not usually switch sites unless the original one was eliminated (e.g. closing of a dump). Locations used by second- or third-year birds during summer and/or winter were often the locations to which respective birds dispersed after they had become breeders (consistency = 90%, n = 121). Most (96%) of the post-breeding adults dispersed to the same location each year. Adults generally remained at respective locations until just prior to reoccupation of breeding territories. Of 203 breeding adults sighted on the coast both in September and in

Table 5. Foraging-site fidelity by Farallon Western Gulls, 1978-1981.

| | Age Class (yr) | | | |
|---|---|---|---|---|
| | 1 & 2 | 2 & 3 | 3 & 4 | 5-10[a] |
| Gulls sighted during 2 consecutive summers (n) | 96 | 135 | 61 | 191 |
| Gulls sighted both summers at same location (<25 km (n)[%]) | 36 (37) | 81 (60) | 48 (79) | 183 (96) |
| Gulls sighted during 2 consecutive winters (n) | 110 | 63 | 39 | — |
| Gulls sighted both winters at same location (<25 km (n) [%]) | 49 (45) | 49 (78) | 37 (95) | — |
| Seasons Combined | | | | |
| Males | | | | |
| Total observed (% showing fidelity) | 55 (45) | 59 (69) | 30 (80) | 68 (97) |
| Females | | | | |
| Total observed (% showing fidelity) | 69 (33) | 80 (66) | 41 (85) | 75 (91) |

[a] Sightings were from 15 August through 15 October.

October, 176 (87%) were seen at the same locations in both months. The remaining 13% were sighted during September in areas outlying the SFBA, and then resighted in the SFBA during October. These adults usually flew directly to coastal foraging sites; gulls sighted on consecutive days when dispersing averaged 109 ± 26.5 kilometers/day, (range = 35-170 kilometers, n = 5). Many gulls dispersed to locations closer to SEFI; gulls using sites less than 100 kilometers from SEFI were not considered in the above calculation. Foraging site fidelity did not vary significantly between sexes of any age class ($P < 0.05$).

Coastal Habitat Preference

Dumps were the most important coastal foraging habitat of all age-classes during all seasons (excluding first-year birds during summer; Table 6). Numbers of first-year birds foraging at dumps increased gradually through the year, while those of second- through tenth-year gulls was highest during summer through midfall, and lowest during late fall through midwinter (Figure 7). For each age class, the percent of gulls found at different foraging habitats varied significantly between seasons ($P < 0.001$, general habitat was excluded from the analyses; Table 6). The differences were due to a greater percentage of each age class foraging at dumps during fall/winter compared to spring/summer. Significant differences in foraging habitat use were found

Table 6. Foraging habitat use by Farallon Western Gulls, 1979-81.

| Age class and Period | Total censused (n) | Habitat Use (%) | | | |
|---|---|---|---|---|---|
| | | Dump | Fishing port | Oceanic | General |
| First-year | | | | | |
| Summer | 897 | 25 | 38 | 23 | 14 |
| Autumn/winter | 2,803 | 53 | 19 | 9 | 19 |
| Second-year | | | | | |
| Spring/summer | 2,022 | 34 | 22 | 27 | 17 |
| Autumn/winter | 1,330 | 58 | 10 | 15 | 17 |
| Third-year | | | | | |
| Spring/summer | 1,248 | 36 | 19 | 31 | 14 |
| Autumn/winter | 763 | 63 | 10 | 14 | 13 |
| Fourth-year | | | | | |
| Spring/summer | 804 | 50 | 15 | 23 | 12 |
| Autumn/winter | 635 | 69 | 10 | 10 | 11 |
| Fifth-tenth-year | | | | | |
| Spring/summer | 2,263 | 60 | 13 | 17 | 10 |
| Autumn/winter | 2,155 | 71 | 9 | 9 | 11 |

