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INTERBREEDING AND EVOLUTION IN THE LARUS GLAUCESCENS - LARUS ARGENTATUS COMPLEX ON THE SOUTH COAST OF ALASKA

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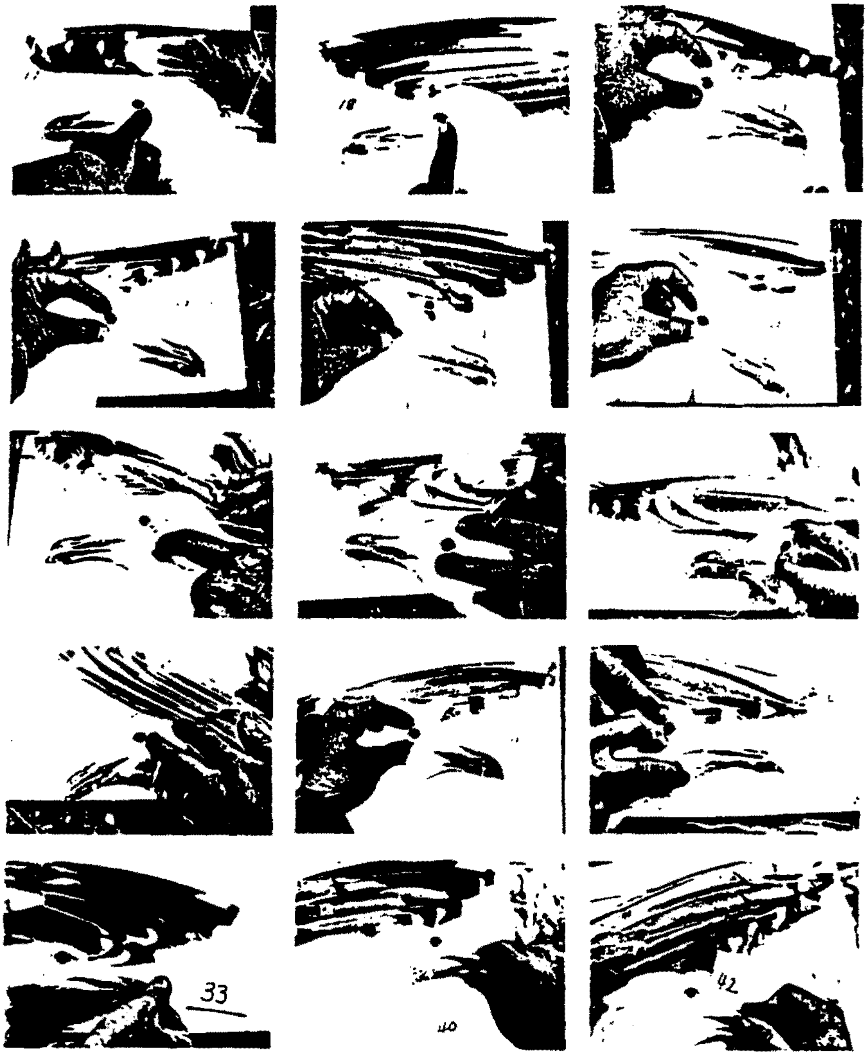

Frontispiece. Sympatric *Larus* gulls from Dry Bay, mouth of the Alsek River, 75 km SE of Yakutat, Alaska. Note the variation in the pattern (extent) of melanin deposition in the subterminal portions of the outer primary feathers, and the intensity of melanin in the same area.

INTERBREEDING AND EVOLUTION IN THE *Larus glaucescens* - *Larus argentatus* COMPLEX ON THE SOUTH COAST OF ALASKA

by

Samuel Merrick Patten, Jr.

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ABSTRACT

Isolating mechanisms, in speciation theory, are characteristics of individuals that prevent successful interbreeding with individuals of different species. Previous studies have shown that certain large white-headed gull populations (genus Larus) are isolated from other such populations by pre-mating mechanisms such as species recognition and nesting habitat selection. Species recognition in these Larus gulls is influenced by such morphological characteristics as the colors of the iris and orbital ring (or eyelid) and the pigmentation of the outer portions of the main flight feathers (the primaries).

This study investigated a 480-km zone of overlap and hybridization on the south coast of Alaska between the Glaucous-winged Gull Larus glaucesens and the Herring Gull Larus argentatus for evidence of species recognition and for differences in nesting habitat selection. The basic method was observation in the field of 2649 breeding adult gulls (361 argentatus, 374 hybrids, and 1914 glaucescens) in coastal and interior Alaska, British Columbia, and the Yukon. Further, 165 breeding adult gulls were collected and photographed in the field (15 argentatus, 51 hybrids, and 99 glaucescens) and the mating patterns and nesting habitat selection of 718 pairs (172 argentatus, 51 mixed, and 495 glaucescens pairs) were studied. Finally, the reproductive productivity of 933 pairs of gulls (78 argentatus, 391 glaucescens, and 464 mixed pairs including at least one integrade per pair) was investigated. In addition, 506 study skins were examined from the entire breeding range of glaucescens (208 individuals) and North American argentatus (298 individuals) which are maintained in museums in Alaska, British Columbia, Washington State, Washington, D.C., and New York City.

Analysis involved statistical and qualitative comparisons of iris and orbital ring colors and primary feather pigmentation among eight populations, distributed from 58° to 62° N lat. Clutch size, hatching success, and fledging success were compared among pure types and integrades for evidence of hybrid inviability.

Individual gulls were highly variable in primary feather pigmentation. Wing hybrid indices (WHI) ranged from 1 to 6 (various shades of gray to black). The WHI means gradually increased from an offshore island *glaucescens* population (WHI 1.2) through intermediate coastal populations (WHI 1.91 to 4.12) to an interior population of *argentatus* on a boreal lake (WHI 5.9).

The range of iris coloration varied from very dark brown to yellow (Munsell 2.5YR to 5Y hues). A progressive change in mean iris color, as with primary feather pigmentation, was also related to geographic location. Iris hybrid indices ranged from a mean of 6.3 to 9.0: brown to yellow.

"Pure types" of *argentatus* in southern Alaska had yellow, uniformly pigmented orbital rings of Munsell hue 5Y. *L. glaucescens* "pure types" had dark pink or vinaceous orbital rings of Munsell hue 5R. Seven hues were observed between these two extremes, ranging from a mean of 1.3 (dark pink) to 8.9 (yellow).

The extreme variation in primary feather pigmentation, and iris and orbital ring colors in *glaucescens* populations indicated species recognition was not functioning as a complete isolating mechanism between *glaucescens* and *argentatus*. Interior (*argentatus*) populations displayed much less variation in these key characters. The inference of long-term gene flow from Herring Gull into Glaucous-winged Gull populations was therefore direct and unavoidable.

The nesting habitat preference exhibited by Herring Gulls for freshwater conditions did not isolate this form from Glaucous-winged Gulls breeding near river mouths and in recently deglaciated fjords. Both Glaucous-winged and Herring Gulls displayed considerable flexibility in nesting habitat selection, breeding together on flat gravel bars, sloping grassy hillsides, and on cliff faces.

Mating patterns within mixed colonies were significantly assortative, including integrades selecting like types as mating partners. However, mixed pairs compared to pure pairs showed no statistical difference in mean clutch size (2.98 vs. 2.93) and fledging success (1.47 vs. 1.40).

Four hypotheses for the existence of a narrow hybrid zone between *argentatus* and *glaucescens* were explored for the best explanation for the data collected. These postulates are the ephemeral-zone, the hybrid superiority, the dynamic equilibrium, and the ecotone-disclimax hypotheses. The "best fit" for the southern Alaskan *Larus* situation involves a combination of the elements of the dynamic equilibrium hypothesis and of the ecotone-disclimax hypothesis.

This and other recent studies of the Western Gull (*Larus occidentalis*) and the Glaucous Gull (*Larus hyperboreus*) and the Slaty-backed Gull (*Larus schistisagus*) expand the concept of the circumpolar *Formenkreis* by extending that concept to include the entire North Pacific rim. This study also designates the Glaucous-winged Gull as a semispecies to the circumpolar Herring Gull superspecies and concludes that the appropriate taxonomic treatment for the Glaucous-winged Gull is *Larus [argentatus] glaucescens*.

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DEFINITIONS[1]

adaptive radiation
: Evolutionary divergence of members of a single phyletic line into a series of different niches or adaptive zones.

allopatric
: Populations separated in space, occupying mutually exclusive but often adjacent geographical areas.

allopatric hybridization
: The interbreeding of two previously isolated populations in a zone of contact. "Secondary intergradation" (a more neutral term) is used where the interbreeding populations have not reached species level.

assortative mating pattern
: The preferential choice of individuals of similar phenotype as mating partners.

backcross
: The result of a hybrid individual of the F_1 or subsequent generations mating with an individual of one of the two parental types.

biological species concept
: Populations of living organisms, organized into natural groupings of interbreeding or potentially interbreeding populations, which are presumed to share coadapted gene complexes (which see).

chroma
: The degree of departure of a given hue from a neutral grey of the same value in the Munsell System of Color Notation. Chroma scales depend upon the strength (degree of saturation) of the sample evaluated.

chick
: A young bird from the time of hatching until fully fledged; technically known as a "pullus" or "local."

circular overlap
: The phenomenon in which a chain of contiguous and interbreeding populations curves back until the terminal links overlap with each other and behave as good species, that is, non-interbreeding. A circular overlap is known as "ring species."

cline
: A geographic gradient in a measurable character, or gradient in gene, genotype, or phenotype frequency. Two or more clines may operate simultaneously and not necessarily on the same axis; the

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[1]Sources: (Endler, 1977; Thomson, 1964; Mayr, 1963).

cline for each character is theoretically independent of the others. Often, however, there is a rather strong correlation among several characters.

coadapted gene complex
A group of genes in a population adapted to a particular environment, which interact together, and enhance survival and/or reproduction in that environment.

conjunction
A connection of two or more subspecies, incipient species, or species to each other along narrow bands or by steep clines.

cross
In genetics, the mating or the offspring of the mating of two individuals of different strains, races, or species.

dispersal
The roughly random and non-direction small-scale movements made by individuals rather than groups, continuously, rather than periodically, as a result of their daily activities.

distal
That portion of a limb or body member or appendage most distant from the center of the body.

ecotone
A habitat created by the juxtaposition of distinctly different habitats; an edge habitat; the area of transition between different habitats; an area of overlap in environments of different types.

ethological
Behavioral, particularly with reference to species-specific behavior elements, the phenotypes of which are largely determined genetically.

F_1
The first generation offspring of a cross (which see).

F_2
The offspring of matings between F_1 individuals; the second generation offspring of a cross.

F-ratio
The statistic appropriate to the analysis of variance, used to evaluate the significances of differences between population means.

fitness
The ability of an organism to survive and reproduce; the survival value and reproductive capacity of a given phenotype relative to other phenotypes in a population.

fledging
The term usually applied to the acquisition by a young bird of its first true feathers; when the process is complete the bird is 'fledged' and may for a short time be described as a 'fledgling'. Often implies that an individual can fly when fully fledged.

Formenkreis
Kleinschmidt's term for an aggregate of geographically representative (allopatric) species and subspecies.

founder principle
The principle that the founders of a new population contain only a small fraction of the total genetic variation of the parental population. The differences are enhanced by different evolutionary pressures in the areas occupied by the two populations, acting in different population genetic environments; the result in increased divergence.

gene flow
The exchange of genetic factors between populations; the movement of genetic information between and among populations.

genotype
The totality of genetic factors that make up the genetic constitution of an individual; as contrasted to phenotype.

geographic barrier
Any terrain that prevents gene flow between populations.

habitat selection
The capacity of a dispersing individual to select an appropriate (the species-specific) habitat.

hue
The notation of a color in the Munsell System which indicates its relationship to a visually equally-spaced scale of 100 hues. The hue notation in this study is based upon three color-names: Red, Yellow-Red, and Yellow.

hybrid
The offspring of a cross of individuals belonging to two unlike natural populations. Usually 'hybrid' and hybridize are limited to two species rather than races or subspecies, where the term intergrade is usually applied.

hybrid index
A method for analyzing variation in dissimilar yet interbreeding populations, resulting from secondary contact and hybridization of those populations, with greatly increased variability in morphology. See also 'zone of overlap and hybridization'.

incubation period
The time between onset of incubation of an egg and the date of hatching. May be based on the lowest egg period in a clutch; on the average egg period, the range, or the longest. In gulls, the first day of steady incubation of a clutch is the day the last egg is laid. The last day of incubation is considered to be the day preceding the one on which the eggs begin to hatch. Alternatively, the number of days calculated from the last egg laid to the last young hatched.

integradation
The formation or existence of character gradients between groups of populations, by means of gene flow.

integrade
An individual which is the product of a cross between different parental types and which displays characters intermediate between those of the parental types. Some intergrades may be the offspring of very similar intergrade parents.

introgression
The incorporation of genes and the resulting characters of one species into the gene pool of another species.

iris
The pigmented main portion of the eye, beneath the orbital ring (eyelid) and surrounding the pupil; plural irides.

isolating mechanisms
Properties of individuals that prevent successful interbreeding with individuals belonging to different populations. Pre-mating isolating mechanisms in gulls may be species recognition, nesting habitat selection, and timing of breeding. Post-mating isolating mechanisms may include such factors as hybrid inviability or reduced fitness.

locus
The location of a given gene on a chromosome.

long call
A series of loud calls given by a gull, associated with a series of postures, combining vocally elements of both sexual display and aggressive defense of territory.

mantle

The back, scapulars, and secondary wing coverts of a gull, together presenting an area of distinctive color, which extend from the primaries (not included) across the rest of the wings and back. The word is used as a general topological term describing appearance.

melanin

A protein which forms usually dark pigments. The substance results from the interaction of the enzyme tyrosinase and the chemical substrate tyrosin.

migration

The relatively long-distance movements made by large numbers of individuals in approximately the same direction at approximately the same time, and usually followed by a return 'migration'. Compare with gene flow and dispersal.

monotypic

A term used of a species, indicating only one subspecies or form.

Munsell System of Color Notation

(See hue, value, and chroma; also Appendix III).

niche

The constellation of environmental factors into which a species (or taxon) fits: the outward projection of the requirements of an organism; its specific way of utilizing its environment. In other words, what the organism does, instead of where it lives (the habitat).

orbital ring

The fleshy portion of the eyelid of a gull visible when the eye is completely open. The orbital ring forms a circle around the opened eye, and is variously colored.

parapatric

Two or more subspecies, incipient species, or species which are in contact over a very narrow zone.

phenotype

The totality of characteristics of an individual, which results from the interaction of genotype and the environment. (See 'genotype').

philopatry

The tendency, or drive of an individual to return to its home area, both for breeding and wintering locations. In German, Ortstreue (true to district).

population
Used here in a general sense, any group of organisms of a single species.

primary(ies)
The main flight feathers of a bird, on the distal end of the wing; ten in number in gulls, and borne on the manus (carpometacarpus and distal phalanges). (See 'secondary').

range
The geographical distribution of a species.

Rassenkreis
A group of subspecies separated by clines. Some of its subspecies may be reproductively isolated from each other. The German equivalent of a polytypic species, -- not a 'circle of races'.

remex (pl. remiges)
Those feathers which have direct ligamentous connections to the wing bones, including both primaries and secondaries.

secondary(ies)
Any one of the flight feathers borne on the ulna, as contrasted with the 'primaries' (which see), borne on the manus.

secondary contact
The rejunction of partially diverged populations diverged from a common ancestor.

secondary intergradation
Morphological intergradation between two geographical forms that at one time diverged in isolation.

selection pressure
The environmental resistance leading to differential survival and reproduction of genotypes.

semispecies
The component species of superspecies (Mayr); also, populations that have acquired some, but not yet all, attributes of species rank; borderline cases between species and subspecies. The second aspect of the definition is the appropriate use here.

Sewall Wright Effect
The tendency in small populations for random variations to become fixed through random drift. The effectiveness of weak selection is low in small populations, which may thus exhibit unusual characteristics.

species group
An array of closely related species, usually also with partially overlapping ranges. (See also 'superspecies').

stasipatric speciation
A process of speciation, originating at a small local colony, either at the periphery of the distribution area of the ancestral species, or inside it. If members of this colony possess high fitness, they subsequently spread and may displace the ancestral form.

step cline
A cline with a very rapid change in gene frequency separating two regions with a relatively small change in gene frequency with distance. (See 'cline').

subspecies
An aggregate of local populations of a species, inhabiting a geographical subdivision of the range of the species, and differing morphologically from other populations of the species. Various criteria are used to distinguish among species, among which are rules suggesting that 75% to 95% of the individuals of a subspecies should be distinguishable from other such subspecies.

substrate
The geological formation, usually with vegetation superimposed, upon which a gull colony rests (i.e., sand dunes, rock cliff face, gravel bars, etc.).

subterminal
As applied to the wing tip pattern of gulls, that (usually dark) portion of the main flight feathers (the primaries) just medial of the feather tips.

superspecies
A monophyletic group of entirely or essentially allopatric species that are too distinct to be included in a single species.

sympatry
The occurrence to two or more populations in the same area; the existence of a population in breeding condition within the range of another population. As opposed to allopatry (which see).

synchronous breeding
The tendency of all members of a population of colonial birds to reproduce within a short period of time of each other. It is an adaptive anti-predator strategy, also necessary if the optimal breeding period is of short duration because of weather and climate.

territory
An area defended by an animal against other members of the same

species, and occasionally against members of other species.

Throwback
That component of the "Long Call" in certain gulls (e.g., *Larus argentatus*) in which the head is moved rapidly back to the rear through an arc extending over the back, from a low, nearly horizontal frontal position. (See "Long Call").

value
The notation of a color in the Munsell System, indicating the degree of lightness or darkness in relation to a neutral grey scale, extending from absolute black to absolute white.

zone of overlap and hybridization
An area of secondary intergradation occupied by numerous hybrids and both parent forms as well. The parental phenotypes must occur in numbers sufficient to preclude their representing extreme recombinant phenotypes.

zygote
A fertilized egg; the cell (individual) that results from the fertilization of an egg cell; a diploid cell formed by the union of male and female gametes.

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1.0 INTRODUCTION

This study is an investigation of the zone of overlap and hybridization in Alaska of two taxa traditionally known as the Glaucous-winged Gull (Larus glaucescens Naumann) and the Herring Gull (Larus argentatus smithsonianus Coues). The Glaucous-winged Gull resembles the Herring Gull in size and plumage characters, with certain observable exceptions, i.e., the subterminal portions of the outer primary feathers are light grey in glaucescens and black in argentatus; the iris of typical glaucescens is dark brown while that of typical argentatus is yellow, and the orbital ring of glaucescens is pink while that of typical argentatus is yellow. The Glaucous-winged Gull breeds along the Pacific Coast from Washington State north to Norton Sound, Alaska, and west along the Aleutian chain to the Commander Islands (USSR). The Herring Gull, a widely distributed circumpolar taxon, breeds in northwestern North America on boreal lakes and rivers in interior Alaska, British Columbia, and the Yukon. The ranges of the two taxa overlap on the south coast of Alaska (Fig. 1).

As a general rule, breeding populations of the two taxa are separated by high mountain ranges dividing the ecologically distinct coastal (glaucescens) and interior (argentatus) regions of the Pacific Northwest and Alaska. Williamson and Peyton (1963) discovered interbreeding between Glaucous-winged and Herring Gulls in the Cook Inlet region, near Anchorage, Alaska, but the extent and degree of contact between these gulls was left unresolved. Williamson (MS) subsequently studied the morphology of gull populations southwest of Cook Inlet, but the coastline of the Gulf of Alaska remained univestigated. The location of gull colonies and their species composition in this region was not known until

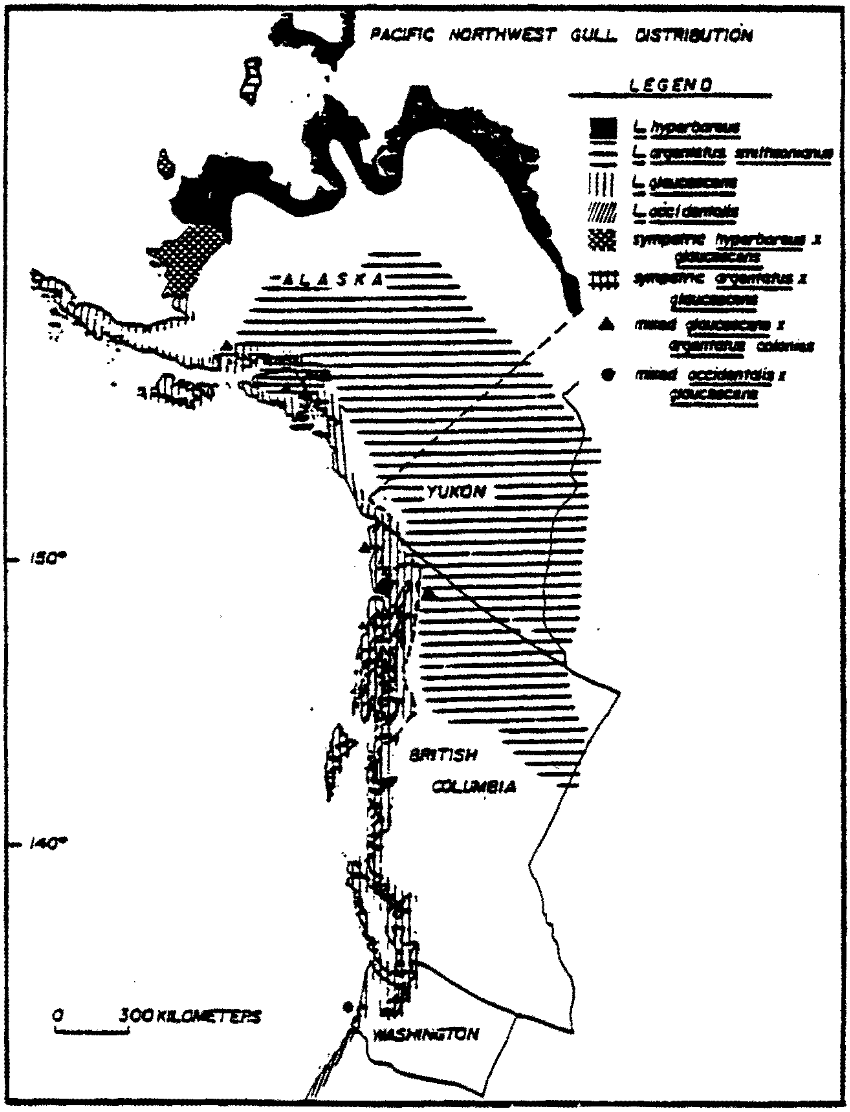

Fig. 1. Pacific Northwest gull distribution. The ranges of glaucescens and hyperboreus overlap in western Alaska; glaucescens and argentatus in southern Alaska; glaucescens and occidentalis in western Washington State. (L.a.vegae breeds on St. Lawrence Island).

the present study. Early observations (Patten and Weisbrod, 1974) of mixed pairs and intermediate morphs in recently deglaciated fjords and at river mouths in the Glacier Bay and Yakutat area of southeastern Alaska indicated the need for a survey of coastal and interior gull colonies between Juneau and Prince William Sound. Subsequent surveys were conducted to determine the possibility of additional sympatry, hybridization, or intergradation between the two gulls. Nesting habitat selection, mating patterns, and reproductivity of pure types and intergrades in this region required study to establish the potential functioning of pre- and post-mating isolating mechanisms (cf. Definitions, p. xiii). Furthermore, most aspects of the reproductive biology of _glaucescens_ and _argentatus_ in Alaska were completely unknown.

The existence of intergrades as well as pure types in the study area required a comprehensive explanation to include an examination of the theoretical hypotheses for the existence of a narrow hybrid zone in southern Alaska. The question of the stability or transitory nature of the contact became important to this aspect of the study. This necessitated research into the geological and ecological conditions characteristic of the coastline of the Gulf of Alaska. If conditions were static, then hybridization should theoretically be a transitory phenomenon.

The information gathered during this study is related to the larger problem of gull relationships within the circumpolar _Formenkreis_, or the circle of interbreeding races of the Herring Gull group extending around the Northern Hemisphere (Stresemann and Timofeeff-Ressovsky, 1947). Where the terminal ends on the circle overlap in Western Europe, extreme variant races, the Herring Gull (_L. argentatus_) and the Lesser Black-backed Gull (_L. fuscus_) act as good species (Paludan, 1951; Goethe, 1955). Previous studies of the *Formenkreis*, which have focused on Palearctic aspects of the *L. argentatus - fuscus* complex, have assumed the simple continuity of *argentatus* populations in North America, and have not even considered hybridization between sympatric forms. However, recent investigations on the West Coast have indicated that the Glaucous-winged Gull (*L. glaucescens*) interbreeds with the Glaucous Gull (*L. hyperboreus*) in western Alaska (Strang, 1977), with the Herring Gull in southern Alaska (Williamson and Peyton, 1963; Patten and Weisbrod, 1974), and with the Western Gull (*L. occidentalis*) along the Washington and Oregon coasts (Hoffman, Weins, and Scott, 1978)(Fig. 1). Russian studies indicate that a fifth species, the Slaty-backed Gull (*L. schistisagus*) interbreeds with a form of the Herring Gull (*L.a. vegae*) on the Pacific Coast of Siberia (Portenko, 1963; Kistchinski, pers. comm.). The evolutionary status of these gulls (subspecies, semispecies, stabilized hybrid forms, or locally differentiated races of a single species) required additional study.

The Glaucous-winged Gull is thus potentially important as a "key" taxon, interbreeding with at least three other populations in the Nearctic *Larus* complex, while the Herring Gull represents the presumed ancestral form. The previously uninvestigated south coast of Alaska provided an unparalleled opportunity to study the contact between the Glaucous-winged Gull and the Herring Gull in a little-known environment.

The intent of this study was therefore, to contribute to the knowledge of the evolution of *Larus* gulls, provide additional knowledge on the area of contact between Glaucous-winged and Herring Gulls, and to expand the concept of the circumpolar *Formenkreis* to include additional large white-headed gulls interbreeding in narrow zones of sympatry along the North Pacific rim.

2.0 CURRENT STATE OF KNOWLEDGE

2.1 General

The complex morphology and evolution of *Larus* gulls have long attracted the attention of ornithologists in Europe and North America. The literature on this topic is divided here for clarity into three parts reflecting geographical areas: the Holarctic-Circumpolar region, the Nearctic-Pacific Coast region, and the North Pacific rim. Supporting literature is presented in the form of a section on theories of hybridization, as related to this study, and a practical section in which aspects of the allopatric breeding biology of *argentatus* and *glaucescens* are compared to assist in understanding the selective forces which may act upon interbreeding populations in the study area. Scientific and common names, typical characteristics, and distributions of some large white-headed gulls discussed below are included in Table 1 for ease of understanding.

2.2 Geographical Areas

2.21 Holarctic-Circumpolar Region

The morphology of Eurasian *Larus* has been studied at least since the early 1930's. Consideration of the evolution of morphological differences among *Larus* populations has led to the concept of the *Formenkreis* as developed by Stegmann (1934) and expanded by Stresemann and Timofeeff-Ressovsky (1947). Geyr von Schweppenburg (1938), Voipio (1954), Voous (1959), Johansen (1960) and Kist (1960) have further studied the origin of the pink-footed gulls of the *L. argentatus* group and the yellow-footed *L.* (*argentatus*) *cachinnans* group. These authors agree that during the Pleistocene an ancestral *Larus argentatus* population was divided into two refugia by the East Siberian Ice Barrier. The pink-footed *argentatus* group was forced to the east side of the barrier, and populations of this

TABLE 1

Scientific and Common Names, Typical Characteristics, and Distributions of Some Large White-headed Gulls Mentioned in Text[1]

Name		Typical Characteristics					Distribution
Scientific	Common (English)	subterminal portions of primary feathers	iris	orbital ring	mantle	feet & legs	
Larus argentatus	Herring gull	black	yellow	yellow/orange	grey	pink	Northern Hemisphere
L.a. smithsonianus	"	"	"	"	"	"	North America
L.a. argentatus	"	"	"	"	"	"	Northern Europe
L.a. vegae	"	"	"	variable pink/orange	"	"	Northern Siberia
L.a. taimyrensis[2]	"	"	"	pink	variable grey	pink/yellow	Northcentral Siberia
L.a. antelius	"	"	"	"	dark grey	yellow	Northwest Siberia
L.a. omissus	"	"	"	"	grey	pink/yellow	Northeast Europe
L.(a) cachinnans[3]	"	"	"	red	dark grey	yellow	Black & Caspian Sea Basins, Kazakhstan
L.(a) mongolicus	"	"	"	red	dark grey	pink/yellow	Mongolia

[1]Sources: Stegmann, 1934; Stresemann & Timofeeff-Ressovsky, 1947; Voipio, 1954; Johansen, 1960; Kinsky, 1963; Smith, 1966; Hoffman, pers. comm.; Kistchinski, pers. comm.

[2]This form may represent an intermediate zone between vegae and antelius, not a subspecies (Kistchinski, pers. comm.).

[3]The common opinion of Soviet biologists is that this form deserves full species status as Larus cachineus, and that mongolicus is a subspecies of cachineus (Kistchinski, pers. comm.).

TABLE 1 (Continued)

Name		Typical Characteristics					Distribution
Scientific	Common	subterminal primaries	iris	orbital ring	mantle	feet & legs	
Larus glaucescens	Glaucous-winged Gull	grey	brown	pink	grey	pink	Pacific Northwest Coast of N. America
Larus occidentalis	Western Gull	black	yellow	yellow/ orange	dark grey	pink	Washington State, Oregon, California coasts
L.o. livens	"	"	"	yellow	very dark grey	yellow	Baja California
Larus schistisagus	Slaty-backed Gull	"	light to medium brown	orange/ red	grey	pink	Pacific Coast of Siberia
Larus fuscus	Lesser Black-backed Gull	"	yellow	vermillion	"	yellow	Northwest Europe
Larus hyperboreus	Glaucous Bull	white	"	yellow	light grey	pink	Circumpolar
L.h. barrovianus	"	"	"	"	darker grey	"	Northwestern Canada, Northern & Western Canada
L.h. pallidisimus	"	"	"	"	very pale grey	"	Eastern and Northern Siberia
Larus glaucoides kumlieni	Kumlien's Gull	variable grey	variable dark to light	reddish purple	grey	"	Baffin Island, North-western Quebec
Larus thayeri	Thayer's Gull	grey to black	dark	pink	grey	"	Eastern Canadian Arctic

form later dispersed over the Bering Land Bridge to the North American continent. This immigration led to the gradual development of the pink-footed American group, including the Glaucous-winged Gull (L. glaucescens) and the Western Gull (L. occidentalis). Later, the ancestral argentatus population expanded across the North American continent along the southern edge of the retreating continental glacier until it reached the Eastern Seaboard. Post-glacially, L. argentatus (sensu stricto) moved north-eastward, crossed the Atlantic, and colonized northwestern Europe.

Populations of the yellow-footed, dark-mantled cachinnans-fuscus group, displaced westward and southward by Siberian glaciers, spread into a refugium in the Aral-Caspian area. From this region, cachinnans populations dispersed into the Mediterranean, and fuscus populations moved into northwestern Europe before the post-Pleistocene invasion of argentatus from North America. In northwestern Europe, argentatus and fuscus became sympatric, thus completing the circumpolar circle of Larus populations (Formenkreis) (Fig. 2). The present European populations of argentatus and fuscus, while sympatric, are generally reproductively isolated, as would be expected from their long period of geographic isolation.

2.22 Nearctic-Pacific Coast Region

Research on the morphology of the Nearctic argentatus group has focused on two major geographical areas: the High Arctic, and more recently, the Pacific Coast. The Eastern Nearctic forms, L. hyperboreus, L. thayeri, L. kumlieni, and L. argentatus, are reproductively isolated by time of breeding, nesting habitat selection, and species recognition among these species which have been sympatric since the end of the Pleistocene (Smith, 1966b). However, on Iceland, recently colonizing populations

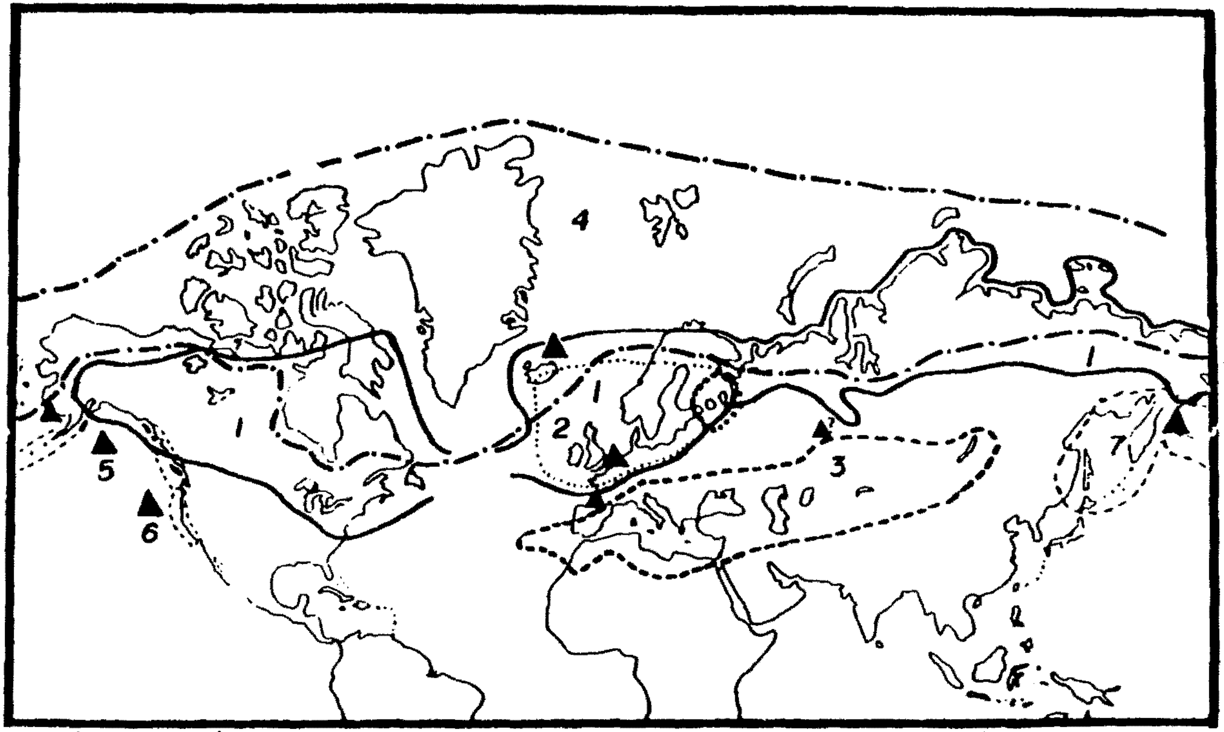

Fig. 2. Circumpolar argentatus - fuscus Formenkreis. Herring Gulls and Lesser Black-backed Gulls are sympatric with only occasional hybridization in Western Europe, while connected by a series of interbreeding populations in Asia. 1) argentatus 2) fuscus 3)(a.) cachinnans 4) hyperboreus 5) glaucescens 6) occidentalis 7) schistisagus. ▲ Hybridization occurs between the following taxa: 1 x 2 (occasional; Western Europe); 1 x 3 (Central Siberia); 1 x 4 (Iceland); 1 x 5 (Southern Alaska); 4 x 5 (Western Alaska); 5 x 6 (Washington and Oregon); 1 x 3 (SW France) 1 x 7 (Koryak Highlands).

of *argentatus* are freely interbreeding with *hyperboreus* (Ingolfsson, 1970). This contact, which has occurred since about 1925, is related to the development of high seas fisheries, and the concurrent spread of the British Herring Gull to Iceland (Ingolfsson, 1970).

The North American West Coast forms, *occidentalis* and *glaucescens*, have been studied by Dawson (1909) who first found evidence of extensive hybridization on the outer Washington Coast; Pearse (1946), who noted possible hybridization on the outer coast of Vancouver Island, and Scott (1971) who found mixed pairs of Western and Glaucous-winged Gulls and extensive hybridization on Destruction Island, Washington. Hoffman, Weins, and Scott (1978) surveyed the gull colonies of the outer Washington and Oregon coasts to determine the extent and range of overlap and hybridization, and found that mating patterns of gulls on Destruction Island were generally assortative, with individuals pairing with mates similar to themselves, although exceptions occurred frequently. They also reported that as a result of their one-year study that gull pairs containing at least one hybrid individual demonstrated apparently greater hatching success than pairs composed of pure Glaucous-winged or Western Gulls.

Swarth (1934) studied the morphology of *glaucescens* and *hyperboreus* breeding at Nunivak Island, Alaska. He considered all *glaucescens* on Nunivak Island showed evidence of interbreeding with *hyperboreus*, and some *hyperboreus* displayed morphological characteristics of *glaucescens*. Strang (1977) believed the variation in color patterns of the irides, orbital rings, and primary feathers of adult *hyperboreus* on the Yukon-Kuskokwim Delta was the result of hybridization with a darker form, presumably *glaucescens*. However, neither Swarth (1934) nor Strang (1977) found mixed pairs of hyperboreus and glaucescens. Williamson and Peyton (1963) and Patten and Weisbrod (1974) found intergrades and mixed pairs of argentatus and glaucescens in southern Alaska.

2.23 North Pacific Rim

Portenko (1963; cf. Vaurie, 1965) found the Slaty-backed Gull (Larus schistisagus) of northern Japan, the Kurile Islands, and the Kamchatka Peninsula interbreeds with a Siberian form of the Herring Gull (L.a. vegae) in the Koryak Highlands on the Pacific Coast of Siberia.

Williamson (1967) considered occidentalis, glaucescens, smithsonianus, vegae, and schistisagus all to be races of the Herring Gull in the North Pacific Ocean and Bering Sea. However, mating patterns were not analyzed between any of these forms, nor was hyperboreus included in this group.

Until the present study, the circumpolar Formenkreis concept (postulating a series of interbreeding populations of Larus gulls) has been incomplete, because of the lack of sufficient information concerning the gull populations of western North America. In particular, the importance of glaucescens as a "key" taxon, interbreeding with every other large white-headed gull with which it comes into contact on the breeding grounds, has not been previously emphasized.

2.3 The Breeding Biology of Herring Gulls and Glaucous-winged Gulls

The breeding biology of Herring Gulls (L. argentatus) in Europe and eastern North America has been studied in detail. Nesting habitat selection is flexible (Drury and Nisbet, 1972; Drury and Kadlec, 1974) and includes marshes (Burger, 1977), sand dunes (Tinbergen, 1960) and cliff faces (Goethe, 1960; Emlen, 1963; Harris, 1970) in both freshwater and marine environments. Modal clutch size is three. Conspecific predation accounts for most of the egg loss. Hatching success is usually 60 to 80 percent, including egg loss to predation and failure to hatch. Critical factors affecting fledging rate are chick loss through cannibalism, chick mortality because of aggressive behavior of adults, and weather conditions during the breeding season. Herring Gulls in eastern North America raise an average of one fledged chick per year (Keith, 1966; Kadlec and Drury, 1968). There is little information available to date on the breeding biology of argentatus in western North America.

The breeding biology of the Glaucous-winged Gull in the Pacific Northwest and Gulf of Alaska has been studied by Schultz (1953), Vermeer (1963), Ward (1973), Patten (1974), Hunt and Hunt (1976) and Patten and Patten (1975, 1976, 1977, 1978). Results of these West Coast investigations indicate breeding characteristics of "pure" glaucescens are quite similar to those of argentatus in characteristics which are presumably genetically determined, i.e., nesting habitat selection, time of breeding, and clutch size, as well as those parameters which fluctuate from year to year, such as hatching success (60-80%) and fledging success (usually averaging one chick per pair per year). The Glaucous-winged Gull, in addition, has the same plumage sequences as the Herring Gull (Schultz, MS), and similar adaptability to urban environments (Ward, 1973), although breeding populations of Glaucous-winged Gulls are generally confined to coastal environments.

There is a strong tendency for adult gulls, including argentatus and glaucescens, to return to natal colonies to breed, suggesting a degree of isolation between members of adjoining colonies (Gross, 1940; Paynter, 1949; Tinbergen, 1953, 1961; Drost et al., 1961; Ludwig, 1963;

Vermeer, 1963). In general, evidence to date indicates that the breeding biologies of glaucescens and argentatus are remarkably similar, although argentatus exhibits a greater tolerance for both marine and freshwater conditions than does glaucescens, which distinctly prefers marine habitats.

2.4 Narrow Hybrid Zones in Vertebrates

Studies of interbreeding reveal that most vertebrate hybrid zones, including those of gulls, are characteristically narrow, suggesting the applicability of general principles. Moore (1977) listed four hypotheses which are pertinent to the theoretical aspects of interbreeding between argentatus and glaucescens in southern Alaska.

The ephemeral-zone hypothesis states that hybridization is a transitory phenomenon and will end either in fusion of the hybridizing taxa by means of introgression or speciation (Dobzhansky, 1940; Sibley, 1957; Wilson, 1965; Remington, 1968). Known examples of stable hybrid zones, such as the contact between the Carrion Crow (Corvus corone) and the Hooded Crow (C. cornix) in central Europe, and the relationship between the flickers (Colaptes auratus auratus and C.a. cafer) on the Great Plains, provide evidence against this hypothesis for birds (Mayr, 1963; Short, 1965, 1969, 1970; Moore, 1977). Short (1970) pointed out that ephemeral zones as opposed to stable zones (see below) are the exception rather than the rule in avian hybrids.

The dynamic-equilibrium hypothesis postulates stable hybrid zones (Bigelow, 1965). This hypothesis reconciles the existence of narrow hybrid zones with the concept of coadapted gene complexes, and states that if two populations have diverged to the point where hybrids suffer depressed fitness, gene flow through the hybrid zone into the parental populations should be inhibited by selection. Where selection gradients are steep, intergradation should be restricted to a narrow zone between the parental populations. Gene flow from parental populations into the hybrid zone could "swamp" alleles which cause individuals to avoid hybridizing, and thus hinder the evolution of isolating mechanisms. Selection might also be slow, giving the appearance of a stable zone.

The hybrid superiority hypothesis states that the range of a hybrid population is determined by the extent of the environmental conditions within which the hybrids are superior (Anderson, 1949; Muller, 1953; Grant, 1971). Short (1972) suggested that hybrids are actually more "fit" than their parental types in stable hybrid zones, although strong selection may occur in parental populations against immigrant genes.

The ecotone-disclimax hypothesis postulates that hybrids can succeed in some areas, such as ecotones, or perpetually disturbed habitats, where competition from parental types is weak (Anderson, 1949). A related concept suggests stable hybrid zones are narrow because they tend to occur in ecotones which are themselves narrow (Moore, 1977).

The data collected in the contact zone between *glaucescens* and *argentatus* in southern Alaska is explored in light of the above hypotheses. The "best fit" of the southern Alaskan situation may involve combinations of one or more hypotheses, particularly the last three.

3.0 DESCRIPTION OF STUDY AREAS

3.1 The General Environment

This study was conducted in southern Alaska, northwestern British Columbia, and southwestern Yukon. The principal area examined was the south coast of Alaska between Juneau and Prince William Sound (Fig. 3). Earlier research in the Glacier Bay area, 110 km NW of Juneau, Alaska, had revealed interbreeding between Glaucous-winged and Herring Gulls (Patten and Weisbrod, 1974). This suggested a considerably larger zone of contact than that postulated by Williamson and Peyton (1963). The narrow coastal zone between Cordova and Juneau was therefore investigated in my study to determine the degree of contact between these gulls. This coastal region, between 30 - 160 km wide and 480 km long, oriented NW to SE along the Pacific Coast, is delimited by the Chugach - St. Elias Ranges to the east, the Pacific Ocean to the west, Prince William Sound to the north, and Icy Strait to the south. The investigation included all six major gull colonies within this area. Colonies outside the coastal zone of contact, i.e., on Middleton Island offshore in the Gulf of Alaska, and in Lake Louise in southcentral Alaska, were also studied for comparative purposes (Fig. 3).

The south coast of Alaska is a wild, relatively uninhabited stretch of North Temperate shoreline. It exhibits dramatic changes in relief, with high mountain ranges to 5800 meters in proximity to marine environments. Fjords, bays, river deltas, and occasional sandy beaches are characteristic of this coastline. Basic factors affecting climate are similar at practically all points along the coastal study area (United States Department of Commerce, 1963). The climate is west coast marine, with nearby ocean areas

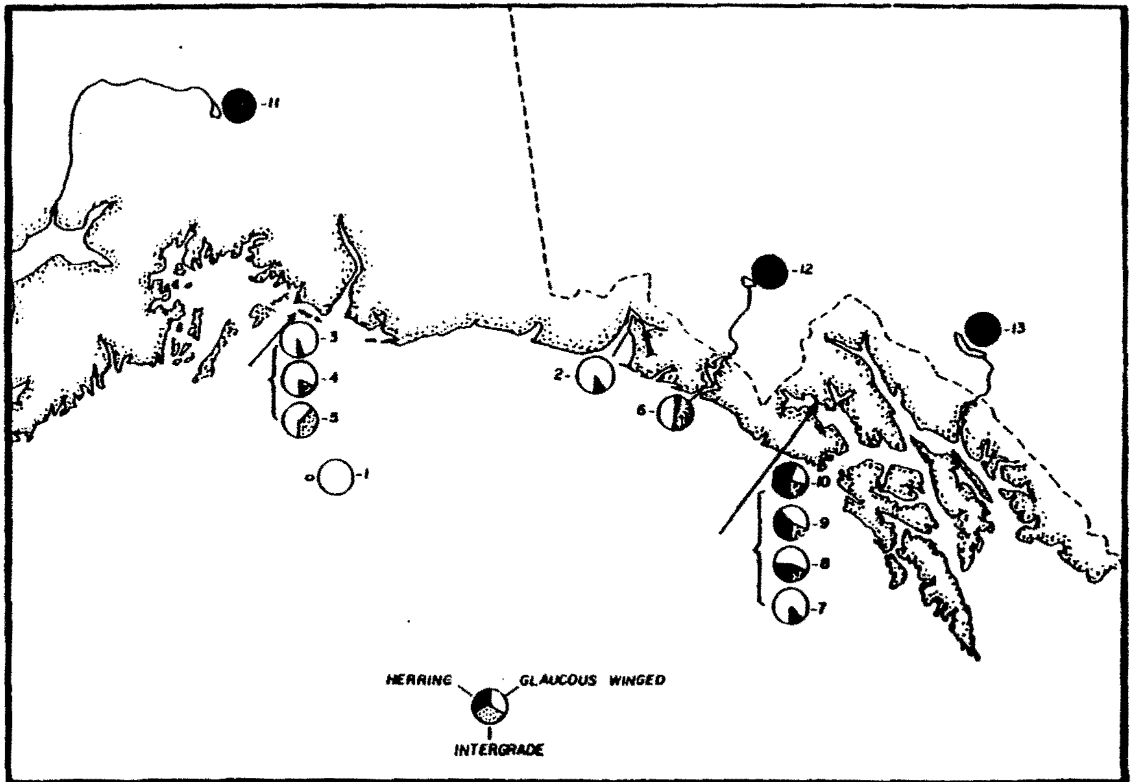

Fig. 3. Frequencies of Herring Gulls, Glaucous-winged Gulls, and intergrades as revealed in 1971 - 1978 surveys in southern Alaska, southwestern Yukon, and northwestern British Columbia. Refer to Table 4 for a key to colony identification numbers.

moderating daily and seasonal temperatures at, and near, sea level.

The area is exposed to frequent low pressure systems moving out of the Gulf of Alaska, providing abundant precipitation. The altitude of the rugged Fairweather, St. Elias, and Chugach Mountain Ranges intensifies precipitation on the coastal slopes as the prevailing westerly winds move the moisture-laden air onshore. Glacier Bay Ranger Station receives 225 cm precipitation annually (Streveler and Paige, 1971); Yakutat 338 cm (Alaska Geographic, 1975); and the Copper River Delta 250 cm (USDC, 1963). Maximum precipitation over the entire area usually occurs from August through November. Snowfall occurs principally from November through March and has an average annual depth ranging from 310 cm to 866 cm, with means at Yakutat of 370 cm and at Cordova of 317 cm (USDC, 1963). Much greater amounts of snowfall in the mountains have caused the formation of glaciers. The activity of the glaciers, in combination with major earthquakes (see below), has created a dynamically changing environment.

The northern interior region of the Pacific Northwest extends from northern British Columbia through southwestern British Columbia to south-central Alaska. This boreal region lies to the N and NE of the coastal range of mountains, and is characterized by a continuous belt of high plateau country, dotted with occasional lakes. The climate is much drier and more severe than the coast, with extreme summer and winter temperatures. Interior lakes and rivers freeze during the winter, forcing Herring Gulls to winter at sea. Coastal waters, by comparison, are generally ice-free.

3.2 Individual Study Sites

A description of the geological and ecological conditions of the individual study sites is essential to a thorough understanding of the effectiveness of the extrinsic barriers between Larus populations, the response of these populations to rapid environmental changes, and the time since contact between previously isolated forms.

3.21 North Marble Island in Glacier Bay

The entire Glacier Bay area was covered, until about 200 years ago, by a massive ice sheet that may have been more than 1300 m thick in places (Streveler and Paige, 1971). The ice has retreated rapidly since 1792, uncovering large terrestrial and marine areas. North Marble Island lies in the middle of the fjord known as Glacier Bay. North Marble Island is 110 km NW of Juneau, and supports the largest gull colony in the Bay (500 pairs) (Fig. 4). North Marble is about 600 m long and 300 m wide, and is surrounded by deep, cold, highly oxygenated waters and strong tidal currents. The island emerged from glaciation about 130 years ago (Streveler, pers. comm.), and has undergone rapid vegetative succession from exposed rock to young maritime spruce forest as have other areas along Glacier Bay (Fig. 5). However, gull nesting activities on the east, west, and north sides of the island have restricted the succession to a resistant meadow barley (Hordeum brachyantherum), which forms 70% of the ground cover on these sloping meadows. In marked contrast, other parts of the island are covered with spruce. The arrested succession suggests that pioneering gull populations colonized the island shortly after deglaciation.

3.22 Dry Bay

The gull colony (500 breeding pairs) at Dry Bay, 75 km SE of Yakutat and 150 km NW of North Marble Island, is located 4.8 km upriver from the mouth of the Alsek River on flat gravel bars in a rapidly changing, mixed alluvial-marine habitat (Figs. 6 - 7). The Alsek River rises

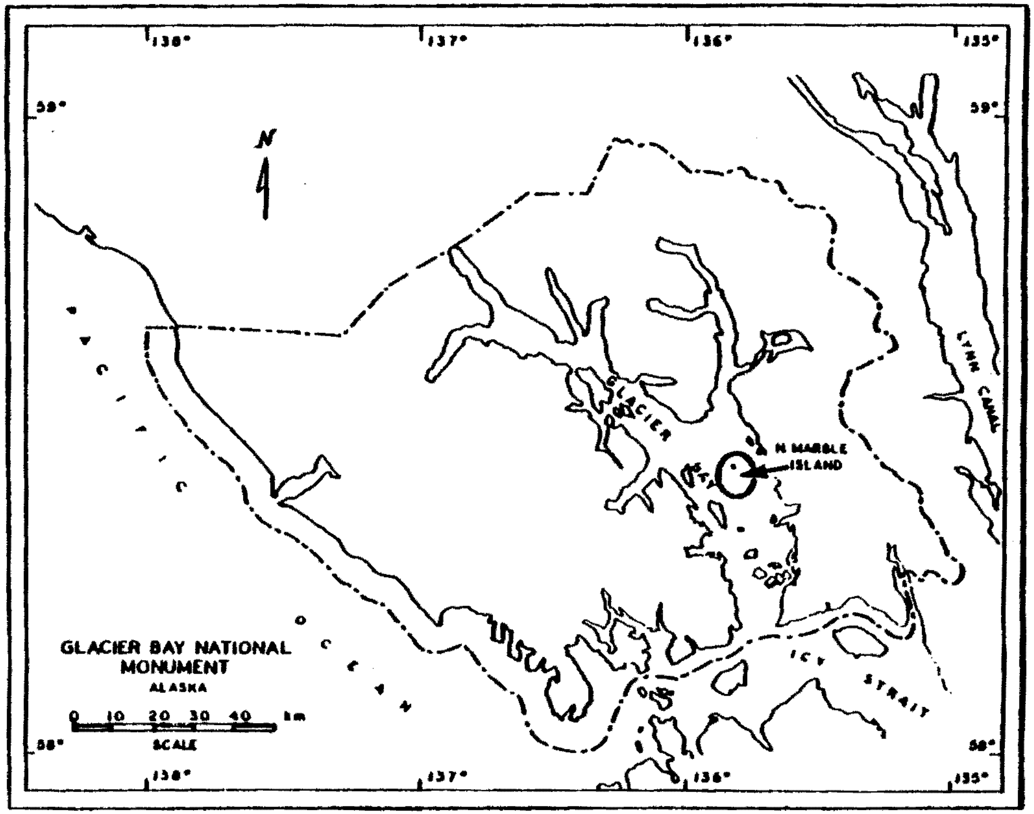

Fig. 4. North Marble Island lies in the middle of Glacier Bay and contains large marine bird nesting areas.

Fig. 5. North Marble Island is about 600 m long and 300 m wide, and is surrounded by deep, cold, highly oxygenated waters and strong tidal currents. The island emerged from glaciation about 130 years ago and has undergone rapid vegetative succession from exposed rock to young maritime spruce forest. However, gull nesting activities on the east, west, and north sides of the island have restricted succession to a resistant meadow barley (Hordeum brachyantherum).

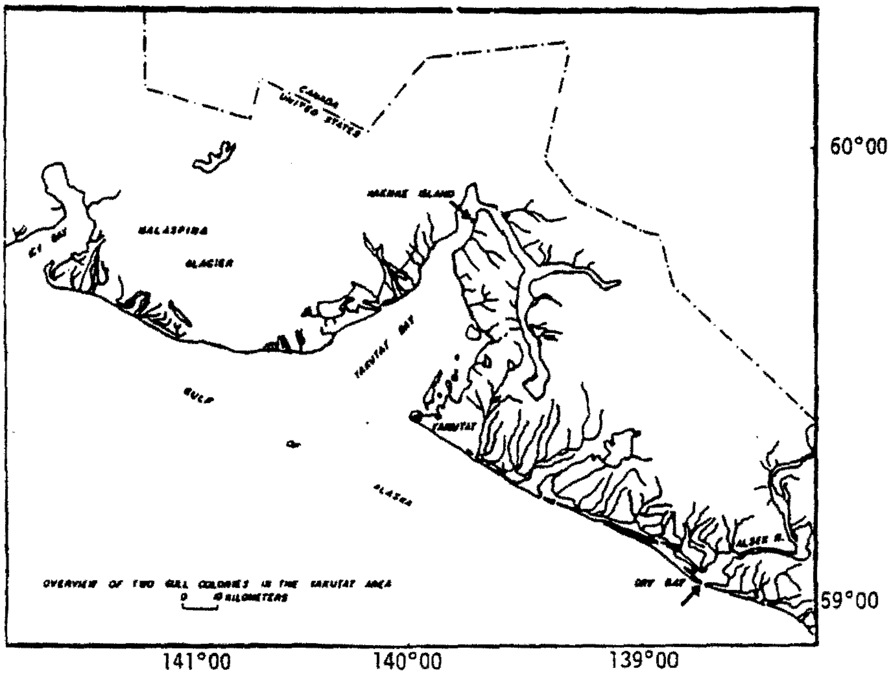

Fig. 6. Two gull colonies in the Yakutat area are located at Dry Bay, 75 km SE of Yakutat, and at Haenke Island, 50 km NE of Yakutat.

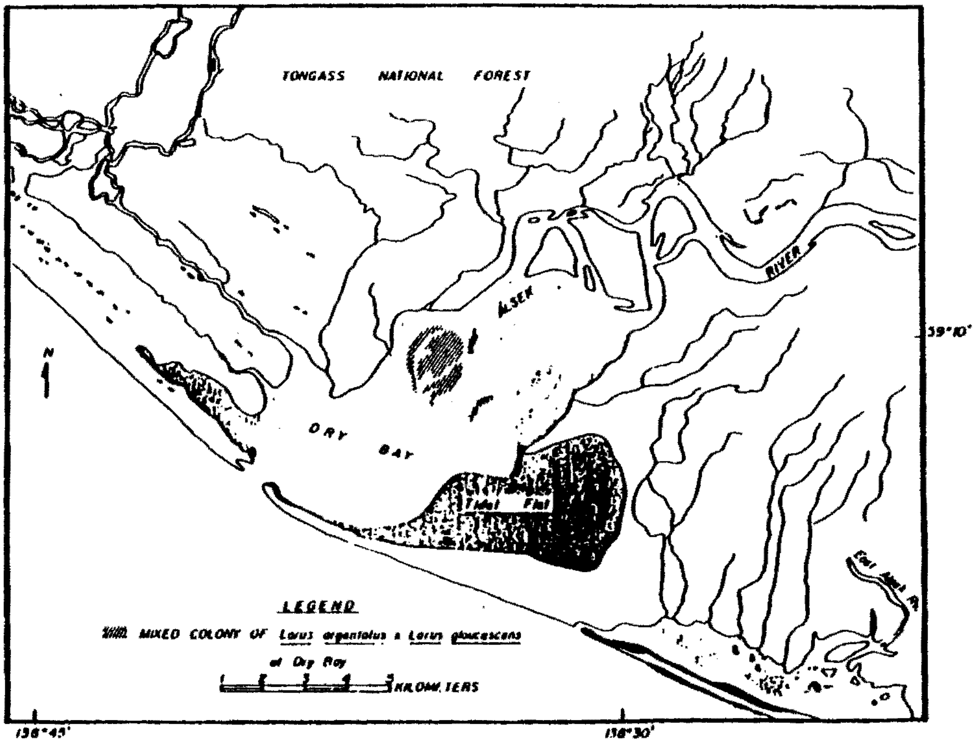

Fig. 7. The gull colony (500 pairs) at Dry Bay is located 4.8 km upriver from the mouth of the Alsek River on flat gravel bars.

in the Yukon, but also partially drains the Fairweather Range. It has carved one of the major breaks through the range of high mountains which separates the coastal and interior environments of the Pacific Northwest.

Dry Bay is the delta of the Alsek River. The river level at Dry Bay changes dramatically in response to rainfall and snowmelt. In some years, late summer high water stages wash completely over the gravel islands (Mork, pers. comm.). Water surrounding the gull colony is fresh, although silty, and carries ice floes from the Alsek Glacier, 28 km upstream. In Fall and Winter, powerful southeast storms cover the delta with heavy rains or snow. Winter winds with velocities greater than 160 kph drive over waves over 20 m in height onto the outer beaches at Dry Bay, occasionally inundating the delta with salt water.

Dry Bay is a geologically active, earthquake-prone area. Dry Bay apparently was not glaciated during Pleistocene times, but may have been the location of catastrophic flooding within the last 1000 years from the melting of glaciers which impounded lakes in the interior Yukon (Brogle, pers. comm.). A minor earthquake caused the mouth of the Alsek River to shift 1 km to the west in 1975 (Alaska Geographic, 1975). The gravel islands of the Alsek River Delta at Dry Bay are also subject to considerable repositioning because of frequent changes in the course of the river. Vegetation on the gravel bars is a sparse mixture of alluvial and maritime forms, dominated by red fescue (Festuca rubra) and river beauty (Epilobium latifolium), but includes beach rye (Elymus arenarius mollis).