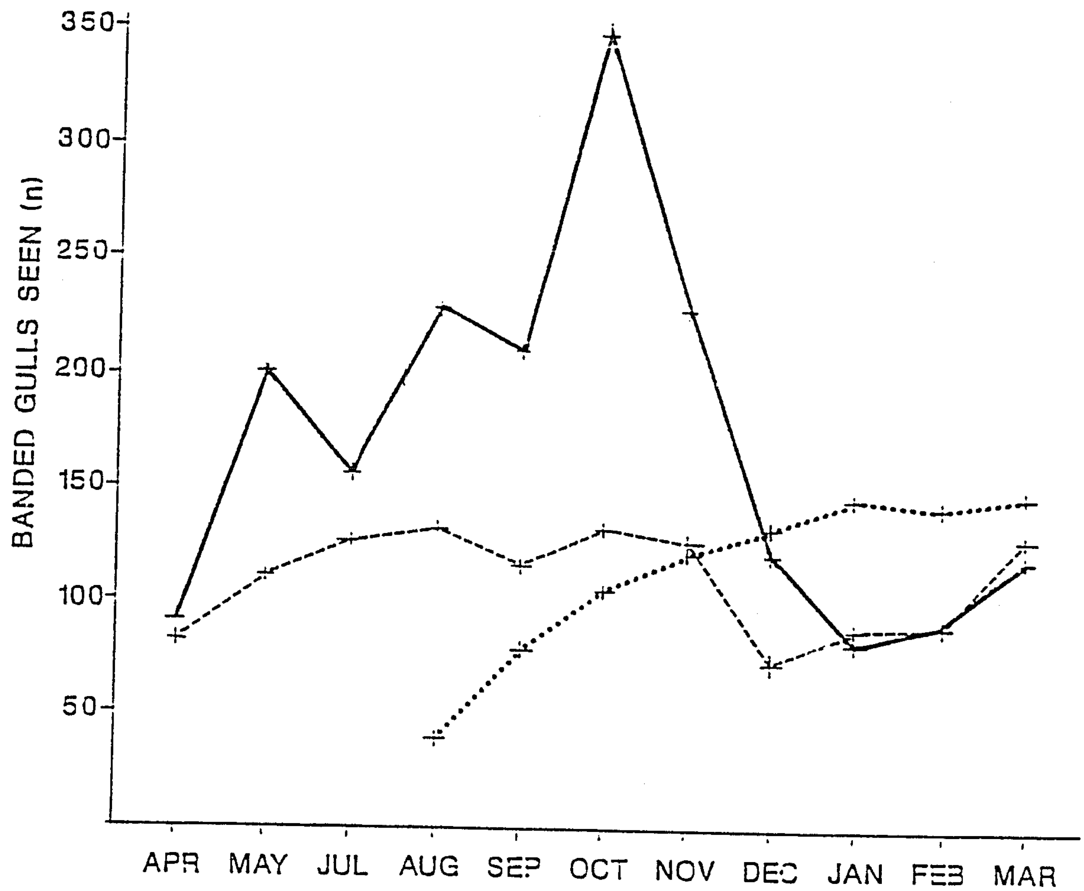


Figure 7. Monthly counts of 3 age classes of banded Farallon Western Gulls at coastal dumps of California and Oregon, 1979-1981. Counts are given as the total for the two years. Solid line = fourth- through tenth-year birds, hatched line = second- and third-year birds, dotted line = first-year birds.

between each age-class (seasons grouped $P < 0.001$, general habitat was excluded from the analyses) except second- and third-year birds ($P > 0.05$). Differences between first- and second-year gulls were due to increase with age in use of dumps and oceanic habitat, and decreased use of fishing ports. Differences between third- through tenth-year birds were due to increased use of dumps with increase in age. First-year birds also showed significant between-year differences in preference for dump and oceanic habitat ($P < 0.01$, Figure 8). Habitat preference by different cohorts, however, showed distinct patterns. For example, the 1978 cohort, which relied heavily on dumps during their first summer, continued to do so in its second (1979) and third (1980) summers. This preference differed significantly from that of other subadult cohorts (1976, 1977, 1979 and 1980 cohorts, grouped) which relied more on oceanic habitat ($P < 0.001$).

During spring/summer, second-, third-, and fifth- through tenth-year males fed on terrestrial food sources (garbage and fish offal) more often than females ($P < 0.05$, general habitat was excluded from the analyses, Table 7). Differences were not significant between sexes of first- and fourth-year birds during spring/summer or between sexes of any age-class during fall/winter ($P > 0.05$).