3.23 Haenke Island

Haenke Island, located in Disenchantment Bay, 50 km NE of Yakutat, is often completely surrounded by pack ice from the nearby Hubbard Glacier

(Figs. 6, 8, 9). The glacier which once filled Yakutat Bay has shown massive expansions and contractions within the last 1000 years (Alaska Geographic, 1975). Haenke Island (1.6 x 1.0 km) has little level ground, and is covered with brushy vegetation dominated by alders (Alnus crispa). The north side of the island, facing the Hubbard Glacier, gradually inclines to an elevation of 75 m, and then drops precipitously, forming a south-facing cliff, where 200 pairs of glaucescens breed on a series of narrow terraces. Vegetation on the terraces is composed of grass (Hordeum brachyantherum) and fireweed (Epilobium angustifolium).

Haenke Island, similar to North Marble, is recently deglaciated, as indicated by the predominance of alders, but the exact date of deglaciation is not known. The gull colony at Haenke Island is the most geographically isolated of the sites examined; the St. Elias Range (to 5800 m) and the Malaspina Glacier (larger than the State of Rhode Island) prevent weather conditions of the interior Yukon from influencing the area.

3.24 Copper River Delta

The largest gull colonies in the northeast Gulf of Alaska are located on sandbar barrier islands off the Copper River Delta near Cordova, Alaska (Fig. 10). South of Cordova, the Copper River and the confluent Martin River have deposited sand and mud where they meet the sea, forming a large delta, 50 km wide. A few kilometers off the mouth of the Copper River a series of low sandbar and dune islands forms a partial barrier to ocean storms. These islands have been created by the deposition of sand and mud, and by earthquakes. They are constantly shaped and re-shaped by the counter-clockwise onshore currents of the Pacific Ocean (Fig. 10).

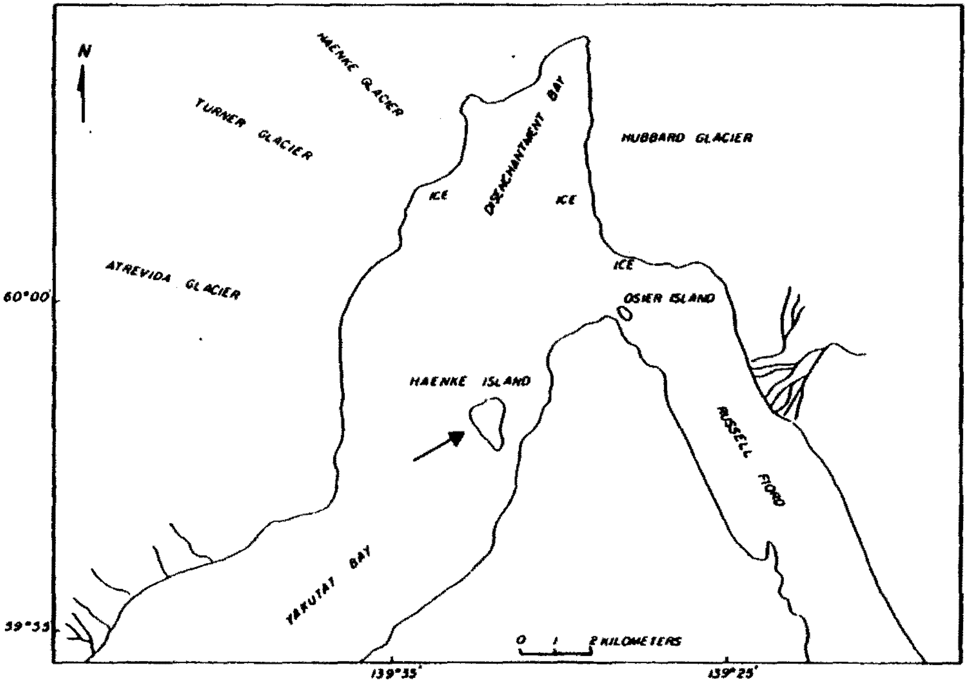

Fig. 8. Map of Haenke Island and surroundings in Disenchantment Bay, near Yakutat Bay, 50 km NE of Yakutat, Alaska. Note the proximity of four major glaciers. The advancing Hubbard Glacier threatens to close Russell Fjord and form a freshwater lake. Haenke Island is located less than 1 km from the mainland.

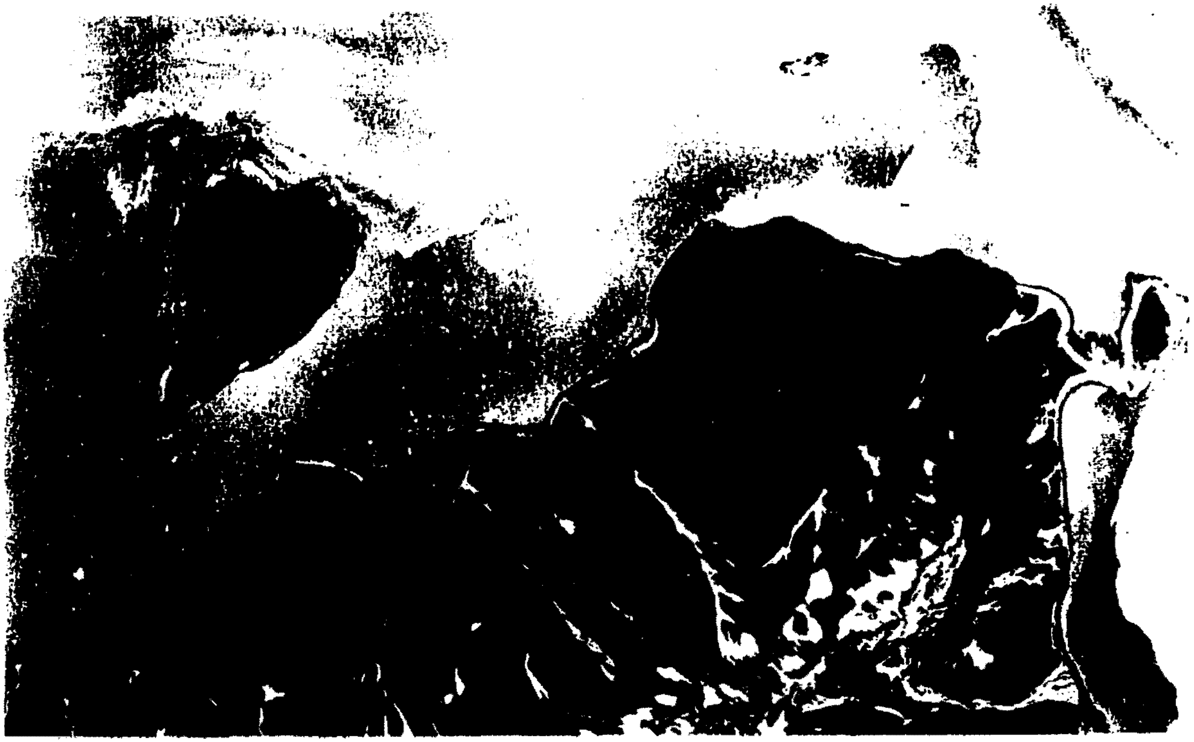

Fig. 9. Aerial photograph of Haenke Island. Note the ice floes and turbid outwash from the Hubbard Glacier. The gull colony at Haenke Island is located on a south-facing cliff (indicated by arrow).

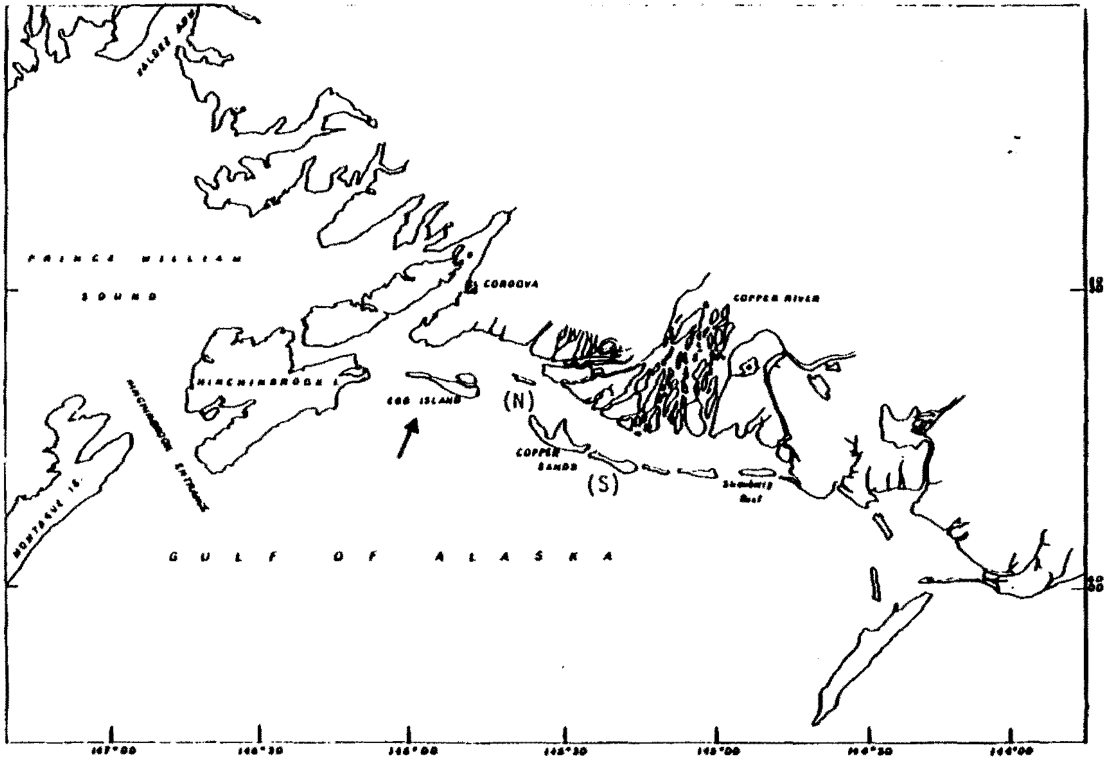

Fig. 10. Map of the Copper River Delta region and Prince William Sound, showing location of Cordova, the Copper River, Egg Island (arrow), Copper Sands (N), Copper Sands (S), and Strawberry Reef.

Janson (1975) wrote of major earthquakes occurring in the Copper River Delta at the end of the last century. The most severe earthquake recorded on the North American continent during modern times occurred in this area of Alaska in 1964. The entire Copper River Delta, including offshore islands, was uplifted an average of two meters in a series of severe shock waves (United States Forest Service, 1975). The abrupt uplift disrupted the complex delta ecosystem and altered the balance between fresh- and saltwater. Nutrient input from saltwater to the delta appreciably diminished and several species of intertidal invertebrates and nesting ducks declined in numbers. Willows (*Salix* spp.) and alders (*Alnus sitchensis*) began to replace grass and sedge marshes in some areas of the delta. Some tidal sloughs dried out (Scheierl and Meyer, 1976).

The sandbar barrier islands at the mouth of the Copper River experienced the same sharp geological forces as the delta itself, but because of the nature of the islands and the marine bird species using them, the resulting changes were quite different. Shallow saltwater channels between islets were eliminated and new ridges of sand dunes were formed, joining islets together. The actual land area of the barrier islands increased because of the uplift. Plant succession began on newly formed dunes, with beach rye (*Elymus arenarius mollis*) forming scattered tufts on the sandy surface. Meadows encroached on dunes as succession continued.

Large colonies of gulls nest on these meadow-covered dunes. The area upon which gulls can nest is increasing, so at the moment, large areas of unoccupied meadows are capable of supporting nesting gulls (Fig. 11). The major nesting islands at the mouth of the Copper River are Egg Island, Copper Sands, and Strawberry Reef.

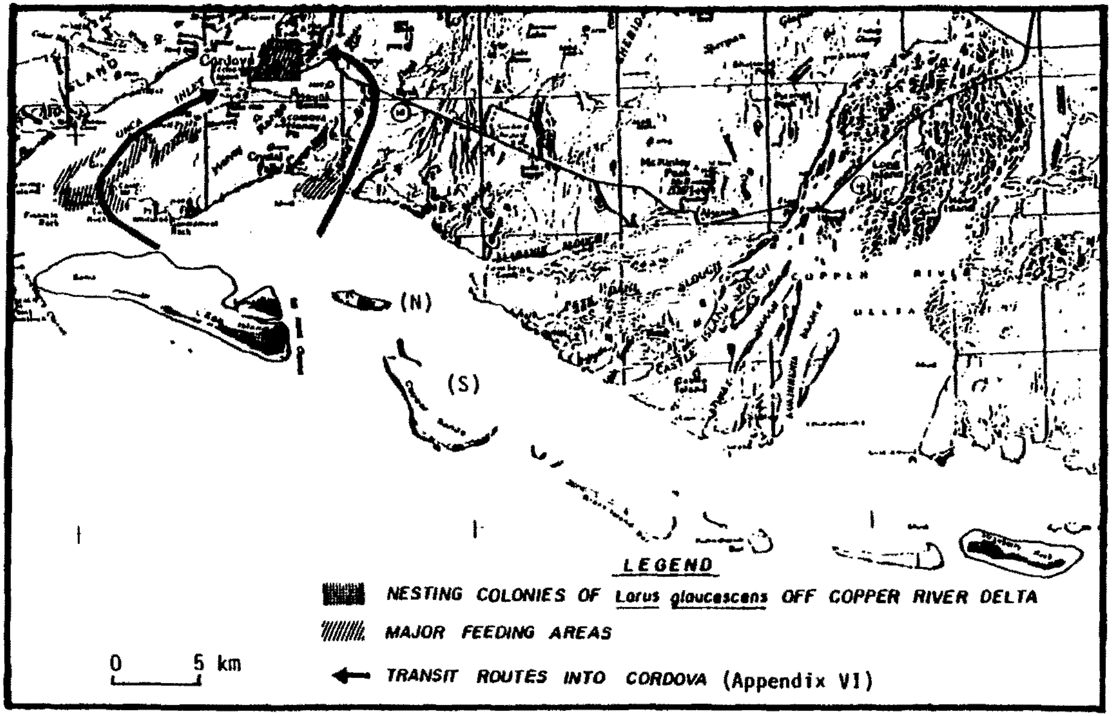

Fig. 11. Egg Island lies 20 km south of Cordova.
Copper Sands consists of two islands: (CS - S) and (CS - N).
Strawberry Reef lies 80 km ESE of Cordova.

Egg Island (10 x 4 km) lies 20 km south of Cordova (Fig. 11). Before the 1964 earthquake, Egg Island was a series of sandbars and dunes, but since the earthquake, with a tremendous increase in surface area, these have coalesced and formed one basic island, which is undergoing colonization by the beach rye *Elymus* (Figs. 12, 13). Egg Island in 1975 - 1978 consisted of a series of dunes on an east-west axis, supporting the largest gull colony in the northeast Gulf of Alaska, approximately 10,000 pairs of *glaucescens*.

Copper Sands consists of two islands: an older island (CS - S) and a new islet (CS - N). Copper Sands (S) is a bar 12 km long, and is one of a series of barrier islands at the mouth of the Copper River. It lies 5 km ESE of Egg Island and 24 km SE of Cordova (Figs. 10 - 11). It consists of a series of unstabilized dunes extending from southeast to northwest. Copper Sands has risen in elevation since the 1964 earthquake, but has much less vegetation than Egg Island. The gull colony of 800 pairs is located on three dunes covered with the beach rye (*Elymus*) at the SE tip of Copper Sands (Fig. 14).

Copper Sands (N) is a small, newly formed island less than a kilometer long. It lies 2.5 km ENE of Egg Island off the mouth of the Eyak River. It did not exist before the 1964 earthquake, but now contains several dunes with 150 pairs of *glaucescens* nesting in the *Elymus* (Fig. 11). Other small barrier islands between Copper Sands and Strawberry Reef at the east end of the delta support few nesting gulls because of the lack of suitable vegetation, a result of intense sand scouring during winter high pressure systems (Isleib and Kessel, 1973; Michelson, 1975). Gulls use these unvegetated islands (Kokinhenik, Softuk, and Grass Island Bar) as resting areas (Fig. 11).

Fig. 12. Before the 1964 earthquake, Egg Island was a series of sandbars and dunes, but since the earthquake, with a tremendous increase in surface area, these have coalesced and formed one basic island. The study area SW of the Egg Island Light is indicated by the arrow (upper right).

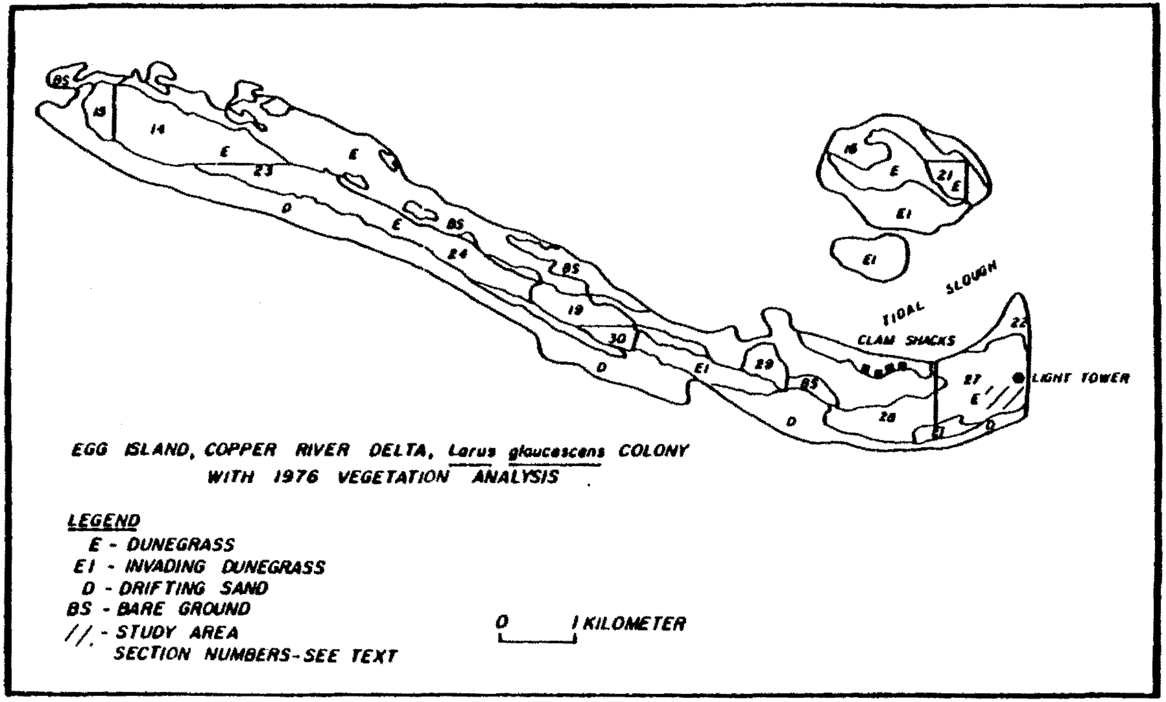

Fig. 13. Egg Island is undergoing colonization by the beach rye grass Elymus (invading dunegrass). The study area was located SW of the Egg Island Light Tower.

Fig. 14. The gull colony of 800 pairs is located on three dunes (arrows) covered with beach rye (Elymus) at the SE tip of Copper Sands (S).

Strawberry Reef, 8 km x 3 km, is the easternmost barrier island at the mouth of the Copper River. It lies 80 km ESE of Cordova and contains the second largest _glaucescens_ colony in the delta, with 2000 gull pairs nesting in the _Elymus_ (Figs. 10, 11, 15). Strawberry Reef is separated from the mainland by shallow tidal channels. The island is undergoing vegetative succession on recently uplifted areas, thus becoming more suitable to nesting gulls. Strawberry Reef, as Egg Island, consists of wide ocean beaches, unstabilized dunes, and mud flats but differs from Egg Island in that it has increasingly large thickets of spruce and alder.

3.25 Middleton Island

Middleton Island (8 km x 1.6 km) is located in the Gulf of Alaska 130 km south of Cordova (Fig. 3). It extends along a NE - SW axis and covers about 890 hectares. The shoreline is nearly surrounded by driftwood, reefs, rocks, and heavy kelp. The bedrock is Cenozoic glacial conglomerate. The surface of the island, dotted with occasional large Pleistocene boulders known as "glacial erractics," consists of a series of step-like terraces above former sea cliffs. The terraces originated during earthquake uplifts, which caused the island to rise above sea level. The last uplift, which occurred during the 1964 earthquake, increased the island's elevation by 4.5 m. The eroding cliffs below the terraces are now bordered by sandy and marshy areas above the intertidal. The terraces merge into dunes above a sandy beach at the north end of the island. The island gradually gains elevation from north to south. At the southern end, rows of conical to ellipsoidal mounds rise to heights of 6 m above the level of the highest terrace, which is approximately 42.5 m above sea level. The climate on Middleton Island

Fig. 15. The gull colony at Strawberry Reef is located on Elymus-covered dunes (arrows). Strawberry Reef is the easternmost barrier island at the mouth of the Copper River and is separated from the mainland by shallow tidal channels.

is mild, but rainy, with prevailing southeasterly gales.

The terraces are covered with wet, grass-forb meadows, dominated by Calamagrostis spp., Carex spp., and Heracleum lanatum. Willows (Salix barclay) and salmonberry (Rubus spectabulus) form thickets on meadow margins and on terrace slopes.

Rausch (1958) reported Glaucous-winged Gulls as non-breeders on Middleton Island. At present, approximately 750 breeding pairs nest primarily in two types of habitat: in an Elymus, driftwood, and boulder mosaic below the eroding cliffs, and in the upland Calamagrostris-covered mounds at the southern end of the island. The driftwood-boulder habitat was exposed by the 1964 earthquake. The glaucescens breeding population in 1978 by no means approached full use of the available nesting habitat of this island.

3.26 Lake Louise

Lake Louise, 8 km x 12 km, lies 51.2 km NW of Glenallen, in the Copper River Basin of southcentral Alaska. Lake Louise drains through Susitna Lake and the Tyone and Susitna Rivers to Cook Inlet (Figs. 16, 17).

A gull colony is situated on a steeply sloping rock known as "Bird Island," 1 km from the west shore of the lake. Bird Island (100 x 20 x 10 m; 0.36 hectare), is radically different in appearance from other spruce-covered islands in Lake Louise. Its vegetation, composed of lichens, mosses, grasses, resistant forbs, and woody vines, indicates disturbed conditions, reflecting heavy, long-term use by birds. Living plants are absent in the peat formation along the island's crest, area of heaviest bird use. At least 77 pairs of Herring Gulls (Larus argentatus smithsonsonianus) and 14 pairs of Double-crested Cormorants (Phalacrocorax auritus) nest on the island. A comparison of photographs taken in 1963 (Hayes, pers.

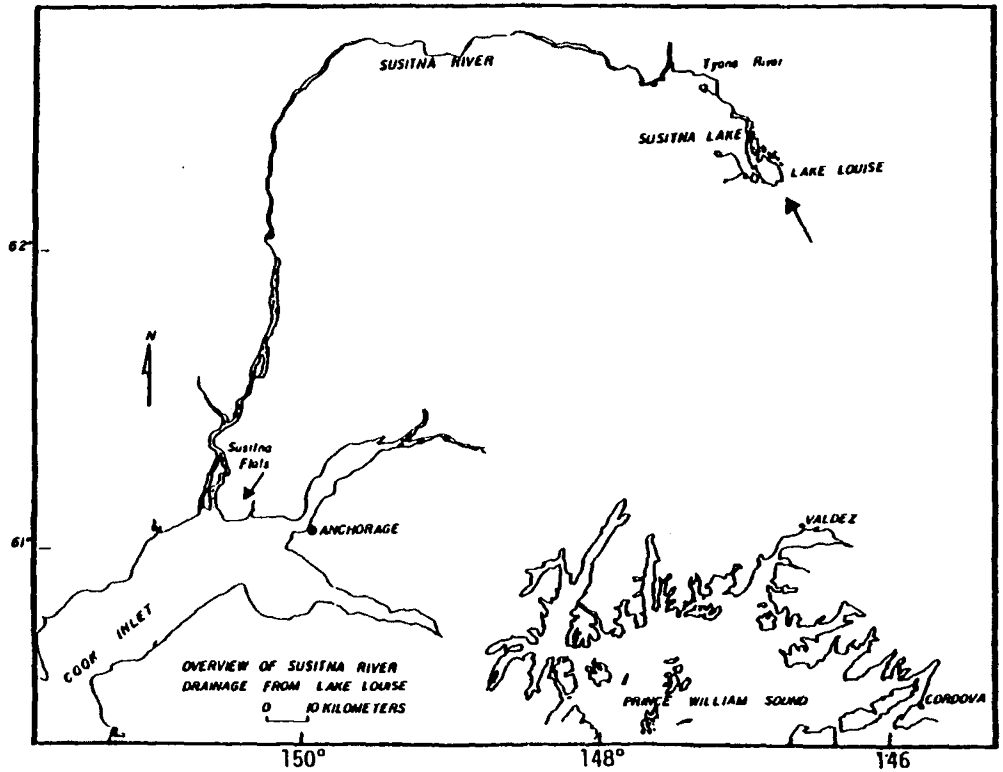

Fig. 16. Overview of Susitna River drainage from Lake Louise to Cook Inlet, showing Prince William Sound, Cordova, Valdez, and Anchorage. Lake Louise and Susitna Flats are indicated by arrows.

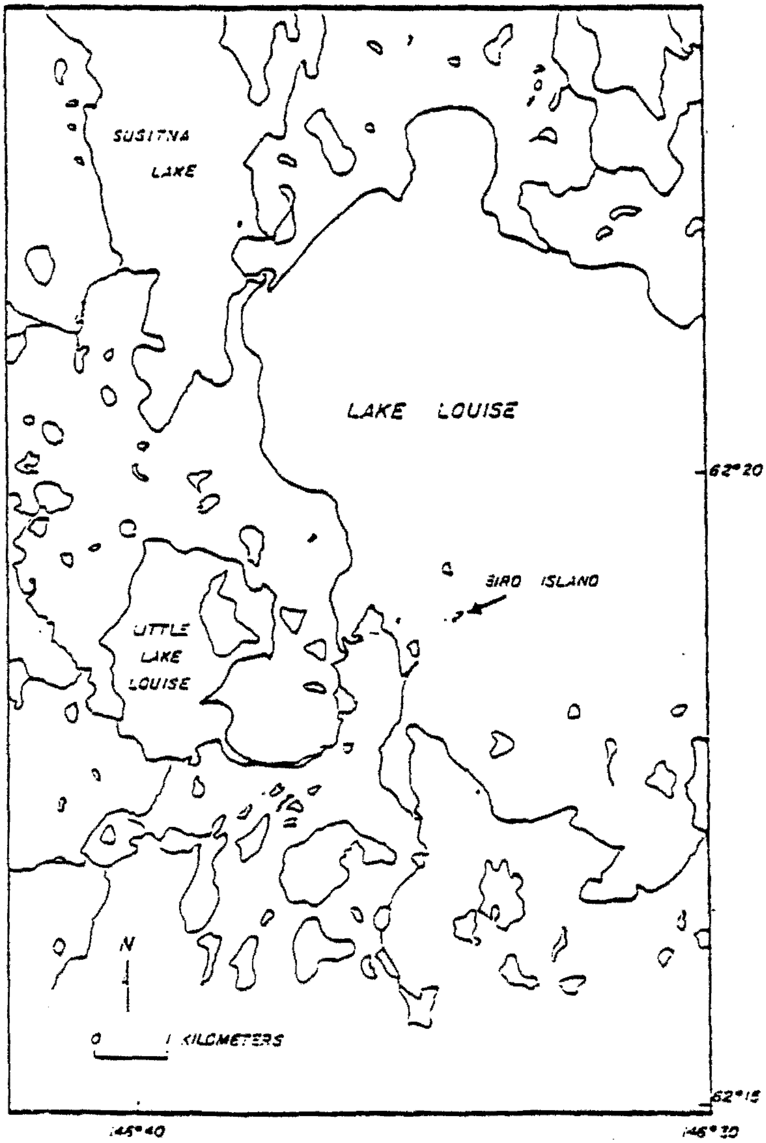

Fig. 17. Overview of the Lake Louise area, showing Susitna Lake and Little Lake Louise. Bird Island (arrow) lies 1 km from the west shore of the lake and contains 77 pairs of Larus argentatus smithsonianus.

comm.) with those of this study, taken in 1978, show little change in the island's vegetation structure. This is in marked contrast to the rapidly changing conditions in gull colonies previously examined along the south coast of Alaska. Gulls and cormorants have inhabited Bird Island as long as local residents can remember and probably centuries longer.

3.3 Summary of Study Areas

The gull colonies with which this study is concerned are located on a series of islands in southern Alaska, extending over 4° of latitude (710 km) from Glacier Bay, northwest of Juneau, to Cordova, and thence inland to Lake Louise in southcentral Alaska. (Other small interior colonies were studied in British Columbia and the Yukon.) (Fig. 3). Aquatic environments include offshore marine, the coast, tidal bays, river deltas, fjords, and freshwater lakes. The geology of the offshore and coastal sites is rapidly changing, influenced by recent deglaciation, major earthquakes, and floods. Vegetation within the colonies, composed of tolerant, resistant invaders of the early successional stages, reflects both disturbance by gulls and rapid environmental changes. Slope and substrate of the gull colonies vary from horizontal gravel bars to nearly vertical cliff faces (Table 2).

One offshore site, Middleton Island, and four coastal colonies, Egg Island, Strawberry Reef, Copper Sands, and Haenke Island, contain only *glaucescens*. Two coastal colonies, North Marble and Dry Bay, contain sympatric and interbreeding *argentatus* and *glaucescens*. The interior colony at Lake Louise is composed of only *argentatus*. Table 3 contains the principal periods of study for these *Larus* colonies.

Table 2 Principal Study Areas -- Larus Colonies in Southern Alaska

Colony	Coordinates N	Coordinates W	Species*	Aquatic Environment	Substrate/Geology/ Slope	Dominant Vegetation
North Marble	58°40'	136°04'	argentatus, glaucescens	tidal bay	recently deglaciated (120 yrs) sloping island	Hordeum meadows
Dry Bay	59°08'	138°25'	argentatus, glaucescens	river delta/ coastal marine	shifting flat gravel bars	sparse alluvial/ maritime mix
Haenke Island	59°58'	139°32'	glaucescens	tidal bay	recently deglaciated island cliff face	Hordeum/Alnus on cliff terraces
Strawberry Reef	60°13'	144°51'	glaucescens	brackish delta/ coastal marine	earthquake influenced low sandbar island	Elymus
Copper Sands	60°18'	145°31'	glaucescens	brackish delta/ coastal marine	earthquake influenced low sandbar island	Elymus
Egg Island	60°23'	145°46'	glaucescens	brackish delta/ coastal marine	earthquake influenced low sandbar island	Elymus
Middleton Island	58°24'	146°19'	glaucescens	offshore marine	earthquake influenced offshore island	Calamagrostris; Elymus, driftwood
Lake Louise	62°20'	146°32'	argentatus	freshwater lake	sloping lake islet	Calamagrostris meadows

* Large white-headed Larus populations during breeding season.

Table 3. Principal Periods of Study for *Larus* Colonies in Southern Alaska

Study Area	Year	Periods of Study
Glacier Bay	1971	17 July - 11 August
North Marble Island	1972	15 May - 14 August
North Marble Island	1973	27 April - 9 August
Outer Coast of Glacier Bay National Monument	1974	23 May - 4 August
Haenke Island	1974	14 - 15 June
Dry Bay	1974	17 - 18 June
Dry Bay	1975	28 June - 3 July
Dry Bay	1977	4 May - 23 July
Egg Island	1975	18 June - 18 August
Egg Island	1976	20 May - 15 August
Strawberry Reef	1976	29 - 30 June
Copper Sands (S)	1976	1 July
Lake Louise	1976	24 - 25 August
Lake Louise	1977	9 - 10 June; 8 - 10 July 1 - 3 August
Lake Louise	1978	1 - 3 August
Middleton Island	1978	19 May - 7 July
Egg Island	1978	16 July - 25 July

4.0 MATERIALS AND METHODS

4.1 Colony Selection

This research involved 28 months field work during eight field seasons (1971 - 1978). Following the discovery in 1971 of hybrid gulls nesting on a cliff face in a recently deglaciated fjord (Patten and Weisbrod, 1974), an extensive survey was conducted (1971 - 1978) to determine location, distribution, habitats and numbers of parental forms and hybrids in breeding populations of gulls between Juneau and Prince William Sound, Alaska (Table 4). The survey indicated three coastal sites (North Marble, Dry Bay, and Egg Island), one offshore site (Middleton Island), and one interior location (Lake Louise) were suitable for intensive study, for reasons of accessibility, recent geological history, and species composition. Each location had distinguishing characteristics and represented the major colony for a considerable geographical area. The offshore and interior sites provided habitats preferred by what are regarded as pure types of Glaucous-winged and Herring Gulls, respectively. The three coastal colonies selected for intensive study presented a gradation of intermediate habitats, from a sandbar barrier island, to a recently deglaciated fjord, to a river mouth connecting coastal with interior environments. Hybridization was expected in all three intermediate habitats. Additional visits were made to three other coastal locations (Copper Sands, Strawberry Reef, and Haenke Island) and two interior sites (Dezadeash Lake, Yukon Territory, and Atlin Lake, British Columbia) to gather supporting information on colony composition and nesting habitat selection. Breeding adult gulls were collected at the eight Alaskan colonies to determine the occurrence and extent of

Table 4. Gull colony survey. The colony numbers correspond to the numbers on Fig. 3.

Colony	Number	Number of Individual Adult Gulls Observed From a Distance				Number of Breeding Adult Gulls Collected, Photographed, and Analyzed in Detail			
		Total	Herring	Hybrid[a]	Glaucous-winged	Total	Herring	Hybrid	Glaucous-winged[b]
Middleton Island	1	116	--	--	116	5	--	--	5
Haenke Island	2	100	--	10	90	10	--	2	8
Egg Island	3	678	--	68	610	56	--	6	50
Copper Sands	4	200	--	50	150	16	--	5	11
Strawberry Reef	5	200	--	75	125	25	--	10	15
Dry Bay	6	224	3	120	101	38	4	25	10
North Marble	7	741	20	30	691	4[c]	1	3	--
Tlingit Point	8	16	4	3	9	--	--	--	--
Sealer's Island	9	35	15	8	12	--	--	--	--
Johns Hopkins Inlet	10	50	30	10	10	--	--	--	--
Lake Louise	11	154	154	--	--	11	11	--	--
Dezadeash Lake, Yukon	12	60	60	--	--	--	--	--	--
Atlin Lake, B.C.[d]	13	75	75	--	--	--	--	--	--
		2649	361	374	1914	165	15	51	99

[a]A gull would probably require a Wing Hybrid Index of 3 - 5 to be recognized as a hybrid in the field and thus these figures are conservative.

[b]Considerable difficulty was encountered in defining "pure" glaucescens in the study area. Most individuals show evidence of introgression (cf. Section 4.5; Figs. 32, 37).

[c]Permit restrictions did not allow collection of more than four gulls in Glacier Bay National Monument.

[d]This colony requires further investigation. Field observations suggested the population was phenotypically argentatus, but study skins in the British Columbia Provincial Museum (BCPM), collected at Atlin Lake in 1916, suggest glaucescens influence.

See Table 5 for further details.

introgression.

4.2 Determination of Isolating Mechanisms

An investigation of pre- and post-mating isolating mechanisms required the analysis of nesting habitat selection, mating patterns, and reproductive productivity of the Glaucous-winged, Herring Gull, and intermediate forms.

4.21 Nesting Habitat Selection

Study plots representative of variations in structural features of the habitat, i.e., slope, substrate, and cover, were established in each of the eight major colonies[1] and in five minor colonies[2] in order to discern potential nesting habitat preferences. The density of nests and the requirement for adequate sample sizes determined the size of each study area, but where possible, the natural features of the habitat defined its borders. The study area on Egg Island (an arbitrary 150 meter square southwest of the USCG Light Tower) was an exception because of the expanse of uniform vegetation covering the island.

4.22 Mating Patterns

Mating patterns were studied for evidence of random or assortative mating. The visual assessment of the variable color characters of the iris and subterminal portions of the primaries of adult gulls in mixed colonies was accomplished by careful study with binoculars and 25 x telescope. The study included 112 nests in two study plots at Dry Bay and 452 nests in four study plots on North Marble.

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[1] North Marble, Dry Bay, Egg Island, Copper Sands, Strawberry Reef, Haenke Island, Middleton Island, and Lake Louise, Alaska.

[2] Glacier Bay, Alaska (Johns Hopkins Inlet, Sealer's Island, Tlingit Point), Atlin Lake, British Columbia, and Dezadeash Lake, Yukon.

4.23 Reproductive Productivity

A total of 933 nests in all colonies were studied for reproductive productivity of Glaucous-winged, Herring Gull, and intermediate forms. The nests under study were marked with numbered forestry stakes at the beginning of each investigation. Numbers of eggs and chicks were recorded during sequential visits to determine clutch size and hatching success. Visits through the colonies averaged every three days during the egg stage, and every four days during the chick stage. The information was recorded in the National Oceanic Data Format 035 "Flat Colony Survey" (Appendix I). Chicks were banded to establish fledging success. The presence of both parental types and many intergrades of variable phenotypes within the colony at Dry Bay required more detailed methods. Chicks of known parentage at Dry Bay were web-tagged with numbered fingerling fish tags immediately upon hatching. The same chicks were banded at three weeks of age, with 2.5 cm tall, butt-end aluminum bands placed upon the left tarsus. The reference numbers were repeated twice vertically around the band (Sladen et al., 1968). A 2.5 cm plastic band, with engraved 3-digit alphanumeric codes (A001-A000) was placed upon the right tarsus, enabling individual recognition of the chicks from distances up to 35 meters. The productivity of "pure" and mixed pairs could be verified by this procedure.

4.3 Mensural Characters

Breeding adult gulls (n = 165) were collected in Alaska to obtain morphological evidence of the occurrence and extent of gene flow between Glaucous-winged and Herring Gulls. The gulls were taken by shotgun after they flew up from nest sites. A vernier calipers, accurate to the nearest

Table 5

Summary of Sample Sizes

(Extension of Table 4)

Adult Gulls Observed from a Distance	Breeding Adults Collected and Analyzed	Pairs Studied for Nesting Habiing Selection & Mating Paterns	Pairs Studied for Reproductive Productivity	Museum Specimens Examined
2649	165[1]	718	933	506

[1] 23 additional gulls, some of which were non-breeders, were captured at the Cordova municipal dump. A comparative analysis of these gulls is provided in Appendix VI.

millimeter, was used to obtain standard measurements of the following characters: culmen length, bill depth at posterior nares; bill depth at posterior nares; bill length from side of the anterior nares to tip; diagonal tarsus length; chord of closed (flattened) wing. Weight was measured by a Pesola gram scale, accurate to the nearest gram. The information was recorded on a Gull Data Sheet devised for this study (Appendix II). Measurements of the same characters have been used in previous gull studies and are of comparative value (Smith, 1966b). Analysis of these characters is contained in Appendix IV. Brood patches and condition of the gonads, noted upon dissection, verified breeding status. Table 5 provides a summary of sample sizes of adult gulls analyzed, museum specimens examined, and breeding pairs studied.

4.4 Investigation of Colorimetric Characters

The investigation of colorimetric characters consisted of recording and analyzing iris, orbital ring, and primary feather pigmentation of 165 breeding adult gulls collected in southern Alaska during this study. Nine additional specimens from Lake Louise, collected by Dr. F.S.L. Williamson, were also analyzed as part of this sample.

4.41 Specification and Description

The colors of the iris, orbital ring, and wing tip influence species recognition in certain large white-headed gulls (Smith, 1966b). A rapid and precise method of identifying and recording these characters was important to the study of variation in freshly collected specimens, and in the investigation of mating patterns. The Munsell System of Color Notation (Munsell Skin, Hair, and Eye Color Charts, Matte Finish Edition) and the Munsell Neutral Value Scale (Munsell Color Co., Baltimore, MD) (Appendix III) were used to provide a basis for objective comparison.

The Munsell Charts were used in the field because gull soft part colors may fade or otherwise change rapidly after a specimen is taken (Fig. 18). The colors of the iris, orbital ring, primaries, tarsi and feet of specimens were described in writing immediately after collection, compared directly to the standard charts of the Munsell Notation, and photographed with Kodacolor II film.

4.42 Analysis

Initial observations of the range of morphological variation and pairing of large gulls in the southern Alaskan contact zone suggested occurrence of second-generation hybrids and backcrosses. An efficient comparison of the interbreeding populations required a method of portraying the variation exhibited by the parental types and intermediate forms. Anderson's (1936) original techniques for analyzing hybridization, consisting of a list of differences between the hybridizing entities, have been gradually refined to a quantitative approach, known as the hybrid index method. This method involves numerical scores for the characters which differ between the two populations (Anderson, 1949; Sibley, 1954). Three separate hybrid indices were created for the analysis of colorimetric characters in this study: the iris (IHI), the orbital ring (OHI) and the wing hybrid index (WHI) primary of feather pigmentation. Further, a composite index (CHI) was developed to provide a more complete investigation of the variation in colorimetric characters.

4.43 Iris Pigmentation

Iris color may function as an important factor in species recognition, and thus as an isolating mechanism among certain large white-headed gulls (Smith, 1966b). Field observations of more than 2600

Fig. 18. The Munsell Charts were used in the field to provide a basis for objective comparison of soft part colors (iris and orbital ring).

individual gulls (Table 4) suggested a considerable degree of variation between dark-eyed glaucescens and light-eyed argentatus phenotypes. For this reason, the variation and distribution of iris pigmentation was analyzed by four different, although related, methods involving qualitative and statistical comparisons of both separate and combined iris parameters. First, a hybrid index (IHI) was created to determine the range of iris colors (cf. Analysis, Section 4.42). For each bird collected, the color of the iris as a whole was recorded on a scale of 1 to 6 to facilitate statistical analysis, with 1 = brown (Munsell 2.5 YR) and 6 = yellow (Munsell 5 Y). Second, the means of the iris color indices were ranked in groups by colony, according to their statistical similarity, as determined by the Duncan's Multiple Range Test (cf. Statistical Procedures, Section 4.6). Third, iris color was subdivided into the separate Munsell categories (parameters) of hue (H), value (V), and chroma (C) (Appendix III), and the frequency distributions of each category in each colony were compared qualitatively among the populations. Fourth, the numerical designations of the three iris parameters were combined to produce the complete Munsell Notation (H V/C = a color) for each individual specimen, and the resulting iris color frequencies were compared qualitatively for each population.

4.44 Orbital Ring Pigmentation

The orbital ring of a gull is that fleshy portion of the eyelid which is visible when the eye is completely open. The orbital ring forms a circle around the opened eye, and is variously colored in different species of gulls. The orbital ring, along with the iris, contrasts against the white head of the gull, and may function as an isolating mechanism among certain species (Salomansen, 1950; Macpherson, 1961; Smith, 1966b).

The variation and distribution of orbital ring pigmentation was examined to determine the possible function as a recognition character between argentatus and glaucescens. Orbital ring pigmentation was recorded on a scale of 1 to 9, with 1 = dark pink (Munsell 5 R) and 9 = yellow (Munsell 5 Y). The scale became the index upon which statistics were computed. Some gulls had uniformly pigmented orbital rings; others had orbital rings composed of two, or occasionally three hues. In such cases the means of the two or three indices were used for analysis. An analysis of variance was used to test the significance of the observed differences among colonies, and subsequently, the means of the eight populations were grouped according to their statistical similarity, as determined by the Duncan's Multiple Range Test. In addition, since statistics based upon means may obscure qualitative differences between populations, the frequency distributions of both uniformly colored and multicolored orbital rings were compared qualitatively by colony.

4.45 Primary Feather Pigmentation

Primary feather pigmentation was recorded by means of a wing hybrid index (WHI) with six categories, developed by Ingolfsson (1970), and modified for this study[1] (cf. Appendix VI). The Index, as used in this study, was based upon the pattern (extent) of melanin deposition in the subterminal portions of the outer primary feathers, and on the intensity of melanin in the same area, as rated by the Munsell Neutral Value Scale. The index included six categories of primary

[1]Ingolfsson defined typical hyperboreus as '0' and typical argentatus as '5'.

feather pigmentation, ranging from typical glaucescens, with primaries the same shade as the mantle (rated as N6/ on the Munsell Scale; an index value of WHI - 1) to typical argentatus, with primaries of intensive black pigment (Munsell N2/; WHI - 6).

The six categories of the wing hybrid index were defined by the varying combinations of the intensity and pattern of melanin on the subterminal portions of the primaries. As the intensity of melanin increased, the pattern included progressively more of the subterminal portions of the outer primary feathers. (The definitions of the categories used are given in Figure 19, and typical examples of the wing patterns are shown in the Frontispiece). Since all gulls were collected during the breeding season, most individuals were molting the innermost primaries (6th and 7th) but not the outermost primaries (8th, 9th, and 10th). In any event, the outermost primaries are most useful in taxonomic discrimination. When an apparent difference occurred in melanin intensity between the old and new outer primaries, the shade of the new primary was used in assigning the index. Feather wear sometimes occurred on the extreme distal tips of the primaries. Occasionally, the wear extended to the apical white spots on the 9th and 10th primaries (known as the "mirrors")(cf. Poor, 1946). However, such feather wear did not change the pattern of melanin on the subterminal portions of the feathers. Fading, which was occasionally observed in museum specimens, slightly altered the intensity of melanin, but was not sufficient to alter the wing hybrid index (i.e., argentatus primaries of Munsell N2/ fade to Munsell N2.25/)[1] (Fig. 19).

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[1]"Greys" fade towards "pale grey"; "blacks" fade towards "brown" (R. Clayborne, pers. comm.).

HYBRID INDEX OF PRIMARY FEATHER PIGMENTATION

MUNSELL NEUTRAL VALUE SCALE

Hybrid Index	Munsell Scale	Verbal Description
0	N7/	primaries lighter than mantle (atypical Cordova _glaucescens_)
1	N6/	primaries same shade as mantle (_glaucescens_)
2	N5/	primaries 1 shade darker than mantle (hybrid)
3	N4/	primaries 2 shades darker than mantle (hybrid)
4	N3.25/	primaries 3 shades darker than mantle (hybrid)
5	N2.5/	primaries blackish (hybrid)
6	N2/	primaries black (_argentatus_)

Fig. 19. Hybrid Index of Primary Feather Pigmentation (WHI). The Hybrid Index is a quantitative approach to analyzing hybridizing entities. The Hybrid Index consists of numerical scores for the characters which differ between the two populations. This Hybrid Index is keyed to the Munsell Neutral Value Scale.

Macpherson (1961) and Barth (1968) noted minor differences in the wing tip patterns of male and female argentatus, i.e., the restricted black pattern of the 9th primary (the "thayeri" pattern) occurred more often in argentatus females than in males. Although these slight differences in primary feather pigmentation were noted in some adult argentatus during this study,[1] the differences were not sufficient to alter the wing hybrid index used in this study.

4.46 Composite Hybrid Index

The scores for the primaries, irides, and orbital rings were added together to produce a "composite hybrid index" (IHI + OHI + WHI = CHI), which allowed a more thorough exploration of the relationships among the eight populations examined. The scores were arranged in such a way that resemblance to argentatus was always high in value, with the highest value for pure argentatus, and a resemblance to glaucescens always low in value, with the lowest value for pure glaucescens. The composite hybrid index obtained was, of course, an arbitrary indication of the "hybridness" (i.e., the relative number of argentatus or glaucescens genes), since the categories were arbitrarily defined. The main concern in defining the categories was to arrive at recognizable objective stages on the Index which could be differentiated from other states.

4.5 Museum Skins

Museum skins (n= 506) of large white-headed gulls (Larus) were examined in the following museums[2]: American Museum of Natural History, (AMNH), New York City; British Columbia Provincial Museum (BCPM),

[1] AMNH 344044 and 358144 provide examples. See Museum Skins, Section 4.5, for an explanation of these abbreviations.

[2] Abbreviations used in the text are given in parentheses.

Victoria; U.S. National Museum of Natural History (USNM), Washington, D. C.; Thomas Burke Memorial Washington State Museum (WSM), Seattle; and the University of Alaska Museum (UAM), Fairbanks. Standard body measurements were taken on the skins examined. Primary feather pigmentation was specified by the Munsell Neutral Value Scale and recorded by a Wing Hybrid Index (cf. Primary Feather Pigmentation, Section 4.45).

In order to delimit the natural variation of glaucescens and argentatus, a large number of presumably pure birds were examined from areas where the two do not overlap. Descriptions in the literature were also used, especially the valuable papers by Poor (1946) and Schultz (MS) on populations of argentatus and glaucescens, respectively. In so doing, considerable difficulty was encountered in defining a "pure" glaucescens population, since the form hybridizes with all other large white-headed gulls which it encounters on the breeding grounds. In fact, a so-called "pure" population of glaucescens may not exist. However, for purposes of this study, the glaucescens population on Middleton Island, Alaska, has been considered the typical or "pure" population, with respect to which comparisons were made.[1]

4.6 Statistical Procedures

Six statistical procedures were used to test for significant differences in the gull data collected during this research. These procedures were the t-test, analysis of variance, Duncan's Multiple Range Test, contingency table analysis, Chi-square tests, and linear regression of

[1]Reference specimens are:

USNM 527864, 527865, 527866, 527867 and 527868.

a dependent variable on a single independent variable.

The t-test was used for comparison of the means of two groups of data. For instance, mensural characters of "pure" types of argentatus and glaucescens were compared by t-test.

If the data contained more than two groups, a further comparison was necessary, using a two-step test. The first step was an analysis of variance, which indicated whether or not there were real differences among the groups. Such real differences among the groups were demonstrated by a significant F-ratio (the statistic appropriate to the analysis of variance). For example, the means of the measurements for bill depth at posterior nares were compared by analysis of variance among male gulls from eight colonies in a search for evidence of relationships. Similarly, the means of the iris color indices (IHI) were compared among the eight colonies and among mixed and pure pairs within the colonies in search of evidence for pre-mating isolating mechanisms.

If the analysis of variance did indicate significant differences between the means of the groups, then a second step, known as the Duncan's Multiple Range Test (DMRT) was needed to complete the analysis. The DMRT is a systematic procedure for comparing group means. This test places group means into statistically similar (homogenous) subsets. A single group can be placed into two adjoining subsets, thereby demonstrating a statistical relationship to both subsets. The DMRT and the t-test are both "robust" (i.e., they assume a normal distribution of means, not samples, and therefore were relatively independent of sample size).

If the data were counts, rather than measurements, the technique employed was the analysis of contingency tables (crosstabulation), and the tests employed were Chi-square tests. For example, three statistical tests were conducted on the mating patterns of the gulls at Dry Bay for evidence of random or assortative mating. Contingency tables were used to display the following joint frequency distributions. First, the index of primary feather pigmentation of each male was compared against that of the corresponding female in 112 pairs. Second, the iris colors of the males were crosstabulated against the iris colors of the females. Third, the indices of primary feather pigmentation and iris color were combined for each individual gull, and the sums for each male were crosstabulated against the corresponding sum for each female (pair by pair) in 112 pairs. The joint frequency distributions were then analyzed by the Chi-square statistic to test whether there was correlation within each pair. A large value of Chi-square implied a systematic correlation among the variables. Where integers of less than 5 occurred in 20% or more of the cells within the crosstabulation, adjacent cells were combined in order not to inflate the value of the Chi-square. In addition, the Chi-square test was used to compare the observed extent of disagreement in iris and primary feather pigment within each of the 112 pairs with that which would be expected by chance, if they were mating without respect to those characteristics.

The regression was used to describe the linear relationship of iris color to primary feather pigmentation since a graph (Fig. 32) suggested a straight-line relationship between these two indices.

In this study, a "p" value of ($p < .05$) was considered statistically significant; ($p < .01$) was considered highly significant, and ($p < .001$) was considered very highly significant.

4.7 Summary

Methods used in this study were similar, although not identical, to those used by other researchers in analyzing hybridization of birds. The hybrid index method, simple to apply, has given satisfactory results in previous cases of hybridization, and has even proven efficient for exploring complex situations (Anderson, 1949; Sibley, 1954; Ingolfsson, 1970; Strang, 1977; Hoffman *et al.*, 1978).

5.0 RESULTS

5.1 Primary Feather Pigmentation

Observations of over 2600 individual gulls in the study area indicated considerable variation in primary feather pigmentation. The range of primary feather pigmentation varied from primaries the same shade of grey as the mantle (WHI 1) to primaries of intensive black pigment (WHI 6) deposited in distinctly delimited subterminal bands. However, mean wing hybrid indices for gull populations appeared to correlate closely with geographic location. A detailed analysis of the degree of primary feather pigmentation of 165 collected gulls included an analysis of variance (Table 6), a statistical comparison (DMRT) of the means for each colony (Tables, 7, 8) (cf. Statistical Procedures, Section 4.6), and a qualitative comparison of the frequency distribution of the indices between each colony (Figs. 20, 21, 22).

Glaucous-winged Gulls from the offshore Middleton Island, apparently farthest away from potential Herring Gull influence, had the lightest wing hybrid index (WHI 1.2), with no indices greater than WHI 1.5 (Table 6). The three Copper River Delta populations, Egg Island (WHI 1.91), Copper Sands (WHI 2.03), and Strawberry Reef (WHI 2.20) displayed progressively intensifying melanin deposits in the subterminal portions of the outer primary feathers. These populations are located from NW to SE across the Copper River Delta in the order listed. Although the Copper Sands and Strawberry Reef colonies had frequency distributions of WHI's which were more like each other than they were like the colony on Egg Island, all three Copper River Delta colonies displayed a high frequency (44 - 60%) of individual gulls with primaries slightly darker than the mantle (WHI 2) (Fig. 20).

Table 6. Hybrid Index of Primary Feather Pigmentation* (WHI) for *Larus* Colonies in Southern Alaska

Colony	Mean	Range	Standard Deviation	Sample Size
Middleton Island	1.20	1.0-1.5	0.27	5
Egg Island	1.91	0.0-4.0	0.69	56
Haenke Island	1.95	1.0-3.5	0.83	10
Copper Sands	2.03	1.0-3.0	0.67	16
Strawberry Reef	2.20	1.0-3.0	0.54	25
Dry Bay	3.10	1.0-6.0	1.56	38
North Marble	4.12	3.0-6.0	1.32	4@
Lake Louise	5.90	5.0-6.0	0.30	11

Analysis of Variance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-ratio
Between Groups	7	188.71	26.96	29.50**
Within Groups	157	143.49	0.91	
Total	164	332.20		

*a Wing Hybrid Index of 1 = "pure" *glaucescens*; a WHI of 6 = "pure" *argentatus* (Fig. 37).

**very highly significant ($p < .001$).

@additional specimens (USNM 16095 and 16097) collected in June, 1899, at Point Gustavus in Glacier Bay, approximately 40 km south of North Marble, have WHI of 3.0 and 2.0, respectively.

Table 7.

Ranked Means for the Wing Hybrid Index*
for *Larus* Colonies in Southern Alaska

(Duncan's Multiple Range Test: $p < .05$ level)

Homogenous subsets (subsets of groups, whose highest and lowest means do not differ by more than the shortest significant range for a subset of that size). There is no significant difference between the means of groups underlined with a single dotted line.

Subset 1 (subterminal primaries same shade as mantle to 1 shade darker)

Group	Middleton Island	Egg Island	Haenke Island	Copper Sands (S)	Strawberry Reef
Mean	1.20	1.91	1.95	2.03	2.20

Subset 2 (primaries 2 shades darker than mantle; extensive melanin)

Group	Dry Bay
Mean	3.10

Subset 3 (primaries 3 shades darker than mantle; extensive melanin)

Group	North Marble
Mean	4.12

Subset 4 (primaries black; distinctly delimited and extensive black pattern)

Group	Lake Louise
Mean	5.90

*A Wing Hybrid Index of 1 = "pure" *glaucescens*; a WHI of 6 = "pure" *argentatus* (Fig. 37).

Table 8. Ranked Means for Wing Hybrid Indices*
for _Larus_ Colonies in Southern Alaska

(Duncan's Multiple Range Test: $p < .01$ level)

Homogenous subsets (subsets of groups, whose highest and lowest means do not differ by more than the shortest significant range for a subset of that size). There is no significant difference between the means of groups underlined with a single dotted line.

Subset 1 (subterminal primaries same shade as mantle to 1 shade darker)

Group	Middleton Island	Egg Island	Haenke Island	Copper Sands (S)	Strawberry Reef
Mean	1.20	1.91	1.95	2.03	2.20

Subset 2 (primaries 2 - 3 shades darker than mantle; extensive melanin)

Group	Dry Bay	North Marble
Mean	3.10	4.12

Subset 3 (primaries 3 shades darker than mantle to black; extensive and distinctly delimited pattern)

Group	North Marble	Lake Louise
Mean	4.12	5.90

*A Wing Hybrid Index of 1 = "pure" _glaucescens_; a WHI of 6 = "pure" _argentatus_ (Fig. 37).

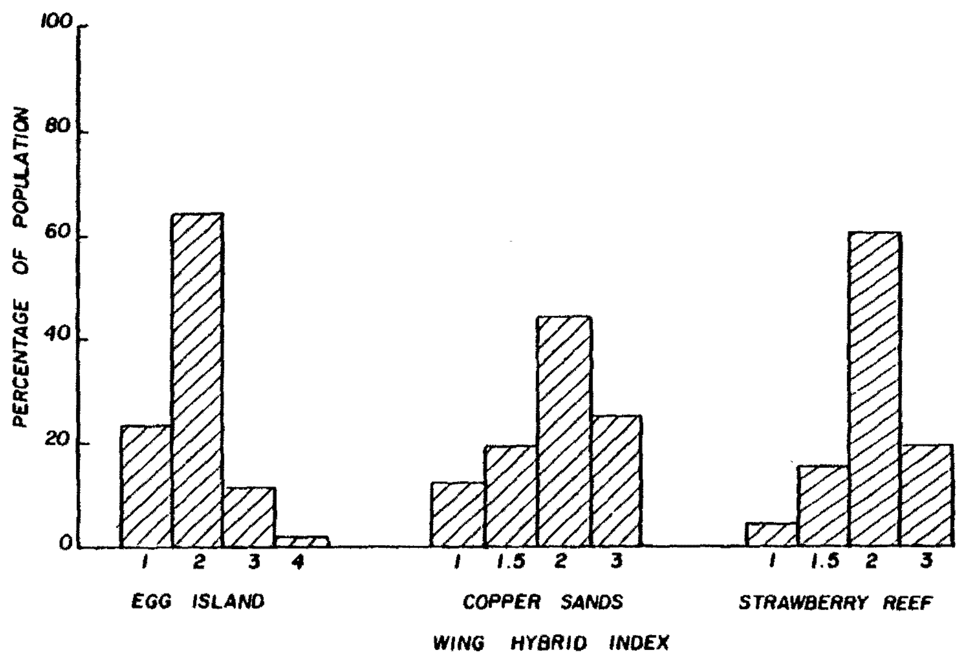

Fig. 20. Although the Copper Sands and Strawberry Reef colonies had frequency distributions of Wing Hybrid Indices which were more like each other than they were like the colony on Egg Island, all three Copper River Delta colonies displayed a high frequency of individual gulls with primaries slightly darker than the mantle (WHI 2).