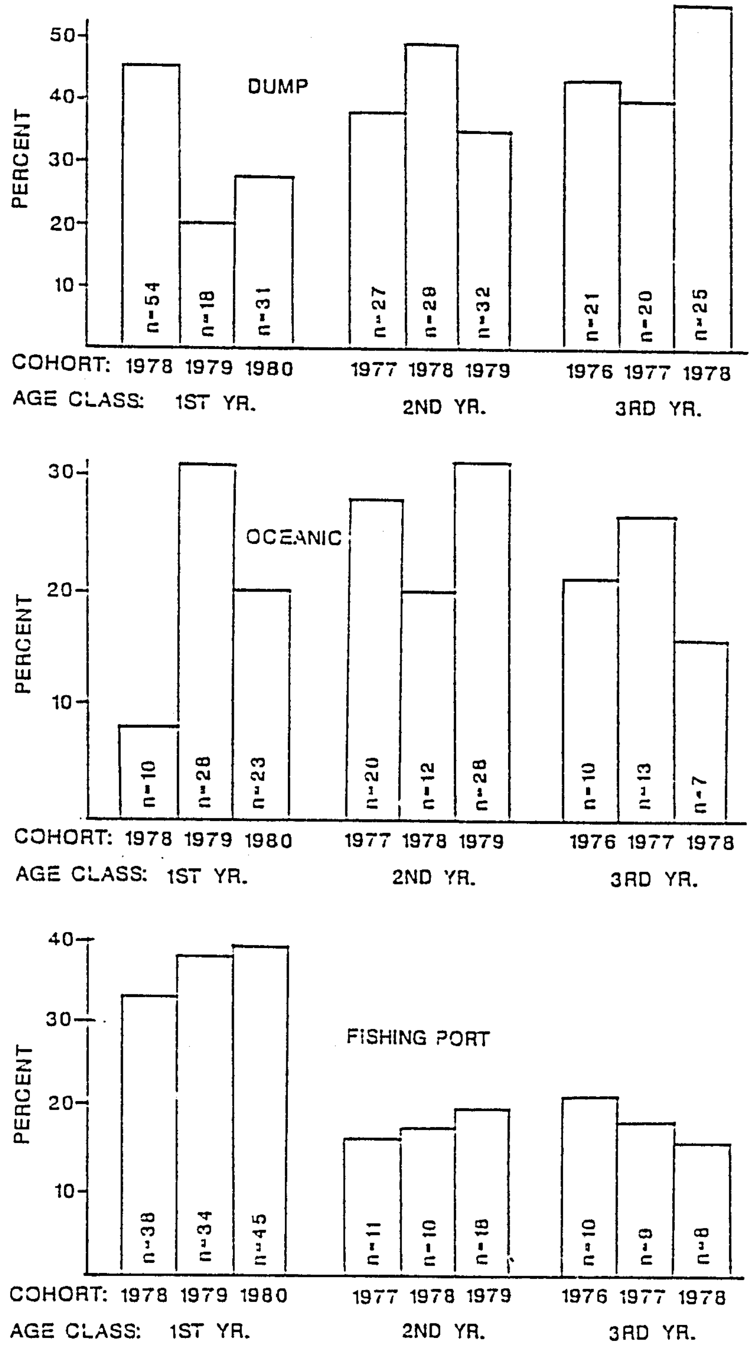


Figure 8. Coastal habitat use by 3 age classes of banded Farallon Western Gulls observed between Florence, Oregon, and Los Angeles, California (September 1978-1980). Percentages are shown as the proportion of the total count of a given cohort at a given age. Values for "general habitat" are not shown.