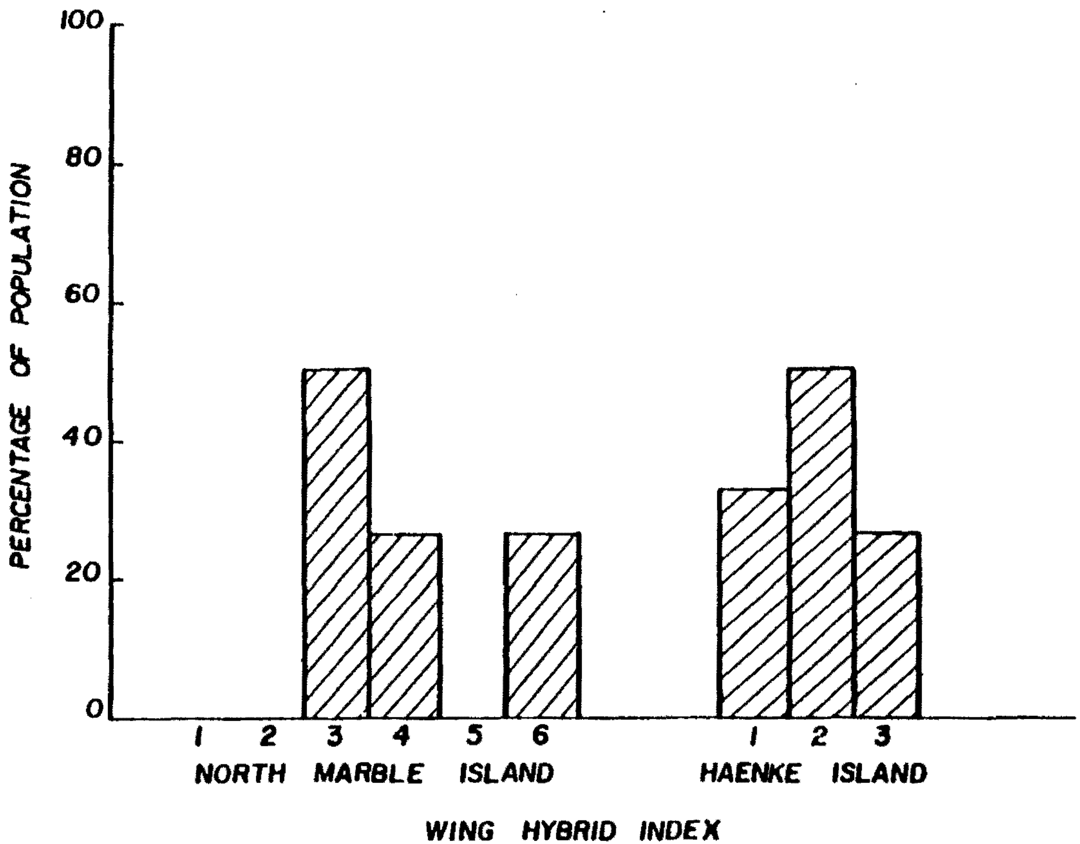

Fig. 21. Frequency distributions of primary feather pigmentation at North Marble Island and Haenke Island.

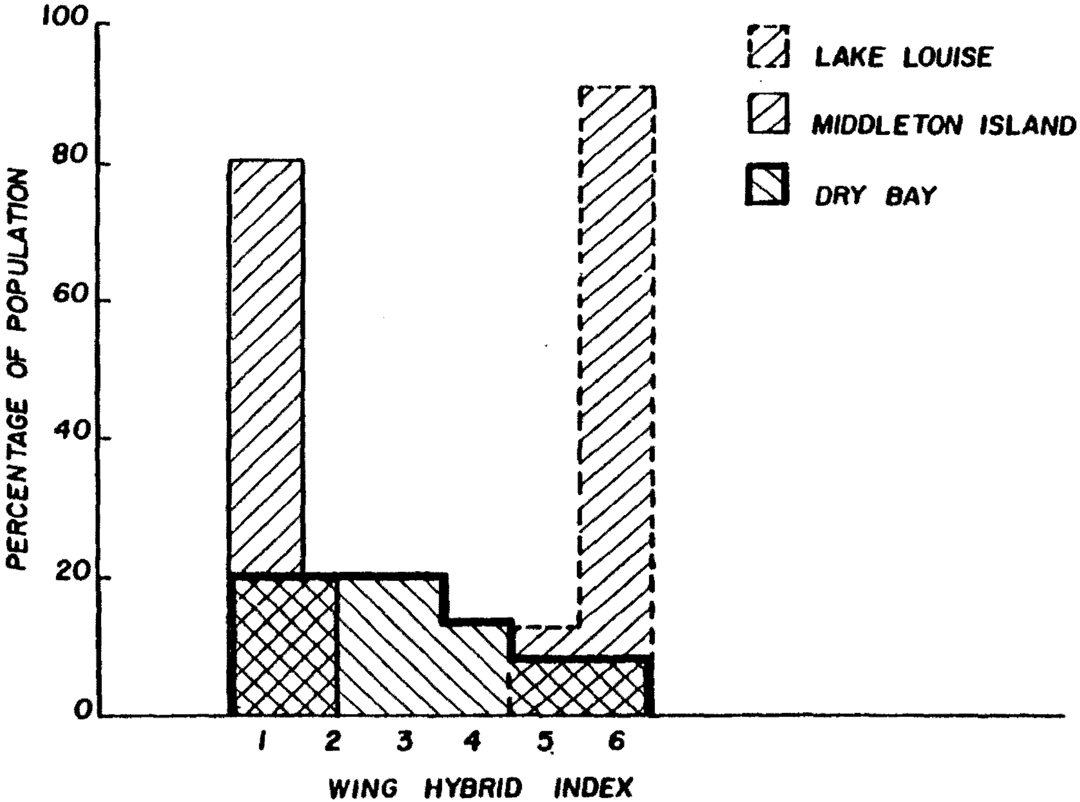

Fig. 22. Frequency distributions of primary feather pigmentation at Lake Louise, Middleton Island, and Dry Bay, Alaska. Middleton Island is a glaucescens colony; Lake Louise is an argentatus colony, and Dry Bay supports sympatric and interbreeding glaucescens, argentatus, and intergrades.

The Haenke Island and Egg Island populations had similar means of primary feather pigmentation (WHI 1.95 - 1.91) but the frequency distributions for these colonies were quite different. Haenke Island birds exhibited equal percentages (40%) of WHI 1 and 2, while the Egg Island colony had fewer birds with WHI 1 (23%) and a much greater concentration of WHI 2 (64%) (Figs. 20,21).

The Dry Bay colony at the mouth of the Alsek River exhibited the complete range of primary feather pigmentation (WHI 1 to 6) (Table 6). The mean wing index (WHI 3.1) was almost exactly midway between *glaucescens* and *argentatus*; although the distribution of the indices was weighted towards *glaucescens*, 72% of the colony was composed of intergrades (WHI 2 - 5). The indices of WHI 1, 2, and 3 occurred in equal proportions (20%), but the indices of WHI 4, 5, and 6 were represented in decreasing proportions (Fig. 22). However, the Dry Bay population had the greatest concentration of WHI 6 (8%) of any coastal group.

The mean wing index for the colony at Lake Louise was WHI 5.9, representative of an *argentatus* population, and the frequency distribution (91% WHI 6) clustered about the mean (Fig. 22).

The F-ratio for the observed distribution of primary feather pigmentation for all colonies was very highly significant ($F = 29.5$, 164 d.f., $p < .001$), indicating real differences among group means (Table 6). Duncan's Multiple Range Test grouped colonies in subsets according to their statistical similarity in mean wing hybrid index (Tables 7 & 8). Middleton Island, Egg Island, Haenke Island, Copper Sands, and Strawberry Reef were included in a homogenous subset (at the 5% level of significance) most resembling *glaucescens*, although exhibiting progressively intensifying melanin in the mean indices of subterminal primary feather pigmentation, in the order listed (Table 7, Subset 1). The mean indices for Dry Bay (WHI 3.1), North Marble (WHI 4.12), and the Lake Louise population (WHI 5.9) were significantly different from each other and from the *glaucescens* subset (at the 5% level), but also displayed progressively intensifying melanin in the subterminal portions of the outer primary feathers in the order listed. Thus there is a progression of increasing *argentatus* influence in primary feather pigmentation (a cline) from the offshore Middleton Island *glaucescens* (WHI 1.2) to the interior Lake Louise *argentatus* (WHI 5.9) through gradually darkening coastal groups (WHI 1.91 to 2.20) and hybrid colonies (WHI 3.1 to 4.12) in fjords and river mouths (Table 8, Subset 2; Figure 36, p. 99).

5.2 Iris Pigmentation

The range of iris coloration included very dark brown (IHI 4), dark brown (IHI 5), brown (IHI 6), light brown (IHI 7), light yellow (IHI 8), and yellow (IHI 9) (Table 9). A clinal change in mean iris color, from brown to yellow, was revealed in the series of colonies studied. As with primary feather pigmentation, the degree of iris color was related to geographic location, although the clines of iris color and primary feather pigmentation were at least partially independent of each other (Fig. 36, p. 99).

The Haenke Island population had the darkest index of iris pigmentation (IHI 6.3) and the least range (IHI 6 - 7) of groups examined (Table 9). The Middleton Island population had the next darkest index (IHI 6.6), but a slightly larger range (IHI 6 - 8). The Egg Island population mean for iris color was slightly higher (IHI 6.86), but the range (IHI 4 - 8) was

Table 9. Hybrid Index for Iris Color (IHI)** for *Larus* Colonies in Southern Alaska

Colony	Mean	Color	Range	Standard Deviation	Sample Size
Haenke Island	6.30	brown	6 - 7	0.48	10
Middleton Island	6.60	light brown	6 - 8	0.89	5
Egg Island	6.86	light brown	4 - 8	0.98	56
Strawberry Reef	7.08	light brown	6 - 8	0.95	25
Copper Sands	7.12	light brown	6 - 8	0.96	16
North Marble	7.25	light brown	6 - 9	1.50	4
Dry Bay	7.79	light yellow	6 - 9	0.81	38
Lake Louise	9.00	yellow	9 - 9	0.00	11

Analysis of Variance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-ratio
Between Groups	7	65.49	9.36	11.77 *
Within Groups	157	124.81	0.79	
Total	164	190.30		

*very highly significant ($p < .001$)

**An Iris Hybrid Index (IHI) of 6 = "pure" *glaucescens*; an IHI of 9 = "pure" *argentatus* (Fig. 37). An exceptional few gulls breeding on Egg Island have very dark brown (IHI 4) and dark brown (IHI 5) irides.

the largest, possibly reflecting the fact that this was the largest colony examined. Copper Sands and the nearby Strawberry Reef colonies shared similar indices of iris pigmentation (IHI 7.08 - 7.12) and similar ranges (IHI 6 - 8). While the mean index for the North Marble Island population was light brown (IHI 7.25), the range expanded to include yellow irides (IHI 6 - 9). The mean index for Dry Bay was IHI 7.79 (light yellow), and the range (IHI 6 - 9) also included brown to yellow irides. The Lake Louise population had the lightest index of iris color (IHI 9 - yellow) (Table 9), although individuals varied in the amount of melanin flecks on the iris.

The F-ratio for the observed distribution of iris colors for all colonies was highly significant ($F = 11.77$, 164 d.f., $p < .001$), indicating real differences among group means (Table 9). However, glaucescens populations were connected to an argentatus population by an uninterrupted continuum of the categories of iris color (Table 11). Only the extremes could be distinguished statistically in the DMRT. The mean of the coastal Haenke Island colony (IHI 6.3 - brown irides) was connected to the mean of the interior Lake Louise colony (IHI 9 - yellow irides) by a "bridge" of intermediate colonies in fjords and at river mouths, i.e., North Marble (IHI 7.25 - light brown) and Dry Bay (IHI 7.79 - light yellow) (Table 10, Subset 2).

5.3 Parameters of Iris Color

Hue, Value, and Chroma are the parameters which define a color in the Munsell System (Appendix III).

5.31 Hue

The hue (H) notation of a color indicates its relationship to a visually equally-spaced scale of 100 hues. The hue notation in this

Table 10. Ranked Means for Iris Color Indices (IHI)* for *Larus* Colonies in Southern Alaska

(Duncan's Multiple Range Test: $p < .05$ level)

Homogenous subsets (subsets of groups whose highest and lowest means do not differ by more than the shortest significant range for a subset of that size). There is no significant difference between the means of groups underlined with a single dotted line

Subset 1 (brown - light brown)

Group	Haenke Island	Middleton Island	Egg Island	Strawberry Reef	Copper Sands	North Marble
Mean	6.30	6.60	6.86	7.08	7.12	7.25

Subset 2 (light brown - light yellow)

Group	North Marble	Dry Bay
Mean	7.25	7.79

Subset 3 (bright yellow)

Group	Lake Louise
Mean	9.00

*An Iris Hybrid Index (IHI) of 6 = "pure" *glaucescens*; an IHI of 9 = "pure" *argentatus* (Fig. 37).

Table 11. Ranked Means for Iris Color (IHI) for *Larus* Colonies in Southern Alaska*
(Duncan's Multiple Range Test: $p < .01$ level)

Homogenous subsets (subsets of groups, whose highest and lowest means do not differ by more than the shortest significant range for a subset of that size). There is no significant difference between the means of groups underlined with a single dotted line.

Subset 1 (brown - light brown)

Group	Haenke Island**	Middleton Island	Egg Island	Strawberry Reef	Copper Sands	North Marble
Mean	6.30	6.60	6.86	7.08	7.12	7.25

Subset 2 (light brown - light yellow)

Group	Middleton Island	Egg Island	Strawberry Reef	Copper Sands	North Marble	Dry Bay
Mean	6.60	6.86	7.08	7.12	7.25	7.79

Subset 3 (bright yellow)

Group	Lake Louise**
Mean	9.00

*An Iris Hybrid Index (IHI) of 6 = "pure" glaucescens; an IHI of 9 = "pure" argentatus (Fig. 37).

**Only the extremes can be distinguished statistically, by lack of membership in a common subset. A statistical continuum is formed if the extremes are excluded.

study is based upon three major hues: Red (R), Yellow-Red (YR), and Yellow (Y), since these cover the range of pigmentation in orbital rings and irides. The range of iris hues included 7.5 YR (brown) (glaucescens), 10 YR (light brown), 2.5 Y (light yellow) and 5 Y (yellow) (argentatus).

The frequency distributions of iris hues were analyzed qualitatively (Fig. 23). Haenke Island had the highest frequency (70%) of brown (7.5 YR) hues. Middleton Island resembled Haenke Island, with a 60% frequency of brown (7.5 YR), but differed by presence of 20% 2.5 YR, light yellow. The Copper River Delta colonies of Egg Island, Copper Sands, and Strawberry Reef shared strikingly similar distributions of brown (7.5 YR), light brown (10 YR) and light yellow (2.5 Y). Both Dry Bay and North Marble populations exhibited strong yellow hues (5 Y). North Marble, compared to Dry Bay, had a higher percentage of brown (7.5 YR) hues. At Dry Bay, the distribution was concentrated around light yellow (2.5 Y). The Lake Louise population had the highest (100%) frequency of yellow hues (5 Y).

5.32 Value

The value (V) is defined as the notation of a color indicating the degree of lightness or darkness in relation to a neutral grey scale. The range of iris values of gulls examined extended from V 3, with abundant melanin obscuring the difference between the pupil and the iris, to V 8, with the pupil clearly visible, with only occasional flecks of dark pigment. Thus dark-eyed gull phenotypes (glaucescens) were represented by V 3, V 4, and V 5, and light-eyed phenotypes (argentatus) by V 7 and V 8.

Haenke Island gulls, with an 80% concentration of V 4, most resembled a "pure" glaucescens population in iris values (Fig. 24). The

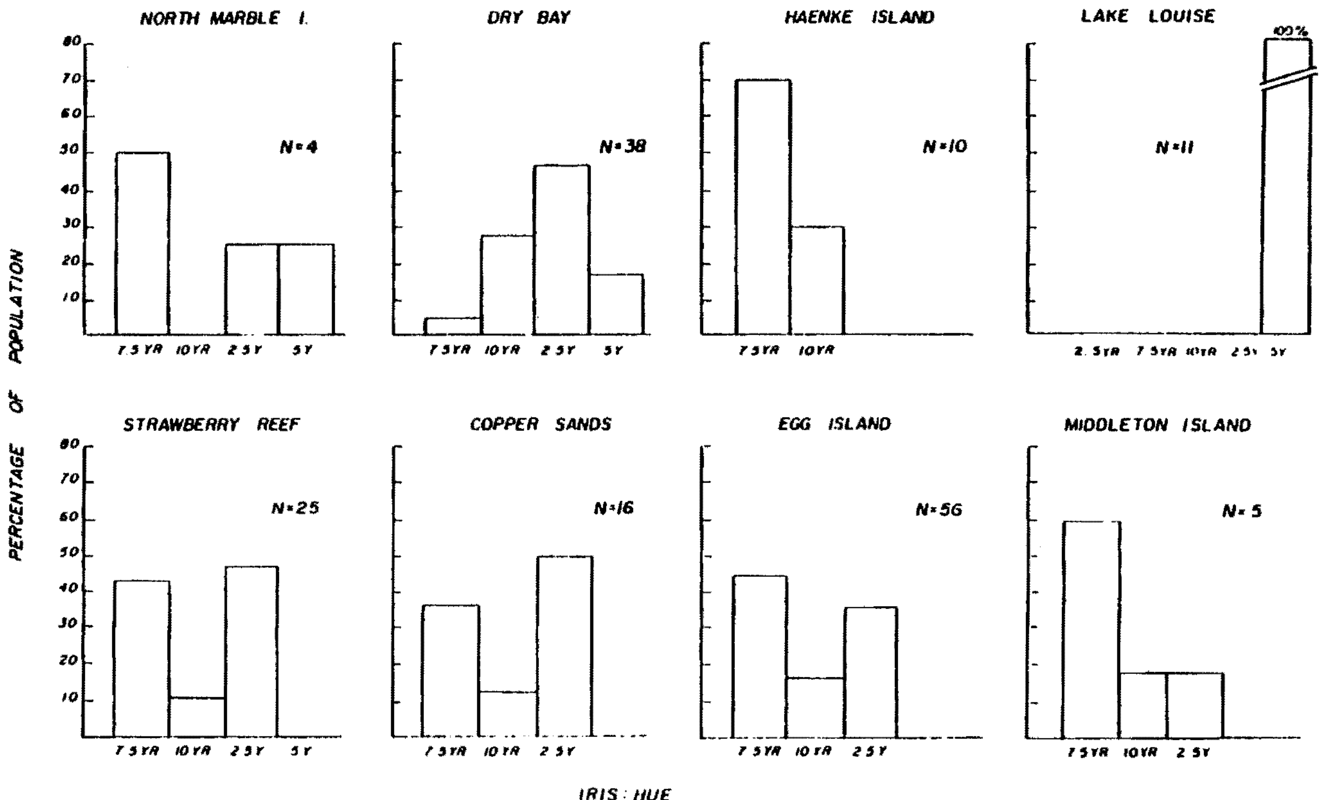

Fig. 23. Frequency distributions of iris hues in eight southern Alaskan Larus colonies. Note the strikingly similar distributions of iris hues in the Copper River Delta populations (Strawberry Reef, Copper Sands, and Egg Island). Haenke Island resembles Middleton Island; Haenke Island and Lake Louise populations are opposite extremes.

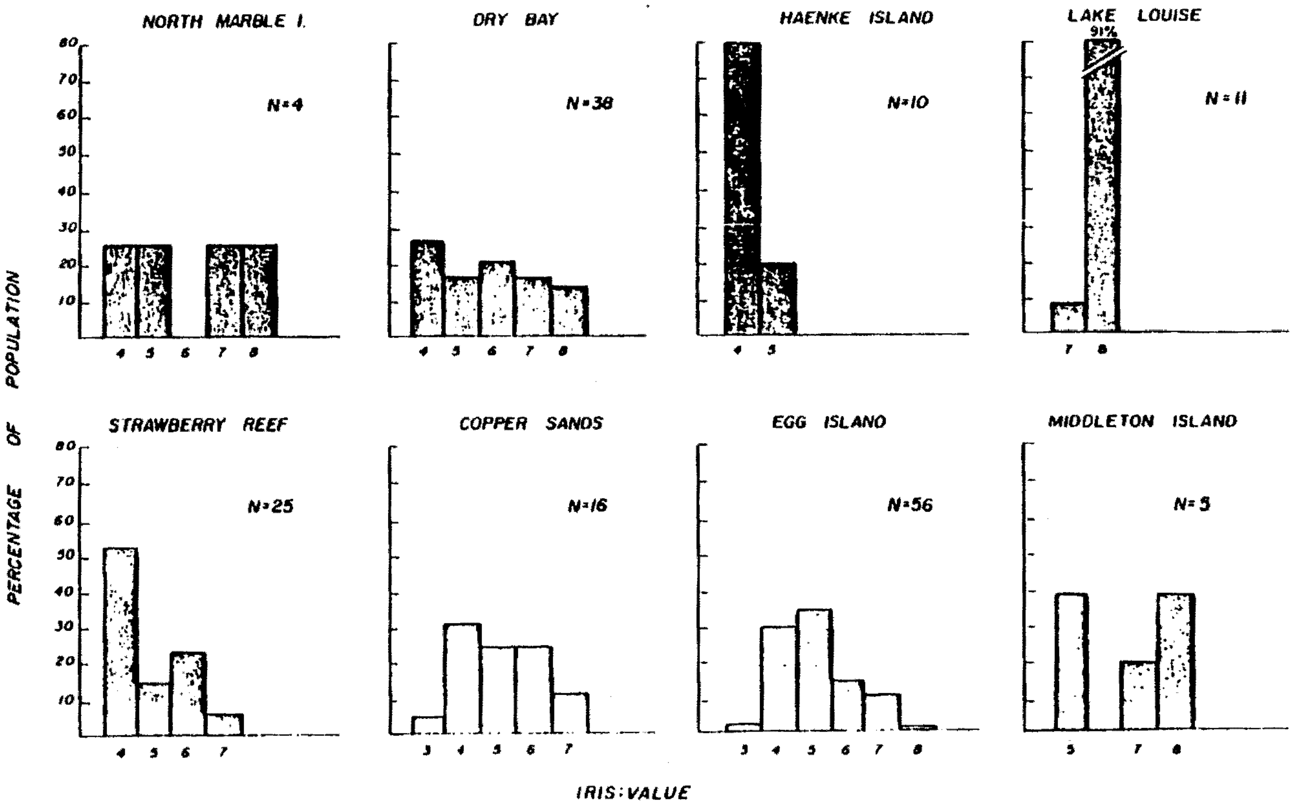

Fig. 24. Frequency distributions of iris values in eight southern Alaskan Larus colonies. Haenke Island and Lake Louise are virtually opposite in the distribution of iris values; the Copper River Delta populations at Egg Island and Copper Sands share similar distributions of iris values; the population at Strawberry Reef is transitional in iris values between coastal glaucescens and the hybrid colony at Dry Bay.

Middleton Island population displayed lighter values, with 40% concentrations at both V 5 and V 8. The remaining coastal populations exhibited frequencies dominated by V 4 and V 5, indicative of glaucescens. The Copper River Delta populations at Egg Island and Copper Sands, as expected, shared similar distributions of iris values. However, on Strawberry Reef, the island at the east end of the Delta, the population was transitional in iris values between the coastal glaucescens colonies and the hybrid colony at Dry Bay. Dry Bay gulls had the broadest and most even distribution of iris values, reflecting the hybrid nature of the population. The North Marble population had a similar even distribution of iris values, although lacking the intermediate value of V 6. The Lake Louise argentatus population, with 91% V 8, was virtually opposite of the distribution of the Haenke Island population at the glaucescens end of the spectrum (80% V 4) (Fig. 24).

5.33 Chroma

Chroma (C) is defined as the degree of departure of a given Munsell hue from a neutral grey of the same value. Chroma scales depend upon the strength (saturation) of the sample evaluated. Iris chroma in gulls in this study did not correlate with other iris parameters. All breeding populations exhibited a concentration on the chroma scale at C 4 (Fig. 25). The range of iris chroma extended from C 2 to C 8, although C 5 and C 7 were absent from all populations, and C 8 occurred at North Marble, only[1].

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[1]The single non-breeding population studied, that at Cordova (Appendix VI) differed considerably in distribution of iris chroma from that of the breeding populations.

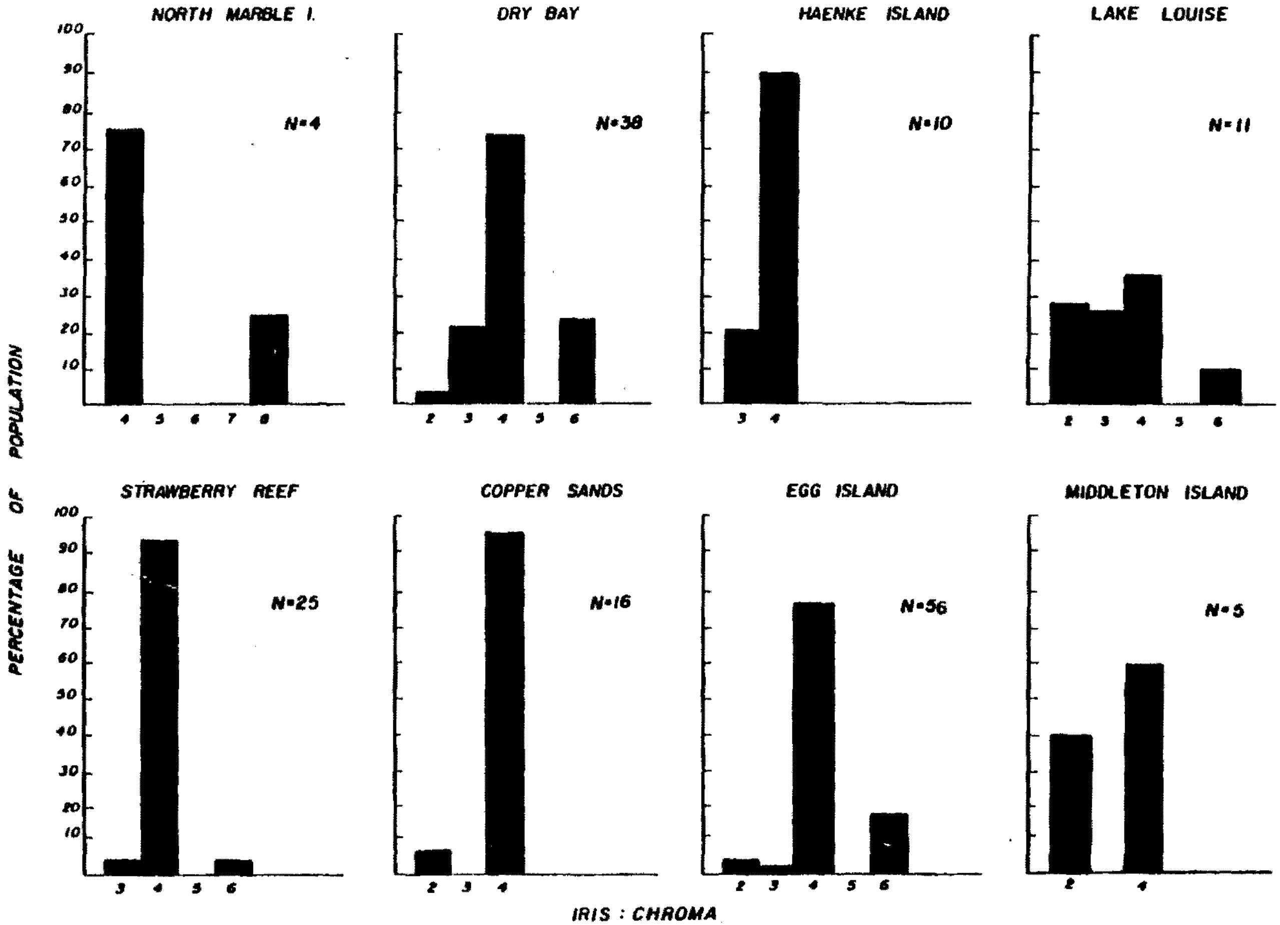

Fig. 25. Frequency distributions of iris chroma in eight southern Alaskan Larus colonies. All breeding populations exhibited a concentration at C 4.

5.34 Combined Iris Parameters (Hue, Value, and Chroma)

Iris color frequencies within individual gull colonies were quite variable, but qualitative comparisons among colonies of the frequencies of the complete Munsell notation revealed degrees of relationship not readily apparent in the comparisons of the individual parameters of iris color.

Haenke Island birds had the greatest concentration of 7.5 YR 4/4 (brown) irides, representing the "purest" population of *glaucescens* studied, as far as iris pigmentation was concerned (Fig. 26) (cf. Primary Feather Pigmentation, Section 5.2). At the opposite end of the spectrum, the Lake Louise population had the greatest concentration of 5 Y 8/4 (yellow) irides, representing an *argentatus* population (Fig. 26).

The colonies at Copper Sands and Strawberry Reef of the Copper River Delta had the most similar distributions of the combined iris parameters, concentrated bimodally at 7.5 YR 4/4 (brown) and at 2.5 Y 5/4 - 5/4 (light yellow) (Fig. 27). Most gulls on Egg Island had iris colors of either 7.5 YR 4/4 (brown) or 2.5 Y 5/4 (light yellow), but the range of the combined iris parameters included 2.5 YR 3/4 (dark brown) to 2.5 Y 7/6 (very light yellow) (Fig. 28). Thus, all three Copper River Delta populations were closely related in parameters of iris color, but the Egg Island population was not as closely related to those on Copper Sands and Strawberry Reef as they were to each other. (The Complete Munsell Notation for iris color in the Copper River Delta colonies thus ranged from dark brown to light yellow: Fig. 29). This finding correlates well with that of the primary feather pigmentation (WHI), orbital ring pigmentation (OHI), and the measurement of bill depth at posterior nares (Appendix VI).

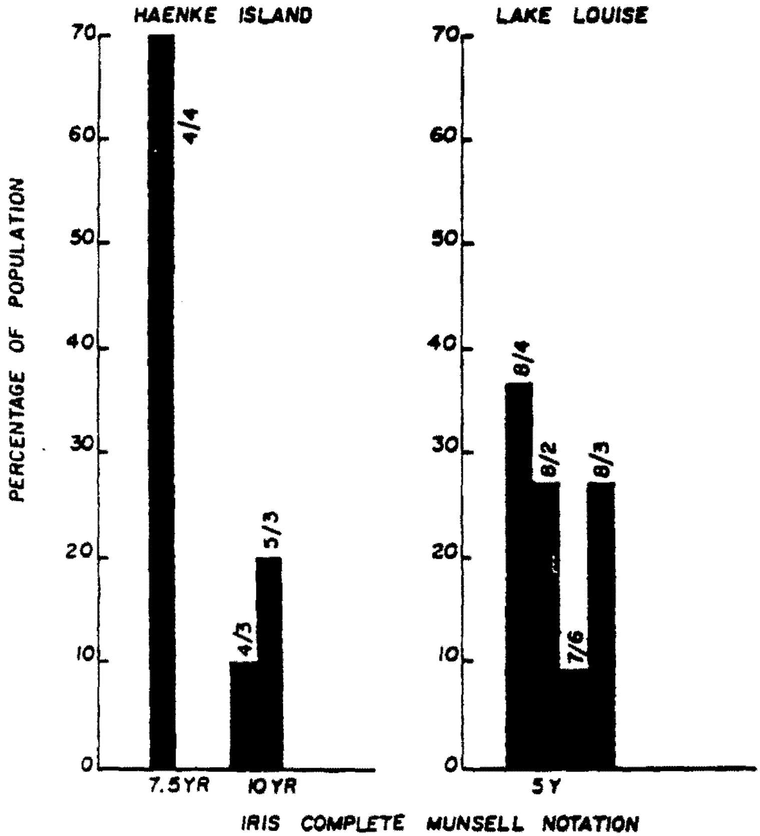

Fig. 26. Complete Munsell Notation for iris color in Larus colonies at Haenke Island and Lake Louise, Alaska. (7.5 YR = brown hues; 10 YR = light brown hues; 5 Y = yellow hues.) Haenke Island gulls had the greatest concentration of 7.5 YR 4/4 (brown) irides. Lake Louise gulls had the greatest concentration of 5Y 8/4 (yellow) irides.

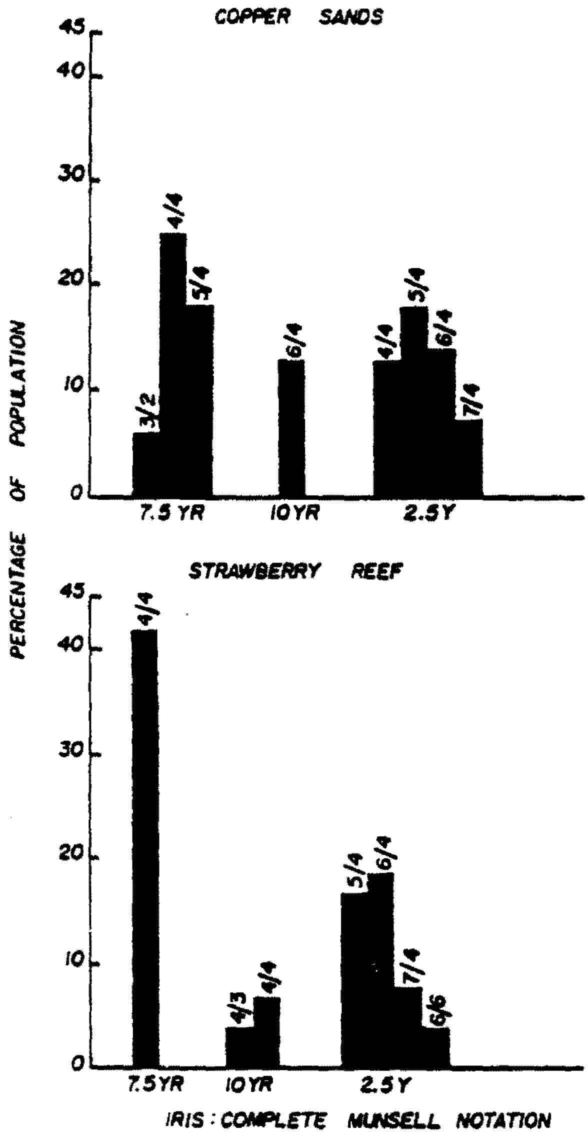

Fig. 27. The gull populations breeding at Copper Sands and Strawberry Reef (Copper River Delta) had similar distributions of iris colors, concentrated at brown and light yellow hues. (7.5 YR = brown hues; 10 YR = light brown hues; 2.5 Y = light yellow hues).

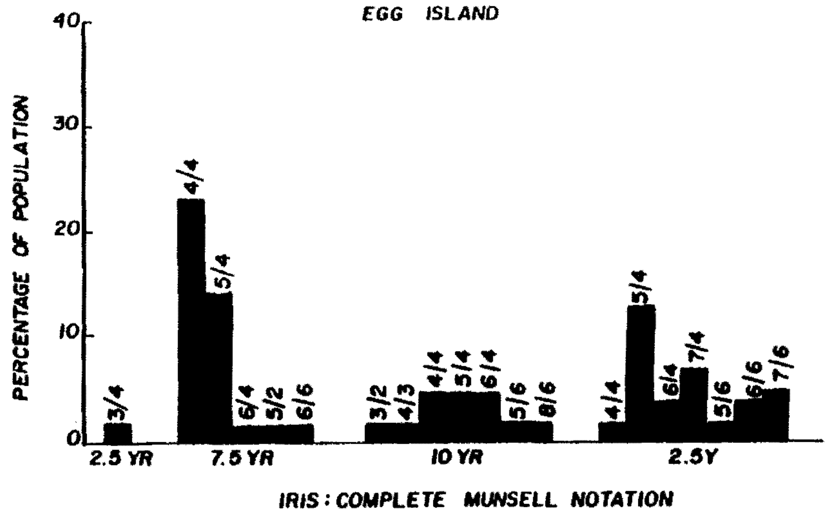

Fig. 28. Frequency distribution of iris colors in Larus gulls breeding at Egg Island, Copper River Delta, Alaska. The distribution of iris colors was concentrated in the 7.5 YR hues (brown) and the 2.5 Y (light yellow) hues, but also included 2.5 YR (very dark brown) and 10 YR (light brown) hues.

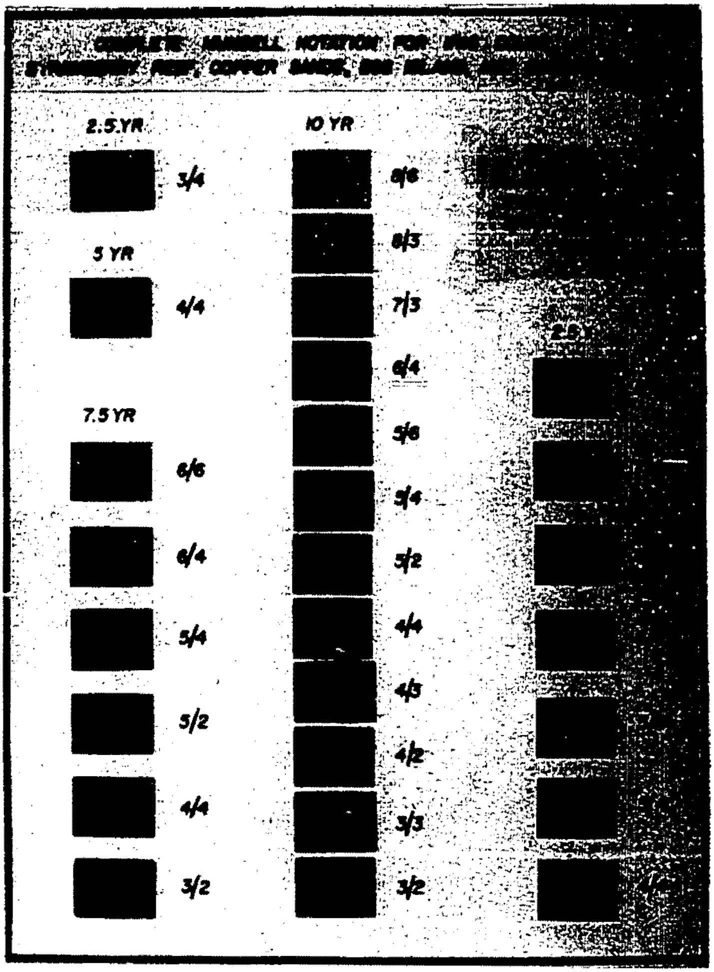

Fig. 29. Iris colors in Copper River Delta *Larus* colonies ranged from dark brown to light yellow.

North Marble gulls had brown (7.5 YR 4/4 - 4/5), light yellow (2.5 Y 7/4), and yellow (5 Y 8/8) irides; Middleton Island gulls had brown (7.5 YR 5/4 - 8/2), light brown (10 YR 5/4) and light yellow (2.5 Y 7/4) irides (Fig. 30).

Dry Bay was distinguished by having the greatest variety of iris colors in any single breeding population studied. The frequency distribution ranged from dark brown to yellow, including twenty intermediate colors (Fig. 31).

5.4 Relationship of Iris Color to Primary Feather Pigmentation

Field observations indicated the possibility of a relationship between primary feather pigmentation and iris color. For example, light-eyed gulls had dark primaries, dark-eyed gulls had light primaries, and gulls with intermediate shades of melanin in their primaries had irides of intermediate shades. However, exceptions were common. (Note that the parental types have contrasting iris colors and primaries).

The iris hue of 188 gulls (both collected and captured) were cross-tabulated against categories of the wing hybrid index (cf. Statistical Procedures, Section 4.6). The relationship was shown to be significant by the Chi-square test, which produced a Chi-square of 27.46, with 16 d.f. ($p < .03$). This relationship can be described by the regression line:

$$y = .5x + 0.13$$

where y is the hybrid index of primary feather pigmentation, and x is the iris hue (Fig. 32).

This regression line describes the actual data; a theoretical line (dotted) connects points for the two "pure" types (Fig. 32). These lines indicate that as the iris color (hue) becomes lighter, there is a statistically significant tendency for the primaries to become darker.

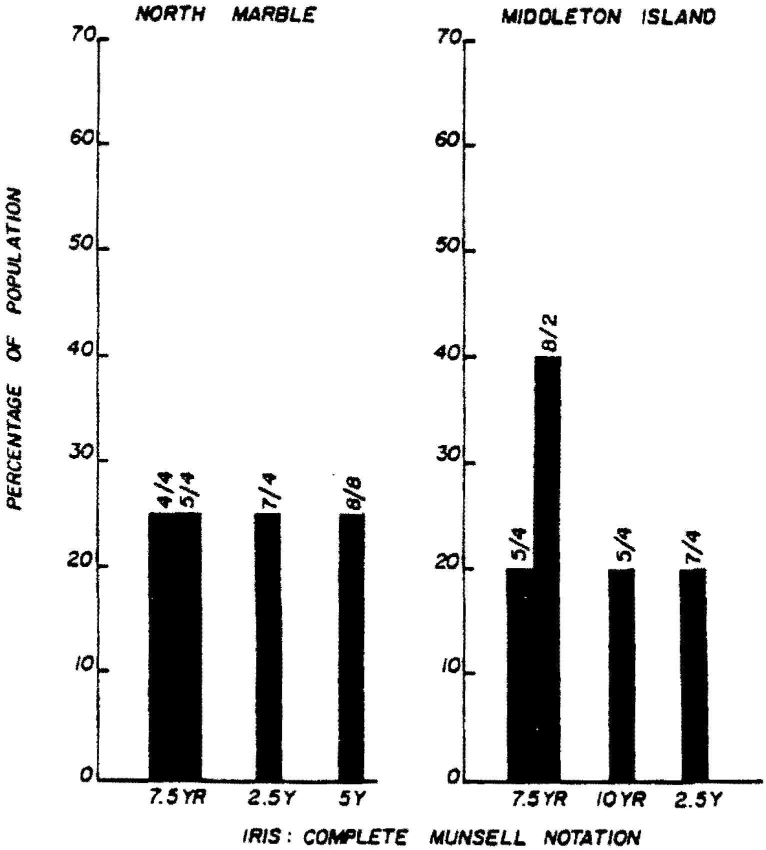

Fig. 30. Frequency distributions of iris colors for Larus gulls breeding at North Marble and Middleton Island, Alaska. (7.5 YR = brown hues; 10 YR = light brown hues; 2.5 Y = light yellow hues; 5 Y = yellow hues). North Marble gulls had brown, light yellow, and yellow irides; Middleton Island gulls had brown, light brown, and light yellow irides.

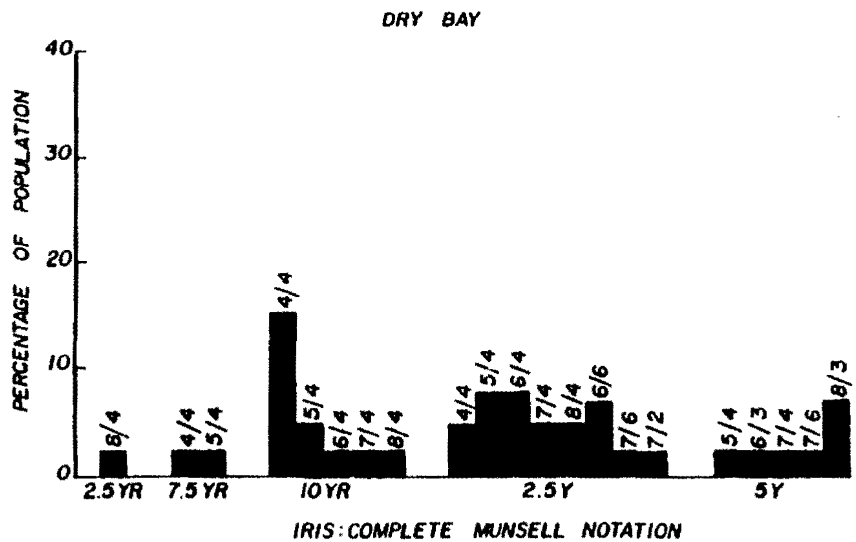

Fig. 31. Frequency distributions of iris colors for gulls breeding at Dry Bay, Alaska. (2.5 YR = very dark brown hues; 7.5 YR = brown hues; 10 YR = light brown hues; 2.5 Y = light yellow hues; 5 Y = yellow hues). Note the concentrations at light brown and yellow hues. Dry Bay was distinguished by having the greatest variety of iris colors (dark brown to yellow) in breeding populations studied.

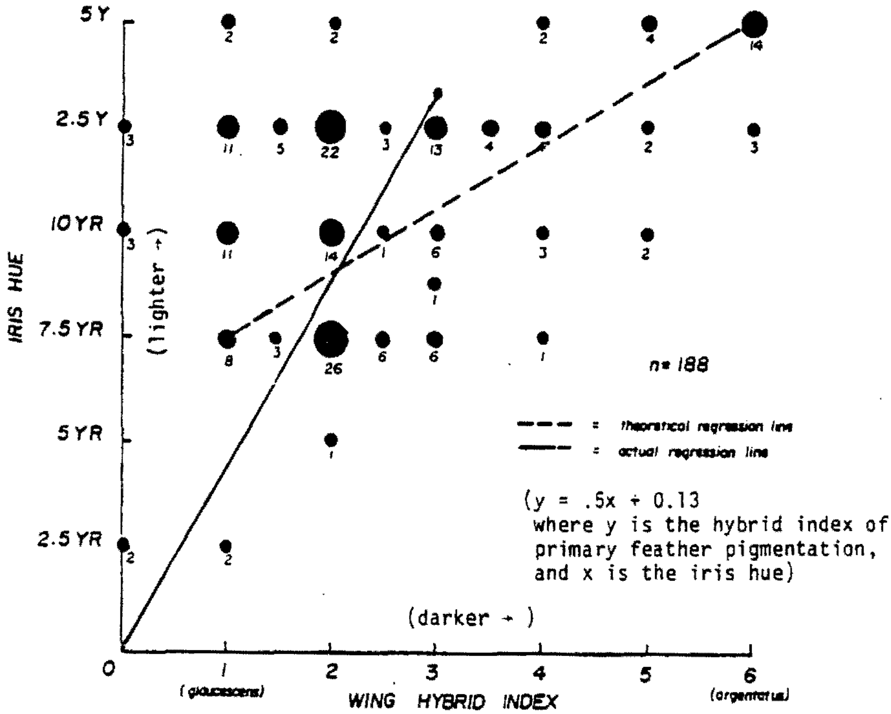

Fig. 32. Iris hues of Larus gulls in southern Alaska plotted against categories of the Wing Hybrid Index of primary feather pigmentation. The solid regression line described the actual data; the dashed theoretical line connects points for the two "pure" types. These lines indicate that as the iris color becomes lighter, there is a statistically significant tendency for the primaries to become darker. However, exceptions were common.

This relationship establishes that the variation and distribution of iris color were correlated with primary feather pigmentation. However, it is not clear whether they functioned independently of, or in conjunction with, each other in species recognition between argentatus and glaucescens, since the two forms were linked by a complete range of intergrades (cf. Analysis of Mating Patterns, Section 5.9).

5.5 Orbital Ring Pigmentation

The "pure types" of Larus argentatus in southern Alaska have uniformly pigmented orbital rings of Munsell hue 5 Y (yellow). Contrastingly, "pure types" of Larus glaucescens have dark pink or vinaceous orbital rings of hue 5 R. However, seven discernible hues were observed between the two extremes, with more than one hue frequently occurring in the same orbital ring. The hybrid index of orbital ring pigmentation (OHI) demonstrated variation among colonies, and qualitative frequencies of orbital ring color demonstrated variation within colonies, but as a general trend, the means of the extreme indices of dark pink and bright yellow could be arranged into a gradation of increasing amounts of yellow pigment (Tables 12, 13, Fig. 36, p. 99).

The Haenke Island population had a mean orbital ring of dark pink (5 R; OHI 1.30); the Middleton Island population had a mean orbital ring color of pink (7.5 R; OHI 2.4); the North Marble Island population had a mean orbital ring color of light pink (10 R; OHI 2.75) (Table 12). Egg Island, Copper Sands, and the Dry Bay populations had similar means of orbital ring indices (OHI 3.66, 4.00, 4.36) of yellowish pink (2.5 YR). The Strawberry Reef population had slightly more yellow present in the mean orbital ring index (OHI 4.60) than did the other Copper River Delta populations or the Dry Bay population (above), with the mean representing

Table 12 . Hybrid Index of Orbital Ring Pigmentation (OHI)** for *Larus* Colonies in Southern Alaska (H 1 + Hue 2 + Hue 3)

Colony	Mean	Munsell Hue	Color	Sample Size
Haenke Island	1.30	5 R	dark pink	10
Middleton Island	2.40	7.5 R	pink	5
North Marble	2.75	10 R	light pink	4
Egg Island	3.66	2.5 YR	yellowish pink	56
Copper Sands	4.00	2.5 YR	yellowish pink	16
Dry Bay	4.36	2.5 YR	yellowish pink	38
Strawberry Reef	4.60	5 YR	pinkish yellow	25
Lake Louise	8.90	5 Y	yellow	11

Analysis of Variance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-ratio
Between Groups	7	376.89	53.84	7.43*
Within Groups	157	1137.01	7.24	
Total	164	1513.90		

*Very highly significant ($p < .001$).

**A "pure" glaucescens has an orbital ring index (OHI) of 1 - 2; a "pure" argentatus has an OHI of 8 - 9 (Fig. 37).

Table 13. Ranked Means for Orbital Indices (OHI) for *Larus* Colonies in Southern Alaska*
(Duncan's Multiple Range Test: $p < .05$ level).**

Homogenous subsets (subsets of groups, whose highest and lowest means do not differ by more than the shortest significant range for a subset of that size). There is no significant difference between the means of groups underlined with a single dotted line.

Subset 1 (dark pink - light pink)

Group	Haenke Island***	Middleton Island	North Marble
Mean	1.30	2.40	2.75

Subset 2 (light pink - yellowish pink)

Group	Middleton Island	North Marble	Egg Island	Copper Sands	Dry Bay	Strawberry Reef
Mean	2.40	2.75	3.66	4.00	4.36	4.60

Subset 3 (yellow)

Group	Lake Louise***
Mean	8.90

*A "pure" *glaucescens* has an orbital ring index (OHI) of 1 - 2; a "pure" *argentatus* has an OHI of 8 - 9 (Fig. 37).

**The only difference in this test between the $p < .05$ and the $p < .01$ levels of significance is the following: at the $p < .01$ level, the Lake Louise group joins Subset 2.

***Aside from these extremes, a statistical continuum is formed.

hue 5 YR, pinkish yellow. The Lake Louise population had a mean orbital ring index (OHI 8.9) representing hue 5 Y (yellow).

The Munsell hues of 7.5 YR, 10 YR and 2.5 Y (light yellowish pink, pinkish yellow, and light yellow) were not represented in orbital rings as population means, but occurred in composite orbital rings (cf. Combination Hues, Section 5.52).

A highly significant F-ratio ($F = 7.43$, 164 d.f., $p < .001$) was produced by the analysis of variance of the hybrid indices of orbital ring pigmentation (Table 12), indicating real differences among group means. The means of orbital ring indices for each colony, together representing a spectrum of colors from dark pink to yellow, were arranged into three statistically similar subsets by the Duncan's Multiple Range Test (cf. Statistical Procedures, Section 4.6). At the 5% level of significance, Subset 1 contained three colonies, Haenke Island (OHI 1.30), Middleton Island (OHI 2.40), and North Marble (OHI 2.75), with OHI means of dark pink to light pink (Table 13). The six colonies in Subset 2, Middleton Island (OHI 2.40), North Marble (OHI 2.75), Egg Island (OHI 3.66), Copper Sands (OHI 4.0), Dry Bay (OHI 4.36) and Strawberry Reef (OHI 4.6) displayed a gradation of orbital ring indices from pink to light yellowish pink. The only colony in Subset 3 was Lake Louise (OHI 8.9; yellow). Statistically, aside from the Haenke Island population (OHI 1.30) and the Lake Louise colony (OHI 8.9) at the extremes, the other colonies occurred in common subsets, and demonstrated a continuum of orbital ring pigmentation (Table 13). Note the sharp step-cline between Strawberry Reef (OHI 4.6) and Lake Louise (OHI 8.9), which was associated with a major mountain barrier, the Chugach Mountain Range (Table 13, Fig. 36).

If orbital ring pigmentation were to function as a species-specific recognition character in this zone of overlap, then variation would be limited. However, the orbital ring proved to be the most variable character examined.

5.51 Solo Hues.

If the orbital rings were uniformly pigmented, they were designated as "solo hues." Haenke Island and Lake Louise populations represented the opposite extremes of dark pink and yellow uniformly pigmented ("solo hued") orbital rings (Figs. 33, 34). Gulls with uniformly pigmented orbital rings were also recorded in the North Marble, Egg Island, and Dry Bay populations. Dark pink (5 R), and 2.5 YR (yellowish pink) were the most commonly represented solo hues (Figs. 33-35) in all colonies except Lake Louise, which contained over 90% uniformly yellow orbital rings. Notable is the range of uniformly colored orbital rings at Dry Bay (dark pink - light pinkish yellow) where gulls with black primaries had solo orbital ring hues of yellowish-pink (2.5 YR), pinkish yellow (5 YR) and light pinkish yellow (10 YR).

5.52 Combination Hues. Some gulls had orbital rings composed of two or three hues. These orbital rings were labeled "combination hues." Orbital rings with a combination of two hues may have similar base hues (5 R - 5 R), but each has its own value and chroma, producing a different color. For example, a pink eye-ring with areas of more intense reddish pigmentation occurs in 20 - 25% of the individuals in the Dry Bay and Egg Island populations (Figs. 34, 35).

Combinations of two hues exclusively were found in the orbital rings of the Copper Sands and Strawberry Reef populations, further demonstrating the close similarity of the adjoining populations (Fig. 35).

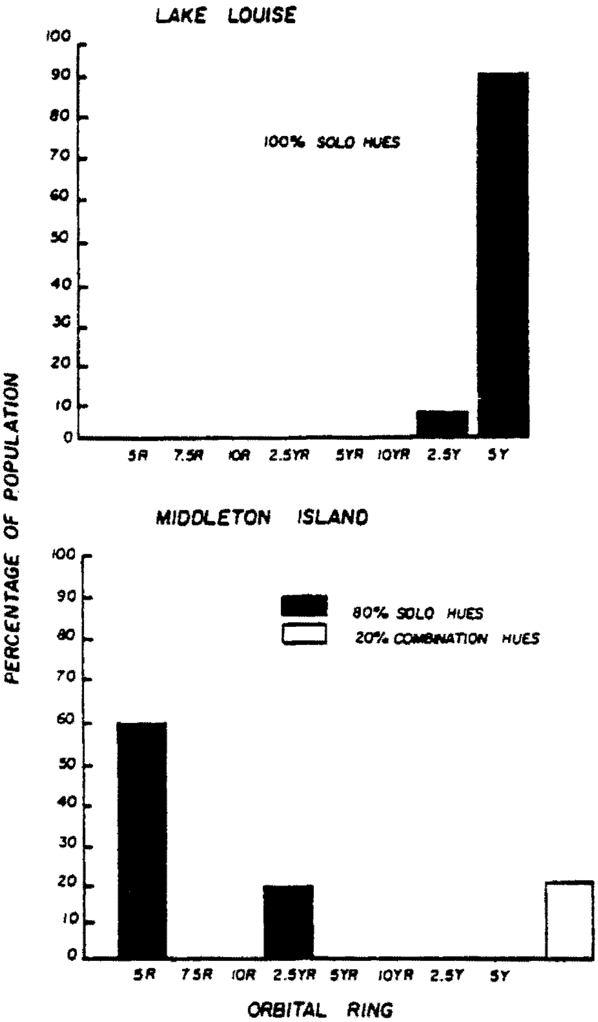

Fig. 33. Frequency distributions of orbital ring pigmentation in Larus populations at Lake Louise, and Middleton Island, Alaska. The Lake Louise population had orbital ring hues concentrated at 2.5 Y (light yellow) and 5 Y (yellow); the Middleton Island population had orbital ring pigmentation concentrated at 5 R (dark pink) and 2.5 YR (yellowish pink), but combination hues were also present.

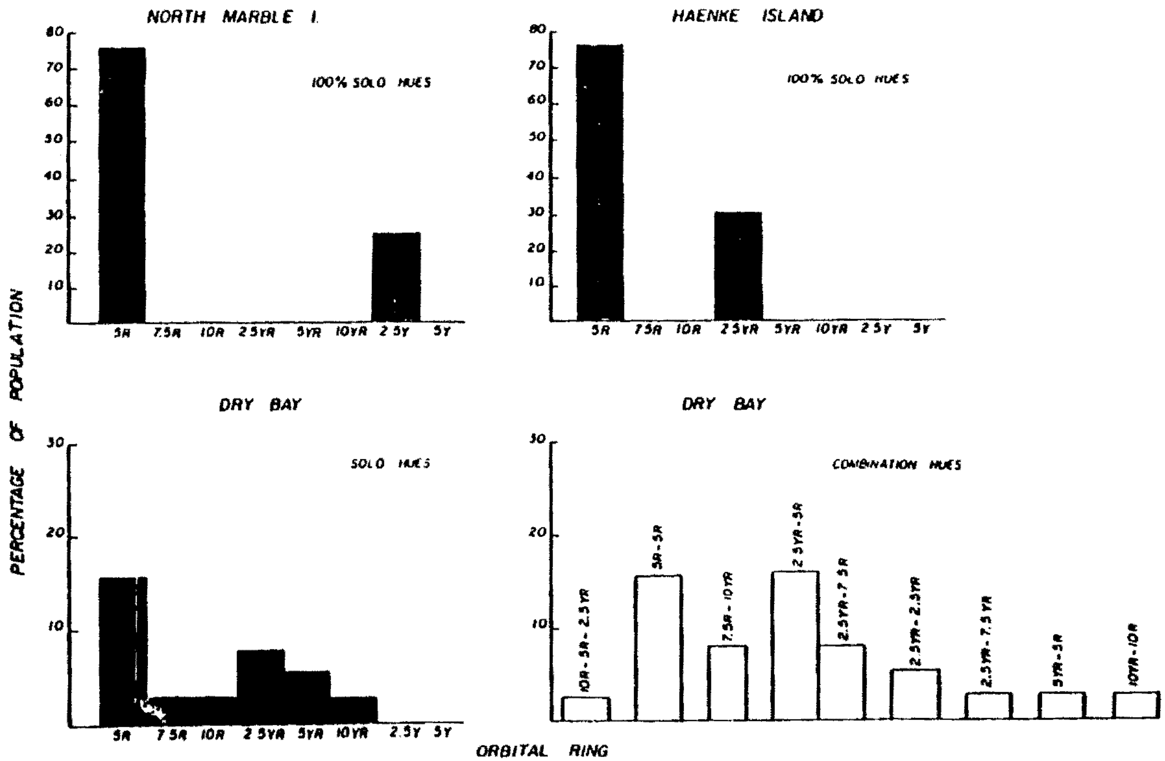

Fig. 34. Frequency distributions of orbital ring pigmentation in Larus populations breeding at North Marble Island, Haenke Island, and Dry Bay, Alaska. North Marble and Haenke Island populations had orbital ring pigmentation concentrated at 5 R (dark pink) hues; Dry Bay was distinguished by having the greatest distribution of solo hues, ranging from 5 R (dark pink) to 10 YR (light yellowish pink) in addition to the most uniformly distributed pattern of combination hues.