Table 7. Sexual difference in the use of terrestrial[a] versus oceanic foraging habitat in Farallon Western Gulls, 1979-81.

| Age-Class and Foraging Habitat | Spring/Summer Males n | (%) | Spring/Summer Females n | (%) | Autumn/Winter Males n | (%) | Autumn/Winter Females n | (%) |
|---|---|---|---|---|---|---|---|---|
| First-year | | | | | | | | |
| Terrestrial | 240 | (75) | 213 | (72) | 329 | (89) | 332 | (88) |
| Oceanic | 80 | (25) | 83 | (28) | 41 | (11) | 45 | (12) |
| Second-year | | | | | | | | |
| Terrestrial | 294 | (70) | 302 | (61) | 176 | (84) | 239 | (80) |
| Oceanic | 126 | (30) | 193 | (39) | 33 | (16) | 60 | (21) |
| Third-year | | | | | | | | |
| Terrestrial | 160 | (69) | 190 | (59) | 120 | (86) | 140 | (82) |
| Oceanic | 72 | (31) | 132 | (41) | 19 | (14) | 31 | (18) |
| Fourth-year | | | | | | | | |
| Terrestrial | 102 | (76) | 104 | (70) | 87 | (91) | 121 | (88) |
| Oceanic | 32 | (24) | 44 | (30) | 9 | ( 9) | 16 | (12) |
| Fifth-tenth-year | | | | | | | | |
| Terrestrial | 219 | (84) | 180 | (77) | 201 | (92) | 207 | (87) |
| Oceanic | 42 | (16) | 54 | (23) | 18 | ( 8) | 31 | (13) |

[a] Terrestrial habitat = dumps and fishing ports.

Gull Densities at Dumps

The numbers of large larids foraging at Oregon and California coastal dumps peaked in January and February (Figure 9). Gull densities at dumps (gulls / metric ton of garbage deposited / hour) were highest in the Oregon region, and decreased with latitude (Figure 10). Densities in SO CAL were about 4 times lower than those in the SFBA, and 10 times lower than those of Oregon.

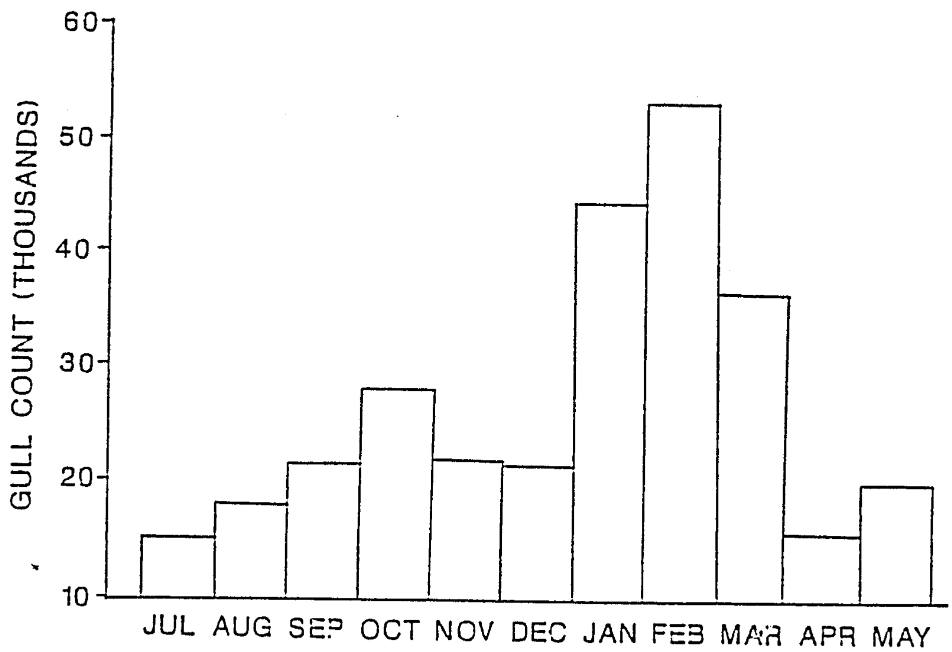


Figure 9. Mean monthly counts of large larids at coastal dumps of California and Oregon, 1979-1981.

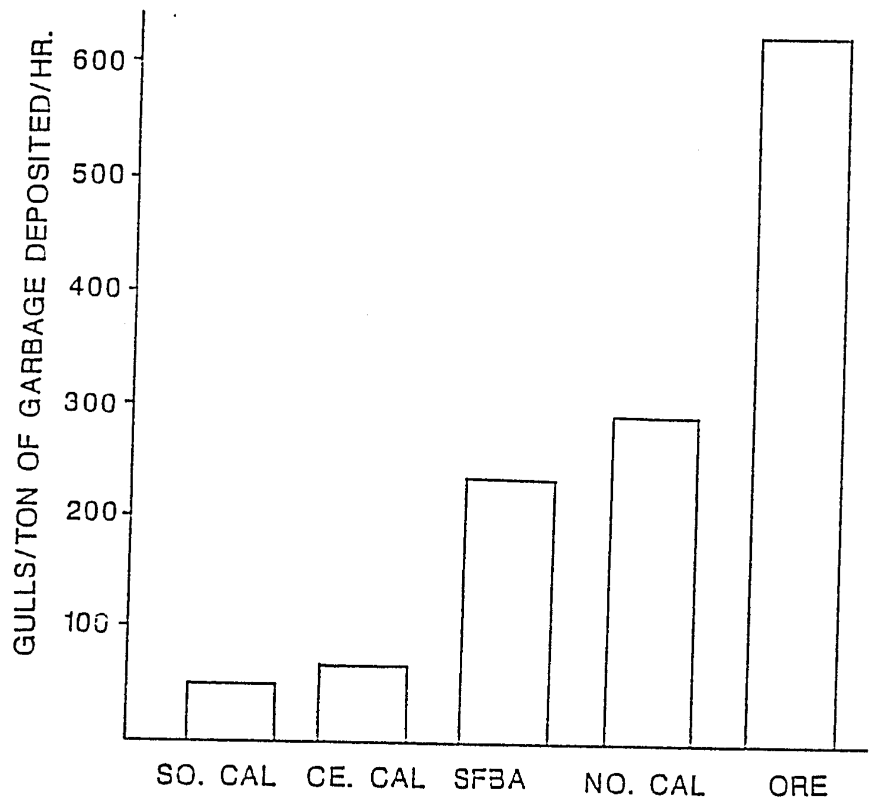


Figure 10. Densities of large larids at coastal dumps of California and Oregon during January and February 1980-1981. Gull densities are given as the mean for the two years. See Figure 1 for location of regions.

# DISCUSSION

Farallon Western Gulls bred during the most productive oceanic period and fed primarily on oceanic prey (Ainley and Boekelheide, in press). These findings are similar to those for Western Gulls that breed on Santa Barbara Island off the coast of southern California (Hunt and Butler 1980). Farallon Western Gulls then dispersed in August-September, coincident with the onset of a period of low ocean productivity. The synchronous nature of their post-breeding dispersal is consistent with severe food limitation (see Lack 1968). Dispersing breeders flew directly to locations at which they resided during the non-breeding period each year. Evidence for similar behavior has been found in Herring Gulls (Coulson and Butterfield 1985). These sites were often where they had foraged as subadult (second- and third-year) birds. By moving to familiar locations, adults probably maximized foraging efficiency and reduced competition through stabilization of concentrations at each location. Maximization of foraging efficiency is particularly important at this time because of the reduced flight capabilities associated with primary molt (Harris 1971, Verbeek 1977, Kilpi and Saurola 1983, Spear in prep).

Breeders foraging in outlying areas began to return to the Gulf of the Farallons in October, although less than 1%

had reoccupied territories at SEFI. The numbers of adults foraging at SFBA dumps peaked at that time. This behavior was likely related to reduced oceanic productivity during fall, as mentioned above, and perhaps continuation of primary molt. A similar influx into local feeding areas prior to territory reoccupation was observed among Herring Gulls in Maine (Schreiber 1968). The sharp decline in numbers of adults at SFBA dumps during the period of territory reoccupation (November-December) probably resulted from several factors. These include severe competition for territory space on SEFI (Pierotti 1981, Hand 1986, Ainley and Boekelheide, in press); arrival of the larger Glaucous-winged Gull (*L. glaucescens*), which comprised up to 50% of the gulls foraging at SFBA dumps during winter (Cogswell 1969, Spear, unpubl. data); slightly increased oceanic productivity during winter; and completion of primary molt, allowing an increased foraging range.