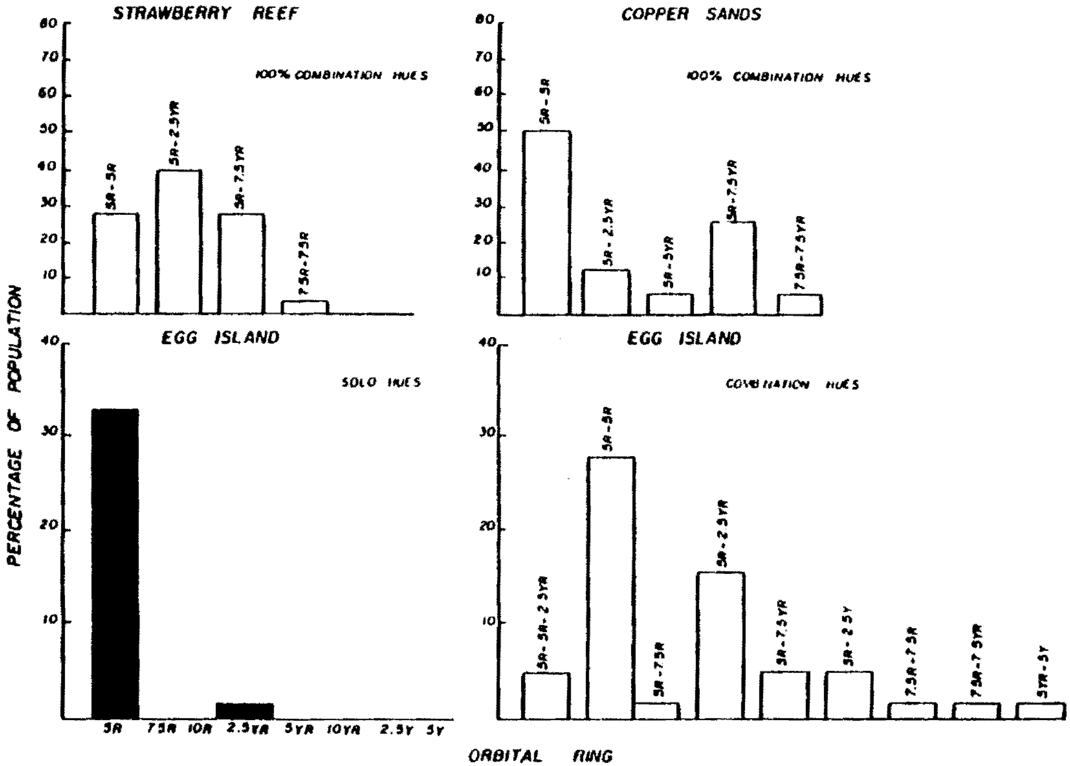

Fig. 35. Frequency distributions of orbital ring pigmentation in Larus populations breeding at Strawberry Reef, Copper Sands, and Egg Island, Copper River Delta, Alaska. Strawberry Reef ano Copper Sands both exhibited 100% combination hues (pink and yellow in similar patterns of deposition). The Egg Island population exhibited solo hues (concentrated at 5 R, dark pink) and combination hues, including some individuals with a combination of three hues in the orbital ring.

A typical pattern in these two populations was an orbital ring with a pinkish hue on the upper rear portion of the eyelid, and a yellowish hue on the lower front portion. Combinations occurring within these two populations were pink with yellowish pink (5 R - 2.5 YR) or pink with light yellowish pink (5 R - 7.5 YR).

Individual gulls on Egg Island and Dry Bay had orbital rings with a combination of three hues. For example, an orbital ring of a pink base color, but with darker pink areas on the upper rear, and yellowish pink on the lower front portion (5 R - 5 R - 2.5 YR), was recorded on Egg Island (Fig. 35). At Dry Bay, an orbital ring with light pink, dark pink, and yellowish pink hues (10 R - 5 R - 2.5 YR) was observed (Fig. 34). Egg Island had the greatest distribution of combination hues, including pink with darker pink areas (5 R - 5 R) and pinkish yellow with yellow (5 YR - 5 Y) (Fig. 35).

The distribution of combination hues at Dry Bay included orbital rings of pinkish yellow with pink (5 YR - 5 R) to orbital rings of a pink base color, with areas of light pinkish yellow (5 R - 7.5 YR). Dry Bay was also distinguished by having the greatest distribution of solo hues, in addition to the most uniformly distributed pattern of combination hues (Fig. 34).

In summary, the possibility that orbital ring pigmentation functions at present as an independent species-specific recognition character between argentatus and glaucescens is considered remote because of the wide spectrum of variation. However, the degree of variation may function as a character for individual or population recognition.

5.6 Composite Hybrid Index

Primary feather pigmentation, iris color, and orbital ring pigmentation, which were analyzed separately to discern relationships between gull populations in southern Alaska, were also unified in a composite hybrid index for a more complete exploration of these relationships (Table 14).

A highly significant F-ratio ($F = 61.01$, 163 d.f , $p < .001$) was produced by the analysis of variance of the composite hybrid indices (Table 14). The offshore Middleton Island population, with the lowest composite index, represented a "pure" glaucescens colony. The interior Lake Louise population, with the highest composite index, was representative of argentatus (Table 14). Between these extremes were three statistically homogenous subsets in the Duncan's Multiple Range Test at both the 5% and 1% levels of significance (Tables 15, 16). Subset 1 contained phenotypic glaucescens populations (Middleton Island, Haenke Island, Egg Island, Copper Sands, and Strawberry Reef). Subset 2 contained hybrid colonies in bays and fjords (Dry Bay and North Marble) and Subset 3 contained only the Lake Louise argentatus population. The coastal glaucescens populations displayed gradually increasing indices, representing darkening of primary feather pigmentation, and increasing yellow pigments in orbital rings and irides (Fig. 36). Strawberry Reef was included in both Subset 1 (glaucescens) and Subset 2 (hybrids) in the DMRT ($p < .01$); the positions of all other populations remained unchanged. Thus the colony at Strawberry Reef displayed a statistical relationship to both coastal glaucescens and hybrid colonies from the results of these criteria. The hybrid colonies were in turn statistically intermediate between argentatus and glaucescens.

Table 14. Composite Hybrid Index (CHI)*
for Larus Colonies in Southern Alaska
(Iris + Orbital Ring + Primary Pigmentation Indices)

Colony	Mean	Range	Standard Deviation	Sample Size
Middleton Island	9.40	8.00 - 12.00	1.29	5
Haenke Island	9.55	8.00 - 12.00	1.21	10
Egg Island	10.39	8.00 - 16.00	1.76	56
Copper Sands	10.40	9.50 - 13.50	1.26	16
Strawberry Reef	11.40	9.50 - 17.00	2.33	25
Dry Bay	13.54	9.00 - 23.00	2.62	37
North Marble	14.12	10.00 - 23.00	6.00	4
Lake Louise	23.82	23.00 - 24.00	0.40	11

Analysis of Variance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-ratio
Between groups	7	1925.73	275.10	61.01**
Within groups	156	703.40	4.51	
Total	163	2629.14		

*A "pure" glaucescens has a Composite Hybrid Index of 8.00 - 9.00; a "pure" argentatus has a CHI of 23.00 - 24.00 (Fig. 37).

**Very highly significant ($p < .001$).

Table 15. Ranked Means for the Composite Hybrid Index (CHI) for *Larus* Colonies* in Southern Alaska (Iris + Orbital Ring + Primary Pigmentation Indices)

(Duncan's Multiple Range Test: $p < .05$ level)

Homogenous subsets (subsets of groups, whose highest and lowest means do not differ by more than the shortest significant range for a subset of that size. There is no significant difference between the means of groups underlined with a single dotted line.

Subset 1 (most like *glaucescens*)

Group	Middleton Island	Haenke Island	Egg Island	Copper Sands	Strawberry Reef**
Mean	9.40	9.55	10.39	10.41	11.40

Subset 2 (hybrid colonies with individual *argentatus* present)

Group	Dry Bay	North Marble
Mean	13.54	14.12

Subset 3 (interior *argentatus*)

Group	Lake Louise
Mean	23.82

*A "pure" *glaucescens* has a Composite Hybrid Index of 8 - 9; a "pure" *argentatus* has a CHI of 23 - 24.

**Note the position of Strawberry Reef, here assigned to a subset most resembling *glaucescens*; compare with Table 16.

Table 16. Ranked Means for the Composite Hybrid Index (CHI) for *Larus* Colonies* in Southern Alaska (Iris + Orbital Ring + Primary Feather Pigmentation Indices)

(Duncan's Multiple Range Test: $p < .01$ level)

Homogenous subsets (subsets of groups, whose highest and lowest means do not differ by more than the shortest significant range for a subset of that size). There is no significant difference between the means of groups underlined with a single dotted line.

Subset 1 (most like *glaucescens*)

Group	Middleton Island	Haenke Island	Egg Island	Copper Sands	Strawberry Reef**
Mean	9.40	9.55	10.39	10.41	11.40

Subset 2 (hybrid colonies with and without individual *argentatus* present)

Group	Strawberry Reef**	Dry Bay	North Marble
Mean	11.40	13.54	14.12

Subset 3 (interior *argentatus*)

Group	Lake Louise
Mean	23.82

*A "pure" *glaucescens* has a Composite Hybrid Index of 8.00 - 9.00; a "pure" *argentatus* a CHI of 23.00 - 24.00.

**Note the position of Strawberry Reef, assigned by the DMRT at the $p < .01$ level to the *glaucescens* and the hybrid subsets, thereby demonstrating a statistical relationship to both classifications. See Discussion, Section 6.4, for a further elaboration of this finding (p. 128 - 135).

Mean Hybrid Indices at Eight Larus Colonies in Southern Alaska

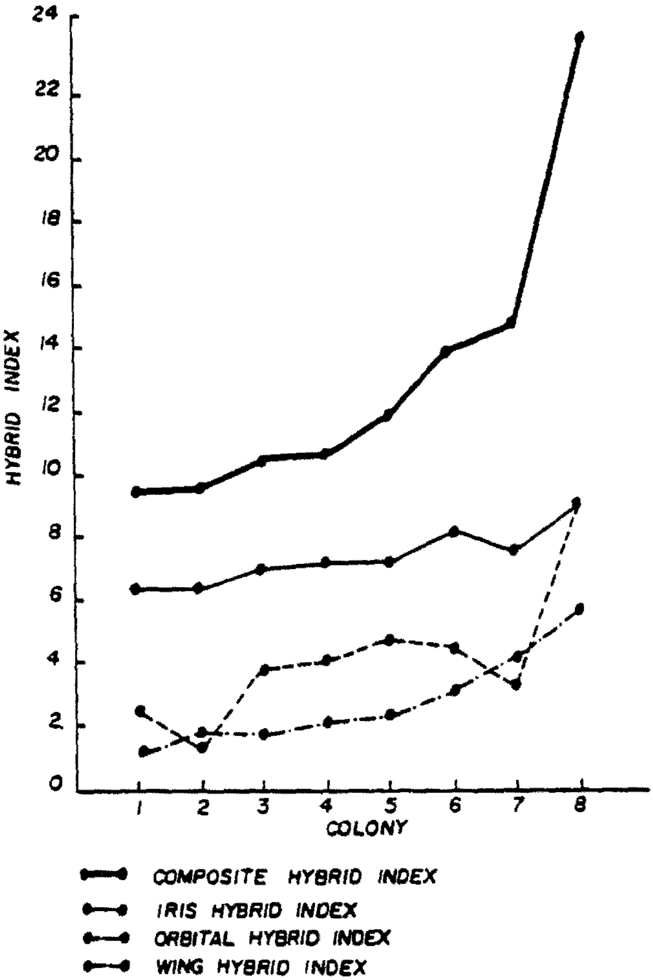

Fig. 36. The coastal glaucescens populations exhibited gradually increasing indices, representing darkening of primary feather pigmentation, and increasing yellow pigments in orbital rings and irides. Note the step-cline in the composite hybrid index between North Marble and Lake Louise (argentatus). (1 = Middleton Island; 2 = Haenke Island; 3 = Egg Island; 4 = Copper Sands; 5 = Strawberry Reef; 6 = Dry Bay; 7 = North Marble; 8 = Lake Louise)

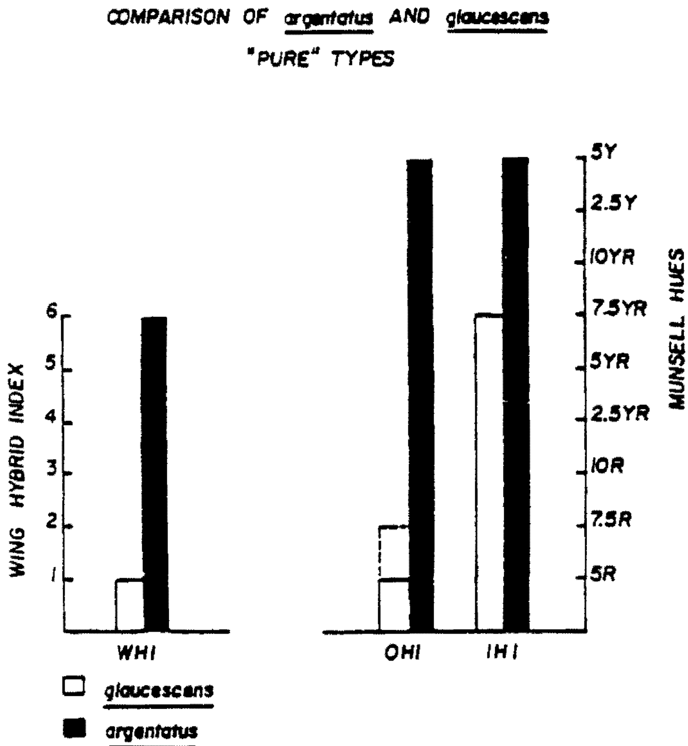

Fig. 37. Comparison of argentatus and glaucescens "pure" types. L. glaucescens have a Wing Hybrid Index of 1: primaries the same shade as the mantle, and no observable pattern of melanin deposition. L. argentatus has a Wing Hybrid Index of 6: primaries of intensive black pigment, in an extensive and distinctly delimited pattern, with melanin deposited along the feather shafts of the 8th, 9th, and 10th primaries. L. glaucescens have an Orbital Hybrid Index of 1 - 2, with dark pink (5R) to pink (7.5 R) hues. L. argentatus have an OHI of 8 - 9, with light yellow (2.5 Y) to yellow (5 Y) hues. L. glaucescens have an Iris Hybrid Index of 6 (7.5 YR), brown hues. L. argentatus have an IHI of 9 (5 Y), yellow hues.

5.7 Nest Site Selection: Slope, Substrate, and Cover

Southern Alaskan argentatus and glaucescens nest on a variety of substrates. In Glacier Bay, argentatus was most often found in fjords close to glacier fronts; glaucescens was concentrated in more marine regions, but also colonized recently deglaciated fjords. L. argentatus and glaucescens were first observed nesting together on fjord cliffs 4 km from the front of the Johns Hopkins Glacier in Johns Hopkins Inlet in Glacier Bay in July 1971 (Patten & Weisbrod, 1974). In 1972-73 argentatus and glaucescens were found nesting together on low rocky islets, flat gravelly hillsides, and sloping grassy meadows in Glacier Bay (Table 17). North Marble Island in Glacier Bay had highest densities of nesting glaucescens on grassy meadows, in which Hordeum was the dominant vegetation. Some nests were located on precipitous sites, approaching 50% slope (Table 18). Small numbers of phenotypic argentatus were scattered through this colony.

Dry Bay, at the mouth of the Alsek River, northwest of Glacier Bay, supported 500 pairs of mixed argentatus and glaucescens nesting on flat gravel bars (Tables 17, 18). The low alluvial islands, washed by high waters in late summer and during winter storms, were of unstabilized substrate. Vegetation was sparse and indicated a combined maritime and freshwater influence (cf. Study Areas, Section 3.22).

Thousands of glaucescens at Egg Island, Copper Sands, and Strawberry Reef, nested on dunes covered with Elymus meadows. Slope of the dunes was shallow, with a mean less than 3%; the highest dunes were only 10 m above sea level (Tables 17, 18).

The glaucescens on Middleton Island were colonizing two habitats; an

Table 17. Nest Site Substrates and Cover in *Larus* Colonies in Southern Alaska, British Columbia, and Yukon Territory

Colony	Species Composition	Substrate/Cover
Glacier Bay colonies:		
Johns Hopkins Inlet	mixed *argentatus* - *glaucescens*	bare cliff face
Sealer's Island	mixed *argentatus* - *glaucescens*	low rocky islet
Tlingit Point	mixed *argentatus* - *glaucescens*	flat gravelly islet
North Marble	mixed *argentatus* - *glaucescens*	sloping grassy hillsides
Dry Bay	mixed *argentatus* - *glaucescens*	flat alluvial gravel bars
Haenke Island	*glaucescens*	grassy cliff terraces
Middleton Island	*glaucescens*	grassy knolls & *Elymus*/boulder/driftwood mosaic
Egg Island	*glaucescens*	*Elymus*-covered dunes
Copper Sands	*glaucescens*	*Elymus*-covered dunes
Strawberry Reef	*glaucescens*	*Elymus*-covered dunes
Lake Louise	*argentatus*	sloping grassy islet, boreal lake
Atlin Lake, B.C.	*argentatus*	low rocky islet, boreal lake
Dezadeash Lake, Y.T.	*argentatus*	forested islet shores, boreal lake

Table 18. Nest Site Slope in *Larus* colonies in Southern Alaska

Colony	Species Composition	Mean	Range	S.D.	Sample Size
North Marble	mixed	16.2	1 - 48	15.7	9
Dry Bay	mixed	0	0	0	112
Egg Island	*glaucescens*	2.8	0 - 8	2.4	186
Lake Louise	*argentatus*	15.9	1 - 50	14.9	50

Elymus-boulder-driftwood mosaic surrounding the island, and on grassy (*Calamagrostris*) knolls at the south end of the island.

The *argentatus* at Lake Louise nested on a grassy (*Calamagrostris*) islet, with slope and substrate similar to that of North Marble, and vegetation similar to that of Middleton Island.

Thus, both allopatric and sympatric *argentatus* and *glaucescens* observed in this study were flexible in nesting habitat selection in coastal southern Alaska and adjoining interior lakes. Nest site substrate included gravel bars and cliff faces, with from 0% to over 50% slope (Table 18). Favored sites for both *argentatus* and *glaucescens* were grassy island slopes. Therefore nest site selection based on structural features of the habitat (slope, substrate, and cover) was not serving as an isolating mechanism between these gulls in the study area.

5.8 Analysis of Mating Patterns

Analysis of mating patterns involved study of pairs at 564 nest sites. At North Marble, 162 gull pairs within four study plots were observed with binocular and telescope in 1972. The study of the pairs revealed the following: 157 phenotypic *glaucescens* pairs; 1 typical *argentatus* (WSM 27430) paired with a "typical" *glaucescens*, and 3 "intermediates" (WSM 27427, 27428, 27429) paired with *glaucescens*.

Gull pairs at 290 nest sites were examined in 1973, and the following were recorded: 276 phenotypic *glaucescens* pairs; 1 pair of *argentatus*; 3 *argentatus* paired with *glaucescens*, and 10 intermediate gulls paired with *glaucescens*. The three *argentatus* paired with *glaucescens* were males; the probability of the single *argentatus* female selecting a mate of like type in this colony was 4/290, or ($p < .01$), suggesting assortative mating.

Mating patterns of 112 pairs within the mixed colony at Dry Bay were studied in detail during May, 1977.[1] The indices of primary feather pigmentation (WHI) and iris color (IHI) of each male were compared to those of the corresponding female in each of the 112 pairs. Further, the combined indices (WHI + IHI) of each male were compared to those of the corresponding female in each of the 112 pairs. Detailed crosstabulations of these three indices are presented in Appendices VIII, IX and X.

Three Chi-square tests were conducted on the distributions of primary feather, iris, and combined indices. The Chi-square test on the observed distribution of primary feather pigmentation indices, compared to that expected by chance (i.e., if the gulls were mating without respect to this characteristic), produced a significant Chi-square of 11.29, with 3 d.f. ($p < .02$) (Table 19). Based upon comparisons of wing hybrid indices, 63% of the pairs at Dry Bay agreed exactly; 18% disagreed by one index value; 8.6% disagreed by two index values (backcrosses), 0.9% by three index values, 1.9% by four index values, and 7.6% disagreed by five index values (mixed pairs). Of the 63% of the pairs with identical hybrid indices, 51 pairs were _glaucescens_ (1 x 1); 12 pairs were intermediates selecting like types (eight 2 x 2 and four 3 x 3); and 3 pairs were _argentatus_ (6 x 6).

The Chi-square test on the observed distribution of iris colors, compared to a random (chance) distribution, resulted in a Chi-square of

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[1]The results and analysis of the mating patterns of the gulls in the mixed colony at Dry Bay were completed before the publication of Hoffman, Weins, and Scott (1978).

Table 19. Chi-square Test of the Comparison of Hybrid Indices of Primary Feather Pigmentation (WHI) of Males Against Females in 112 Pairs of *Larus* Gulls at Dry Bay, Alaska.

	Observed	Expected (by chance)	Chi-square $\frac{(O-E)^2}{E}$
agree exactly (identical WHI)	66	48.45	6.36
disagree by 1 WHI	25	32.96	1.92
disagree by 2 WHI	13	18.80	1.79
disagree by more than 2 WHI	8	11.79	1.22

(Data in Table 50) $\chi^2_{(3\ d.f.)} = 11.29$*

*Significant ($.01 < p < .02$)

4.23, with 3 d.f. (n.s., $p < .05$) (Table 20). This unexpected result is related to the strongly skewed distribution of iris color indices at Dry Bay; most individuals had dark eyes, and therefore any tendency towards mating patterns based on eye color alone could not be established.

However, the observed distribution of the combined primary feather and iris color indices, compared to that expected by chance, resulted in a significant Chi-square of 11.24, with 3 d.f. ($p \leq .03$) (Table 21). Based on comparisons of these combined indices, 56.3% of the pairs at Dry Bay agreed exactly; 19.6% disagreed by one combined index value; 10.7% disagreed by two index values, 5.3% by three index values, and 8% by four or more combined index values.

The results of these tests indicated that the mating patterns of the gulls in this study were assortative, or selective. Gulls in most cases chose mates similar to themselves, but occasionally selected mates of widely different phenotypes, forming mixed pairs and apparent backcrosses. It is apparent that the combination of primary feather pigmentation and iris color was much more important than iris color alone as a factor in mate selection.

5.9 Clutch Size

There is geographic and annual variation in clutch size in gull populations in southern Alaska. The range of clutch size in 933 nests of glaucescens, argentatus, and mixed populations between 1972 and 1978 included means from 2.05 to 2.93 eggs per nest. The extremes both occurred in glaucescens populations (Table 22). The 1975 Egg Island population (glaucescens) was at the low end of the range. Clutch size increased significantly from 1975 to 1976 (Table 22). Analysis of population parameters

Table 20. Chi-square Test of the Comparison of Iris Color Indices (IHI) of Males Against Females in 112 Pairs of *Larus* Gulls at Dry Bay, Alaska

	Observed	Expected (by chance)	Chi-square $\frac{O - E^2}{E}$
Agree exactly (identical IHI)	101	97.70	.11
Disagree by 1 IHI	3	4.78	.66
Disagree by 2 IHI	4	2.05	1.84
Disagree by more than 2 IHI	4	7.47	1.61
	112		X^2 = 4.23*

*not significant ($p > .05$). The distribution is skewed. Most individual gulls at Dry Bay had dark eyes.

Table 21. Chi-square Test of the Comparison of Combined Hybrid Indices (CHI) of Males Against Females in 112 Pairs of *Larus* Gulls at Dry Bay, Alaska (IHI + WHI = CHI)

	Observed	Expected (by chance)	Chi-square $\frac{O - E^2}{E}$
Agree exactly (identical CHI)	63	45.92	6.35
Disagree by 1 (CHI)	22	30.52	2.38
Disagree by 2 (CHI)	12	15.40	.75
Disagree by 3 (CHI)	6	6.3	.01
Disagree by 4 or more (CHI)	9	13.94	1.75
	112		$\chi^2 = 11.24$*

*Significant ($p \leq .03$)

Table 22. Clutch Size in *Larus* Colonies in Southern Alaska

Colony	Year	Species	Number of Nests Examined	Mean Clutch Size
North Marble	1972	mixed	162	2.80
North Marble	1973	mixed	191	2.96
Dry Bay	1977	"pure" (*gl.*)	76	2.93
Dry Bay	1977	mixed	36	2.89
Egg Island	1975	*glaucescens*	153	2.05
Egg Island	1976	*glaucescens*	186	2.56
Middleton Island	1978	*glaucescens*	52	2.88
Lake Louise	1977	*argentatus*	77	2.74
	1972-1978		933 nests	

at Egg Island in 1975 suggested an expanding population with a high proportion of young females, which tend to lay smaller clutches than older adults (Patten & Patten, 1975, 1976, 1977, 1978). The interior Lake Louise argentatus population had an intermediate clutch size of 2.74. The upper extreme in clutch size was the mean of the "pure" glaucescens at Dry Bay in 1977 (2.93). The weighted means for the mixed North Marble Island population were quite high (2.80 in 1972; 2.96 in 1973; combined weighted mean 2.90) (Table 22).

Phenotypes of both parents at 112 nests were determined in two study plots at Dry Bay in 1977 (cf. Analysis of Mating Patterns, Section 5.8). The categories containing at least one intergrade parent were combined for analysis of clutch size. Only one "pure" argentatus x argentatus pair was found at these sites. The analysis of clutch size of "pure" pairs at Dry Bay was therefore confined to glaucescens. However, the clutch sizes of the 77 "pure" pairs of argentatus at Lake Louise have been compared to glaucescens and mixed pairs.

The analysis of variance for clutch size in southern Alaskan Larus colonies produced a highly significant F-ratio ($F = 35.6$, 9 d.f., $p < .001$) (Table 23). The clutch size data were therefore analyzed using Duncan's Multiple Range Test (DMRT) (cf. Statistical Procedures, Section 4.6). (The Dry Bay colony was divided into two groups: "pure" glaucescens and mixed pairs, but the North Marble data were combined as a single mean).

There were four homogenous subsets of clutch sizes for argentatus, glaucescens, and mixed populations in the DMRT ($p < .05$)(Table 24). Subset 1 contained the 1975 Egg Island glaucescens population. Subset 2 contained populations of glaucescens, argentatus, and mixed pairs. Subset 3

Table 23. Analysis of Variance of Clutch Size in Southern Alaskan *Larus* Colonies

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-ratio
Between Groups	9	88.79	12.68	35.57*
Within Groups	923	283.83	0.36	
Total	932	372.62		

*Very highly significant ($p < .001$).

Table 24. Ranked Means for Clutch Size for *Larus* Colonies in Southern Alaska

(Duncan's Multiple Range Test: $p < .05$)

Homogenous subsets (subsets of groups, whose highest and lowest means do not differ by more than the shortest significant range for a subset of that size). There is no significant difference between the means of groups underlined with a single dotted line.

Subset 1	glaucescens			
Group	Egg Island - 1975			
Mean	2.05			
Subset 2	glaucescens	argentatus	glaucescens	hybrid*
Group	Egg Island - 1976	Lake Louise	Middleton Is.	Dry Bay
Mean	2.56	2.74	2.88	2.89
Subset 3	argentatus	glaucescens	hybrid	combined**
Group	Lake Louise	Middleton Is.	Dry Bay	North Marble
Mean	2.74	2.88	2.89	2.90
Subset 4	glaucescens	hybrid	combined	glaucescens
Group	Middleton Is.	Dry Bay	North Marble	Dry Bay
Mean	2.88	2.89	2.90	2.93

*hybrid = pairs containing at least one intergrade gull.

**combined = glau. x glau.; arg. x glauc.; intergrade x glau.; arg. x arg.

contained glaucescens, argentatus, and two mixed populations. Subset 4 contained mixed pairs at Dry Bay, "pure" (glaucescens) pairs at Dry Bay, and the mixed colony on North Marble Island. Within each subset, the clutch sizes were all statistically similar.

At the $p < .01$ level of significance, the homogenous subsets of ranked means for clutch size were reduced to three. Subset 1 remained the 1975 Egg Island population; Subset 2 contained the 1976 clutch size for glaucescens at Egg Island, that of argentatus at Lake Louise, that of glaucescens on Middleton Island, and that of the mixed pairs at Dry Bay. Subset 3 contained the argentatus at Lake Louise, glaucescens at Middleton Island, mixed pairs at Dry Bay, and the mean of the combined colonies at North Marble (Table 25).

Thus, while there were significant annual and geographical differences, populations of argentatus were not significantly different from mixed or glaucescens with respect to clutch size.

5.10 Hatching and Fledging Success

There were three types of egg loss in 933 nests studied in southern Alaskan Larus colonies: (1) eggs which disappeared from the nest because of predation ("lost" eggs); (2) eggs that remained in the nest but failed to hatch; and (3) eggs which pipped but the embryo failed to emerge and died (Table 26).

The most important cause of hatching failure was egg loss to predation, ranging from 4% to nearly 30% of eggs laid. In most cases, egg predation was by other (Larus) gulls. The glaucescens colony at Egg Island (1975-76) and the mixed colony at North Marble (1972-73) did not differ significantly from each other in egg loss to predation, but both

Table 25. Ranked Means for Clutch Size for Larus Colonies in Southern Alaska
(Duncan's Multiple Range Test: $p < .01$)

Homogenous subsets (subsets of groups, whose highest and lowest means do not differ by more than the short-significant range for a subset of that size). There is no significant difference between the means of groups underlined with a single dotted line.

Subset 1	glaucescens				
Group	Egg Island - 1975				
Mean	2.05				
Subset 2	glaucescens	argentatus	glaucescens	hybrid*	
Group	Egg Island - 1976	Lake Louise	Middleton Is.	Dry Bay	
Mean	2.56	2.74	2.88	2.89	
Subset 3	argentatus	glaucescens	hybrid	combined**	glaucescens
Group	Lake Louise	Middleton Is.	Dry Bay	North Marble	Dry Bay
Mean	2.74	2.88	2.89	2.90	2.93

*hybrid = pairs containing at least one intergrade.