During the breeding season, 79% of subadults foraged outside the range of adults foraging from SEFI. These birds' distributions were skewed toward the northern portion of the species' range where oceanic productivity is highest. In fall/winter they were concentrated in the SFBA. Although 60% of subadults were found at dumps during the latter period, the 62% decrease in numbers censused on the coast, compared to those of spring/summer, suggests importance of oceanic habitat as well. This is supported by increased residence in SEFI clubs.

Individual subadults developed foraging habits and site preference as indicated by age-related increase in site fidelity. Similar fidelity also was observed among subadult Glaucous-winged Gulls and Herring Gulls (Sprout 1937, Ferris 1940, Davis 1975). Although site fidelity developed mostly during the second and third years in Western Gulls, feeding conditions during the dispersal period of fledglings apparently had a lasting effect on foraging habits (see also Davis 1975). For example, the 1978 cohort, which relied heavily on garbage in their first summer, maintained this preference unlike other cohorts which hatched during years of more favorable oceanic productivity and subsequently foraged more often at oceanic habitat.

Because adults were concentrated near breeding colonies during spring, subadults moving north probably did not need to move as far as dispersing fledglings (which dispersed during the dispersal period of adults) to find favorable feeding sites. This, and foraging site fidelity, are likely factors explaining range reduction and lack of interannual variation in distributions of subadults compared with first- year birds. Subadults of other larids also exhibit range reduction with age (Spaans 1971, Coulter 1975, Moore 1976, Parsons and Duncan 1978, Southern 1980, Kilpi and Saurola 1983, Coulson and Butterfield 1985). In Western Gulls, this was particularly marked between the third and fourth year. In spring/summer, many of these birds were not seen at habitually used foraging sites. Many of the same gulls appeared at SEFI, where they attempted to acquire territories and mates. A gradual increase in the amount of time nonbreeders spent at SEFI was demonstrated by an age- related increase in the duration of visits to the colony and a decrease in the periods of absence. Vacillation of nonbreeders between SEFI and coastal foraging locations suggests that they lacked feeding skills required in the unfamiliar foraging habitat near the island, or that they were ambivalent about the relative importance of maintaining ties to familiar sites vs. establishing themselves at the colony.

Marked interannual differences existed in dispersal patterns of Farallon fledglings. This has not been investigated in other larid populations, but young Herring Gulls in colonies near large supplies of refuse dispersed shorter distances than those from colonies farther away (Spaans 1971, Kilpi and Saurola 1983). Kilpi and Saurola (1983) concluded that dispersal patterns were related primarily to location of food sources (i.e. food availability). The evidence for Western Gulls suggests thatdifferences in dispersal patterns of fledglings were a function of the availability of oceanic prey, and that the importance of oceanic habitat was not fully appreciated during this study because it was not as accessible as dumps and fishing ports for census. First, the availability of oceanic prey varied markedly between years (reviewed by Ainley and Boekelhiede in press). Food was especially available in a year when most young dispersed north (1979), but was not in one when most dispersed south (1978). In contrast, food availability at dumps and fishing ports varied little and is an unlikely explanation of interannual variation in dispersal patterns. Second, although censuses indicated that fishing ports were preferred by gulls, numbers reached local carrying capacity quickly following post-breeding dispersal. It is not surprising that annual differences in preference for oceanic habitat and dumps accounted for most variation in dispersal patterns. It follows that the southern movement of first-year gulls during fall/winter was probably a response to decreased oceanic productivity. Refuse (the primary alternate food source) in dumps north of the SFBA comprised only 11% of the garbage volume available on the California/Oregon coast. This low figure and an influx of Glaucous-winged Gulls and local adult Western Gulls to coastal dumps resulted in larger numbers of gulls per unit volume of garbage than was the case farther south.

Sexual differences in dispersal patterns and foraging habitat preference by adult Western Gulls probably resulted from several inter-related factors. First, establishing and maintaining breeding territories is primarily the role of males (Pierotti 1981, Hand 1986, this study). It is probably more adaptive for males to move shorter distances. There is evidence suggesting similar patterns in Herring Gulls (Coulson and Butterfield 1986). In addition, with higher wing loading (males, $\bar{x} = 0.548 \pm 0.008$ grams / centimeter, n = 17; females, $\bar{x} = 0.469 \pm 0.003$ grams / centimeter , n = 21; t = 9.67, df = 36, P  0.001), males are probably less well adapted for long distance flights, but with larger body size, are better adapted for defending terrestrial (fixed) food sources abundant in the SFBA (see also Monaghan 1980, Sibley and McCleery 1983).

I believe, like Spaans (1971) and Kilpi and Saurola (1983), that dispersal patterns of gulls are a response to food availability. In the case of Farallon Western Gulls, these patterns appear most related to the fluctuating availability of oceanic prey. Human refuse is an important alternate food source when oceanic productivity is low. Greater interannual variation in dispersal patterns in first-year gulls than in older ones probably reflected the fact that first-year individuals are less capable of exploiting limited resources (see Verbeek 1977, Searcy 1978, Burger 1981 for review of age-related foraging success), and that older individuals became associated with specific foraging locations.

# APPENDIX I

## RELIABILITY OF SEXING FARALLON WESTERN GULLS BY SIZE

Pierotti (1981) found no sexual overlap in weights of 36 Farallon Western Gulls shot at their territories. During May-June 1978-1983, I trapped 172 Farallon gulls of known sex while they incubated eggs on SEFI, and found only a 2.9% sexual overlap in mass. In considering this marked sexual dimorphism, I tested the reliability of sexing these gulls by visual observation.

During 1978-1986, I determined the sex of 520 breeding Farallon Western Gulls (all banded) by observing courtship-feeding of females and copulatory roles of each adult at their territories. During the same period, I sighted 204 of these adults away from their territories, and attempted to sex 170 (83%) by comparing their size to that of Western Gulls nearby. I did not attempt to sex 34 (17%) of the 204 gulls because of poor observation conditions or because they appeared intermediate in size. Similarly, I sighted 159 of the 520 breeding adults on the coast when they were 6 months to 3 years old, and 51 when <6 months of age. By comparing size differences, I attempted to sex 127 (80%) of the 6-month to 3-year-old birds, and 39 (76%) of the younger birds. I did not attempt to sex some birds for reasons given for adults.

Reliability when sexing adults, 6-month to 3-year-old birds, and gulls <6 months old by observing size differences, was 97%, 96% and 92%, respectively (Table 1). Within the three age groups, confidence attained for each sex was over 95%, except 6-month to 3-year-old females (94.3%), and males <6 months old (87.5%). The sex ratio among gulls not sexed by size comparison was not significantly different from that of gulls that were sexed (G test, $P > 0.05$).

Sexing Farallon Western Gulls >6 months of age by observing size differences in live birds is reliable within 95% confidence limits. (For this study the 94.3% confidence attained when sexing 6-month to 3-year-old females was considered acceptable.) Using size comparison for sexing gulls <6 months old was not reliable within the given limits; apparently, many males do not reach adult size until they are six months of age (see also Sayce and Hunt 1987). During my study, however, many (banded) birds sighted when <6 months old were resighted at an age when sexing by size comparison was reliable. Resighting facilitated study of the sex-related dispersal patterns of the younger age group.

Table A1. Reliability of sexing Farallon Western Gulls by size comparison.

| Age | Birds sighted off territory[a] (n) | Birds sexed by size comparison (n) | Birds sexed correctly by size comparison (n) | Birds not sexed when sighted off territory (n) |
|---|---|---|---|---|
| >4 year | | | | |
| Males | 117 | 99 | 97 (98.0%) | 18 |
| Females | 87 | 71 | 68 (95.8%) | 16 |
| 6 months to 3 year | | | | |
| Males | 94 | 74 | 72 (97.3%) | 20 |
| Females | 65 | 53 | 50 (94.3%) | 12 |
| <6 months | | | | |
| Males | 32 | 24 | 21 (87.5%) | 8 |
| Females | 19 | 15 | 15 (100.0%) | 4 |

[a] All birds sighted off territory also were sighted as adults on their SEFI breeding territories and sexed by behavioral observation on those occasions.

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