**combined= glau. x glau.; arg. x glau.; intergrade x glau.; arg. x arg.

Table 26. "Lost," Inviable, and Pipped Eggs Failing to Hatch in *Larus* Colonies in Southern Alaska (1972 - 1978) (in Study Plots)

Colony	Year	Species	Total Eggs	Lost Eggs	Inviable Eggs	Pipped/ Failed to Hatch
North Marble	1972	mixed	455	125 (27.5%)	22 (4.8%)	1 (< 1%)
North Marble	1973	mixed	566	150 (26.5%)	26 (4.6%)	1 (< 1%)
Egg Island	1975	*glaucescens*	313	92 (29.5%)	8 (2.6%)	1 (< 1%)
Egg Island	1976	*glaucescens*	476	104 (21.8%)	9 (1.9%)	1 (< 1%)
Dry Bay "A"	1977	mixed	265	10 (3.7%)	8 (3.0%)	2 (< 1%)
Dry Bay "B"	1977	mixed	63	7 (11.1%)	0	0
Lake Louise	1977	*argentatus*	211	n.a.	13 (6.2%)	2 (< 1%)
Middleton Island	1978	*glaucescens*	150	8 (5.3%)	18 (12.0%)	0

had significantly higher ($p < .05$) higher rates of this type of egg loss than the mixed colony at Dry Bay (Table 26). Data on egg loss to predation were not available for the _argentatus_ population at Lake Louise.

Inviable eggs (1972-78) ranged from 0% at the Dry Bay colony (mixed _argentatus_ x _glaucescens_), to 1.9% in the Egg Island _glaucescens_ population, to 6.2% in the _argentatus_ breeding at Lake Louise, and to 12% in the _glaucescens_ population on Middleton Island. Inviable eggs in the mixed colony at North Marble (1972-73) had similar low frequencies, ranging from 4.6% to 4.8%. Differences between populations in frequencies of inviable eggs were not significant ($p < .05$) (Table 26).

Egg loss caused by eggs which pipped without further emergence of the embryo was well below 1% at every colony (Table 26).

Hatching success for all colonies (1972-78) ranged from 67% to 93% (Table 27). The study colony with the highest hatching success was the mixed population at Dry Bay in 1977. This colony also had the lowest egg loss to predation. Predation was the controlling factor in hatching success in all colonies, with the exception of Middleton Island, where large internest differences (>50 meters) may have reduced attempts at predation by other gulls.

The Egg Island _glaucescens_ population was not significantly different in hatching success or observed chick mortality from the mixed colony on North Marble, but chick disappearance was significantly higher ($p < .05$). This was probably related to the much greater meadow area on Egg Island, which allowed chicks to wander. Dry Bay, because of intense eagle predation, had the highest rate of chick disappearance (Table 27). The North Marble Island colony had the highest percentage of chicks fledged of those

Table 27. Hatching Success, Chick Mortality, and Fledging Success in *Larus* Colonies in Southern Alaska (1972 - 1978)

Colony	Year	Species	Nest Examined	Chicks Hatching	Observed Mortality	Disappeared	Fledged (% of Hatched)	(Mean per Nest)
North Marble	1972	mixed	162	304 (67%)	16 (5%)	5 (2%)	283 (93%)	1.75
North Marble	1973	mixed	191	390 (69%)	31 (8%)	16 (4%)	343 (88%)	1.80
Egg Island	1975	glaucescens	153	254 (69%)	30 (12%)	75 (26%)	157 (62%)	1.03
Egg Island	1976	glaucescens	186	343 (77%)	27 (8%)	108 (31%)	208 (61%)	1.12
Dry Bay "A"	1977	mixed	90	245 (92%)	16 (6%)	95 (39%)*	134 (54%)	1.44
Dry Bay "B"	1977	mixed	22	59 (93%)	2 (3%)	29 (49%)*	28 (48%)	
Lake Louise	1977	argentatus	77	n.a.	--	--	73 --	0.95
Middleton Island	1978	glaucescens	52	123 (82%)	--	--	--	**

*Most chick disappearance was due to sustained eagle predation.

** Chicks on Middleton Island were impossible to follow after hatching because of dense vegetation.

hatching, and the Dry Bay population the lowest percentage (Table 27). However, the final fledging success as measured in chicks produced per nest depended additionally upon the clutch size and hatching success. The analysis of variance for fledging success in eight southern Alaska study colonies produced an F-ratio of 1.81, 7.d.f. ($p < .05$; F-probability = .0816), i.e., differences between colonies in fledging success were not significant (Table 28). There was sufficient variability in fledging success within the colonies studied to eliminate significant differences between the colonies. However, the hybrid pairs within the mixed colony at Dry Bay produced 1.47 chicks per nest, while in comparison the phenotypically "pure" pairs (glaucescens) produced 1.40 chicks per nest ($t = 0.72$; $p > .05$), also not significant.

In summary, although there was significant annual and geographical variability in clutch size in gull populations in southern Alaska, the clutch size and fledging success of "hybrid" versus "pure" pairs within the mixed colony at Dry Bay were not significantly different. Differences in fledging success between colonies of glaucescens and argentatus examined were also not significantly different. Therefore, at these confidence levels, there was no evidence of post-mating isolating mechanisms affecting clutch size and fledging success during the study years.

Table 28. Analysis of Variance of Fledging Success in Southern Alaskan *Larus* Colonies

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-ratio
Between Groups	7	135.67	19.38	1.81*
Within Groups	925	8508.88	10.69	
Total	932	8644.55		

*Not significant ($p > .05$; F-probability = .0816).

6.0 DISCUSSION

6.1 Allopatric Hybridization of Glaucous-winged and Herring Gulls

The interbreeding of two previously isolated populations in a zone of contact is known as allopatric hybridization (Mayr, 1942; 1963). Glaucous-winged and Herring Gulls are virtually allopatric in the Pacific Northwest, occupying largely exclusive but adjacent geographical areas. The contact between these forms is determined by both intrinsic and extrinsic factors. The extrinsic factors originally separating these two gull populations were glaciation and mountain ranges, which even now allow contact only in geographically restricted areas. The Alaska, St. Elias, and Coast Ranges of the Pacific Northwest are now the most important barriers to gene flow between Glaucous-winged and Herring Gulls. The mountains themselves do not provide suitable habitat for gulls and in addition they produce two very different climatic zones, the boreal (subarctic) interior and the west coast marine. But where rivers and recently deglaciated fjords break the mountain barrier, a zone of secondary contact results between the two previously isolated gull populations. Interbreeding occurs in these areas of contact, since complete reproductive isolating did not evolve during their period of separation.

Among the most important intrinsic factors determining the degree of genetic contact between Glaucous-winged and Herring Gulls are nesting habitat preferences. The deliberate choosing of the appropri... habitat can serve as a powerful reinforcement of geographic borders and reduces the probability that new isolation will become established beyond the species border, but for gulls there is a degree of variability in habitat preferences.

Glaucous-winged and Herring Gulls exhibit incomplete habitat segregation along the division between fresh-water and marine environments during the breeding season. Along the coast of Alaska, Herring Gulls have a distinct preference for breeding in restricted fresh-water and brackish conditions such as at the heads of fjords with active glaciers and at river mouths. For example, in Glacier Bay, numbers of breeding Herring Gulls diminish with distance away from active glacier fronts (Table 4, Figure 4). Breeding Glaucous-winged Gulls are generally confined to marine environments, although after the breeding season they may follow major rivers and salmon streams inland. A colony of *glaucescens* breeding on islands in Bidarka Bay, Illiamna Lake, on the base of the Alaska Peninsula (Williamson and Peyton, 1963) and a small population breeding some distance up the Columbia River (Hoffman, pers. comm.) are two known exceptions to this rule.

Nesting habitat selection in gulls is influenced by the interaction of genetic and developmental factors, with individuals preferring to nest in that habitat in which they were hatched (i.e., habitat imprinting). Noseworthy *et al*. (1973) found that young Herring Gulls, after experimental displacement, returned to habitat similar to that in which they were hatched. Tinbergen (1953) found that Herring Gulls returned as adults to nest in the same types of habitat in which they had been raised as chicks. Young adult gulls, breeding for the first time, may initially prefer to return to the colony in which they were raised (i.e., philopatry). If successful in breeding, they return to the same breeding place in subsequent seasons (Southern 1977). Such colony site tenacity has been documented for several gulls, including the Herring Gull in

Europe and the Great Lakes (Tinbergen, 1961; Drost et al., 1961; Ludwig, 1963) and the Glaucous-winged Gull in British Columbia (Vermeer, 1963). Colony site tenacity develops when the environment of the colony sites does not change from year to year, and breeders are successful.

There are two categories of gulls which seek new nesting locations. These are gulls breeding for the first time, and unsuccessful breeders. First-time breeders not returning to their natal site may attempt to breed in a habitat similar to that in which they were raised but at a different location or they may attempt to settle in a site where experienced breeders are nesting (McNicholl, 1975). A gull abandoning an unsuccessful nest site may seek a different location where other birds are nesting or an alternative breeding habitat. First-time breeders and unsuccessful adults demonstrate sufficient flexibility to pioneer new and potentially productive habitats and display a degree of opportunism rather than rigid preferences. The limited availability of nesting habitat in the interior may also encourage Herring Gulls to colonize the coast.

Colonies located in unstable environments have fewer returning experienced adults, but more young birds attempting to breed for the first time. Mixed colonies of Glaucous-winged and Herring Gulls are found on river bars near the coast and in recently deglaciated fjords--notably unstable environments. Site tenacity in such places either has not had time to develop, or the areas are potentially disadvantageous. The river bars may disappear completely, and the fjord sites may become unsuitable because of vegetative succession. Rapid colonization of such newly available and temporarily suitable sites would be of selective advantage. Based on the above, it is believed that pioneering individuals or previously unsuccessful adults colonize such sites on the south coast of Alaska.

Tinbergen (1953), based on his studies of European Herring Gulls, observed that pioneering individuals are among the most susceptible to hybridization because of the paucity of conspecific mates. The eight years of observation upon which this study is based, supported by the findings of Sanger (1973) and Harrington (1975), also indicate that Herring Gulls, hatched on river bars in interior Alaska, migrate to the open sea in the winter. The Herring Gulls, returning from winters at sea, find suitable river-bar nesting habitat at the mouths of rivers within the coastal environment. These river bars, within sight and sound of the marine environment, are colonized by Glaucous-winged Gulls, leading to the breeding of both forms in the same habitat.

6.2 Evolution of Assortative Mating Patterns Without Selective Pressure on Hybrid Offspring

There was widespread evidence of hybridization within the *argentatus* - *glaucescens* contact zone, as indicated by observations of mixed pairs and the great amount of morphological variation in coastal adult *glaucescens* populations. There was also evidence of maintenance of both parental types. Nesting habitat preferences and selection of like types as mating partners were partially formed isolating mechanisms, but did not prevent interbreeding between *argentatus* and *glaucescens*. Definite deviations from random mating were evident, indicating the development of incipient isolating mechanisms prior to contact between the two forms.

Among the most important pre-mating isolating mechanisms is species recognition. It has been postulated that the color of the iris and the orbital ring function in species recognition between large white-headed gulls (Smith, 1966b). The variation and distribution of iris and orbital ring colors make such action unlikely in southern Alaskan *Larus* populations. However, the variability of these characters may function in individual or population recognition. For example, the orbital rings of the Strawberry Reef and Copper Sands populations resembled each other very closely, with combinations of only two hues occurring (yellow and pink in similar patterns of deposition). The three gull populations on the Copper River Delta also shared strikingly similar distributions of iris hues.

Even if intrinsic pre-mating isolating mechanisms were fully developed, pioneering *argentatus*, in the absence of appropriate stimuli from other Herring Gulls, would respond to *glaucescens* in breeding condition rather than not breed at all. The south coast of Alaska was beyond the normal breeding range of most *argentatus*, and the Alaskan Herring Gull population numbered far less than that of the Glaucous-winged Gull. Individual *argentatus*, coming into breeding condition at the end of their dispersal phase on the south coast, may have had difficulty finding conspecific mates.

Mixed pairs are found in recently deglaciated fjords and at river mouths in habitats meeting the preferences of both taxa. Mixed pairs made up 7.6% of the colony at Dry Bay, and only 0.6 - 1% of the colony on North Marble Island. The offspring of these mixed pairs were viable at least to fledging stage (cf. Hatching and Fledging Success, Section 5.10). As evidenced by the great amount of morphological variation exhibited by the coastal adult *glaucescens* (cf. Results, Sections 5.1 - 5.6), it is hypothesized that the *argentatus* x *glaucescens* hybrids survived to adulthood and returned to the natal colony or to the vicinity to breed.

The F_1 individuals mated with individuals resembling the most abundant parental type, glaucescens, forming a backcross, with the full range of variability potentially expressed in their offspring. Apparent backcross pairs, based upon indices of primary feather pigmentation, made up 8.6% of the colony at Dry Bay, and 2% - 3.4% of the colony at North Marble. The progeny of the backcrosses formed pair bonds with bird resembling the hybrid parent, creating a population of intermediates, the recombinants of which resembled the parental types. The recombinant forms resembling argentatus attracted more argentatus from the migration pathway, and interbreeding continued.

Patterns of mating in the mixed colony at Dry Bay were assortative, with frequent exceptions. Based upon comparisons of wing hybrid indices (cf. Analysis of Mating Patterns, Section 5.8), 63% of the pairs at Dry Bay agreed exactly; 18% disagreed by one hybrid index value, 8.6% disagreed by two index values, 0.9% by three index values, 1.9% by four index values, and 7.6% disagreed by 5 index values (mixed pairs). The probability that the single argentatus pair observed on North Marble would be formed, given the number of potentially available glaucescens and argentatus mates, was 1/140, suggesting a high degree of assortative mating.

Harris's (1970) egg fostering experiments on argentatus and fuscus, two closely related species in Britain, also revealed a strong tendency for individuals (especially females) to choose mates similar to the birds that raised them. The most reasonable explanation for this occurrence is that the selection of mating partners is determined by fixation on a parental type. This fixation is incompletely formed, but leads to assortative mating patterns in gulls without differential selection pressure on hybrid offspring along the southern Alaskan coastline. The assortative mating patterns include intergrades selecting like types as mating partners.

6.3 Viability of Hybrid Offspring

The genotype of a species is considered to be an integrated system (coadapted gene complex) adapted to the ecological niche in which a species lives. Gene recombination in the offspring of species crosses could lead to the formation of disharmonious gene complexes (Dobzhansky, 1951). The decreased viability of hybrid offspring lessens the reproductive potential of both interbreeding species. While both *argentatus* and *glaucescens* differ in their preferences for fresh-water and saltwater conditions during the breeding season, both are generalists, filling the role of opportunistic scavengers outside the breeding season. There is no evidence that *argentatus* x *glaucescens* hybrids are any less well adapted to the southern Alaskan coastline than are either of the parental forms, as evidenced by comparisons of clutch size, fledging success, and frequency of intergrades (cf. Results, Sections 5.1 - 5.6 and 5.8). According to theory, any mutation which provides a basis for species recognition will be selected for if hybrid offspring suffer reduced fitness. Such selection leads to the evolution of pre-mating isolating mechanisms. Assortative mating patterns usually evolve if there is a selective pressure against hybrid offspring, which is not the case with *glaucescens* x *argentatus* crosses in the coastal environment. Furthermore, extensive interspecific hybridization in animals normally accompanies the beginning of sympatry, and rapidly declines because of the establishment of antihybridization mechanisms. While contact and hybridization between *glaucescens* and *artentatus* was obviously recent in areas such as Glacier Bay, geological evidence suggests that in localities such as Dry Bay, contact was possible as long as 10,000 years ago. Morphological analyses of adult gulls at the six colonies along the zone of contact indicate widespread gene flow from argentatus into glaucescens populations, with no evidence of hybrid inviability.

6.4 Relationships Between Northeast Gulf of Alaska Larus Populations

The relationships between breeding populations of Glaucous-winged and Herring Gulls in the Northeast Gulf of Alaska have until recently remained unexplored. Evidence of gene flow from argentatus into glaucescens populations, as indicated by colorimetric hybrid indices, was widespread, although the actual contact (interbreeding) between the two populations was found to be restricted. Mixed populations of argentatus and glaucescens displayed degrees of reproductive isolation ranging from occasional interbreeding between pioneering individuals, through intergrades selecting like types as mating partners, to absorption of argentatus into variable populations of glaucescens. The morphological analyses and the reproductive survey revealed that the degree of intergradation was related to the geological and ecological history of the immediate area of the colony. The investigation of the zone of contact thus focused on a study of the unique conditions determining the area of hybridization in this part of Alaska.

Glaucous-winged and Herring Gulls have similar nesting habitat requirements with respect to slope, substrate, and cover, but they differ in their preference for marine and fresh-water conditions. Hybridization occurs in habitats at the interface between fresh-water and marine environments, characterized by disturbed, rapidly changing conditions, such as at the mouths of rivers and in recently deglaciated fjords. Gene flow is particularly evident where migration pathways of argentatus along river valleys cross coastal colonies of glaucescens (cf. Dry Bay population, Sections 5.1 - 5.6). The degree of contact and gene flow between Glaucous-winged and Herring Gulls is discussed below in relation to the environment of six coastal colonies, an interior location -- Lake Louise, and an offshore site -- Middleton Island.

Interbreeding is a transitory phenomenon in recent post-glacial environments such as Glacier Bay. Fjords with retreating glaciers resemble high-arctic environments, where melting of large bodies of ice creates fresh-water conditions unsuitable for Herring Gulls. Interbreeding between Glaucous-winged and Herring Gulls occurs on cliff faces and gravel bars. However, the interbreeding is restricted in time, because of rapid post-glacial successional changes. Growth of alders (Alnus crispa) within twenty years of deglaciation (Streveler and Paige, 1971) was sufficient, in some cases, to cause gulls to seek new breeding habitats. Small numbers of such displaced Herring Gulls enter the larger Glaucous-winged Gull colonies, such as the one on North Marble Island in Glacier Bay. Deglaciated about 120 years ago, North Marble Island is a steeply sloping limestone knoll. Examination of the colony of 500 pairs nesting on grassy (Hordeum brachyantherum) meadows revealed that mixed pairs of argentatus and glaucescens successfully fledged young. The colony was of sufficient size for nesting activities of the gulls to retard vegetative succession. The relative stability of this colony may also have attracted Herring Gulls displaced from other locations in Glacier Bay.

Hybridization at Dry Bay occurred in a mixed alluvial-maritime environment which escaped Pleistocene glaciation. The gull colony of 500 pairs was located on flat gravel bars 4.8 km from the mouth of the Alsek River. The sparsely vegetated gravel bars, colonized by both argentatus and glaucescens were subject to constant river erosion and flooding by winter storm tides. The Alsek River, one of the major breaks through the coast ranges originates in the interior Yukon Lake district, and is a known migration route connecting interior populations of birds and mammals with similar coastal populations (Streveler and Paige, 1971). Dry Bay is a major migration staging area (pers. obs.). Thousands of Herring Gulls, which have wintered at sea, congregate on the gravel bars before moving inland in May, intermixing with coastal Glaucous-winged Gulls in proximity to the breeding colony. Numbers of breeding Herring Gull "pure types" are low in this unstable delta environment, but the percentage of intergrades is high, approaching 50% of the colony. The complete spectrum of primary feather pigmentation (WHI 1 - 6 -- pale grey to black), iris hue (IHI 6 - 9 -- brown to yellow), and orbital ring color (OHI 1 - 9 -- pink to yellow) is evident in a collection of breeding birds from this colony. The population characteristics for this colony are distinctly intermediate between Glaucous-winged and Herring Gulls: subterminal portions of the primaries 2 x darker than mantle (WHI 3.11); orbital rings pinkish yellow (OHI 4.5); and irides light yellow (IHI 7.79). The composite hybrid index was 13.54 ± 2.62, indicating a distinct Herring Gull influence, with considerable population variability. Mating patterns were assortative, including intergrades and pure types generally selecting like types as mating partners. Mean clutch size and fledging success of pure glaucescens pairs (2.93 eggs/nest; 1.40 chicks fledged per nest) and those pairs containing at least one intergrade (2.89 eggs/nest; 1.47 chicks fledged per nest) were not statistically different. The high percentage of intergrades, the spectrum of morphological variation, and the development of assortative mating patterns indicate long-term contact between Glaucous-winged and Herring Gulls in this area.

Haenke Island, deglaciated twice within the last 1000 years, supported a colony of 200 pairs of glaucescens nesting on grassy (H. brachyantherum) cliff terraces. The colony at Haenke Island was separated from interior regions of the Yukon and therefore from Herring Gull contact by the highest peaks of the St. Elias Range (to 5800 m) and by the immense Malaspina Glacier. The glaucescens population exhibited restricted primary feather pigmentation, with subterminal portions of the primaries slightly darker than mantle (WHI 1.95), brown eyes (IHI 6.30) and dark pink orbital rings (OHI 1.3). The Haenke Island gull population, with a composite HI of 9.55 ± 1.21, morphologically resembled the glaucescens population inhabiting Middleton Island (below). Haenke Island was slightly more geographically isolated than other areas examined in this study, and the glaucescens breeding at the site displayed little evidence of prior genetic contact with argentatus.

The populations inhabiting the three major glaucescens colonies of the Copper River Delta (Fig. 10) resembled each other more than any other colonies in the Northeast Gulf of Alaska, and their morphological characteristics indicated prior contact with argentatus. The 1964 earthquake increased the surface area of the barrier islands, which in some cases quickly vegetated with resistant grasses, and was thereupon colonized by expanding populations of glaucescens. The argentatus population which existed on the delta before the 1964 earthquake (Gabrielson and Lincoln, 1959) no longer exists, probably because the balance between fresh and saltwater was altered, with subsequent encroachment of woody vegetation creating habitat unsuitable for nesting Herring Gulls.

Egg Island, with the largest known Glaucous-winged Gull colony (10,000 pairs), was a series of sand bars and dunes before the 1964 earthquake. The island increased tremendously in surface area after the 2 m uplift, with subsequent colonization by the beach rye grass *Elymus*, thus creating unlimited nesting space. Major sources of artificial food (the Cordova canneries and fish-processing houses) within 18 km have contributed to the population increase of 4% per year. In the absence of unusually severe weather conditions and of human predation (egging) in the immediate study area, the low clutch size (2.4) and moderate fledging success (1.08) suggested that the Egg Island breeding population was composed of young adults, probably immigrating from a large area of the southern Alaskan coast.

The gull population at Copper Sands, nesting on three comparatively small *Elymus*-covered dunes, remained relatively stable despite the earthquake uplift because of the lack of sufficient nesting space. The Strawberry Reef population also did not increase dramatically, in this case because of the distance (80 km) to the sources of artificial food at Cordova[1] (Fig. 11).

The populations inhabiting the three Copper River Delta colonies displayed essentially identical frequencies of iris hue. However, the indices of melanin in the subterminal portions of the primaries increased from Egg Island (1.91) to Copper Sands (2.03) to Strawberry Reef (2.20). Similarly, the hybrid indices indicated increasing yellow pigments in the

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[1]Recent reports indicate essentially complete reproductive failure in the gull colony at Strawberry Reef because of brown bear predation (Michelson, pers. comm.).

orbital rings from Egg Island (3.66 -- yellowish pink) to Copper Sands (4.0 -- yellowish pink) to Strawberry Reef (4.6 -- pinkish yellow). Composite hybrid indices reflected the trend: Egg Island (10.39 ± 1.76), Copper Sands (10.40 ± 1.27), and Strawberry Reef (11.40 ± 2.33); the variation in primary feather pigmentation and orbital ring coloration was clinal across the Copper River Delta. The Strawberry Reef population, with more yellow pigments in the orbital rings, and increased melanin deposits in the subterminal portions of the primaries, had the largest standard deviation of the composite hybrid index. Strawberry Reef was the most variable of the Copper River Delta colonies, and the population clearly displayed argentatus influence. Contact with argentatus may have been most frequent here because Strawberry Reef is the closest barrier island to the mainland, to the Copper River (a potential migration route) and thus to freshwater sources, which argentatus prefers.

Gabrielson and Lincoln (1959) reported an argentatus colony on the Copper River Delta, but repeated and comprehensive aerial surveys by Patten and Isleib (pers. comm.) have been unable to locate it. The tremendous habitat alteration of the Delta since the 1964 earthquake may have made the marshes unsuitable for nesting argentatus. Population characteristics of the Copper River Delta glaucescens indicate interbreeding between argentatus and glaucescens when the argentatus population inhabited the delta. In particular, it is apparent that the Strawberry Reef population, which is transitional in characteristics between the Copper River Delta glaucescens and the hybrid population at Dry Bay in the Alsek River, absorbed the genes of the argentatus population formerly inhabiting the Copper River Delta.

Middleton Island is in the Gulf of Alaska 130 km south of Cordova, and 75 km west of Kayak Island (Fig. 3). It has been colonized by 750 pairs of glaucescens within the last 20 years (Hatch, Pearson, and Gould, 1979). A 4.5 meter uplift during the 1964 earthquake exposed a broad band of boulder and log-strewn beach, now inhabited by a glaucescens population displaying essentially no darkening of primary feathers (WHI 1.2), pink orbital rings (OHI 2.4), and brown to light brown irides (IHI 6.6). The composite hybrid index (0.40 ± 1.29) of this colony was the lowest of any group examined in the field during this study, indicating a population of phenotypically pure glaucescens. Furthermore, the mantle and primary feathers of a group of five breeding adult gulls collected at random from Middleton Island are lighter and more uniform than any other glaucescens group in the U.S. National Museum. This includes those glaucescens from Amchitka Island, Alaska, of which USNM 46626 and 466837 serve as examples. The lack of melanin in the subterminal portions of the primaries of the gulls breeding on Middleton Island suggested that this population did not originate from the coastal zone between Cordova and Juneau, but rather from an area without breeding Herring Gulls, such as Kodiak Island.

Lake Louise, in southcentral Alaska, supported the interior Herring Gull colony examined in detail. The colony of 77 pairs was located in a long-term stable habitat, a small, steeply sloping, grassy (Calamagrostris) islet in a boreal lake. Although the slope and vegetative cover of the islet resembled North Marble Island in Glacier Bay, which was colonized by both argentatus and glaucescens, and the grassy knolls on Middleton Island, colonized by glaucescens, there were no glaucescens at Lake Louise. The gulls breeding at Lake Louise were phenotypically argentatus: black subterminal primary bands (WHI 5.9); yellow orbital rings (OHI 8.9) and yellow irides (IHI 9.0); composite HI 23.81 ± 0.4. Observations at additional gull colonies in interior British Columbia and the Yukon supported this conclusion, although Drury (pers. comm.) reported a diminished pattern of primary feather pigmentation of argentatus breeding at Kluane Lake, Yukon Territory, which possibly indicates some gene flow from glaucescens via the Alsek River, although the report needs further investigation. Interior argentatus populations do not show much, if any, glaucescens influence because there is little advantage for glaucescens to colonize the interior.

6.5 Predictions of Additional Gene Flow Between Previously Isolated Larus Populations

The results of this study predict interbreeding in locations other than those reported here, especially where migration pathways of interior argentatus cross coastal glaucescens colonies on river deltas along the Pacific Coast. The coast-river-lake systems in southcentral and southeastern Alaska provide examples (Figs. 3, 16).

The Susitna Flats on Upper Cook Inlet are joined with the interior Lake Louise by the Susitna River. Dry Bay is joined by the Alsek River to the Dezadeash and Kluane Lake districts in the Yukon. The Taku River connects the coastal Taku Arm with the Atlin Lake drainage area in British Columbia. Similar situations are expected in northern British Columbia, for instance along the Stikine River (cf. Webster, 1950). To date (1979), Herring Gulls have not been known to breed south of the edge of the boreal forest in the Fort St. Johns region of northcentral British Columbia, and thus coastal hybrid colonies (argentatus x glaucescens) are not expected in central or southern British Columbia.

The interbreeding between glaucescens and argentatus is currently restricted by geographical conditions and by partially formed premating isolating mechanisms of marine/fresh-water nesting habitat preferences and assortative mating patterns. The rate of hybridization could increase in the Gulf of Alaska if the current level of environmental disturbance, in the form of large-scale fisheries, remains high. The development of intensive fisheries in Alaska within the last seventy years has led to increasing amounts of offal and similar garbage in the environment. Large-scale, foreign-flag, factory ship fisheries have developed off Alaskan coasts within approximately the last fifteen years. These factory ships discharge thousands of tons of fish waste annually into the sea (cf. Wahl and Heinemann, 1979). Onshore in Alaska, at Dutch Harbor, as an example, commercial institutions processed about five million kilograms of crab a week during the 1978 season (Morgen, 1979). These factories also produce vast amounts of organic waste. The resulting food supply will enhance survival of coastal gull populations and potentially accelerate rates of gene flow between previously isolated Larus populations (cf. Ingolfsson, 1970).

6.6 The Geological and Evolutionary History of the argentatus - glaucescens Contact

The Pacific Northwest is divided into two radically different climatic and ecological regions: the coastal and interior environments, which are separated by high ranges of mountains. Both coastal and interior regions of the Pacific Northwest were subjected to profound geological and climatic changes during the late Pleistocene and early Holocene times. Beginning approximately 25,000 years ago, the main Wisconsin glaciation developed and lasted some 12,000 years on the coast and about

3000 years longer in the interior (Borden, 1979). At its maximum extent, the main Wisconsin glaciation buried all of British Columbia as well as adjoining coastal areas in northwest Washington State and southeastern Alaska under the vast Cordilleran Ice Sheet. West of the Cascades, a massive glacial lobe extended from the Coast Mountains of British Columbia southward through the Straits of Georgia and adjoining Puget Sound lowlands, reaching its maximum extent slightly south of 47^{o} N Latitude approximately 15,000 years ago (Borden, 1979).

The ancestral Larus argentatus populations probably came out of eastern Siberia during the early Pleistocene (Stegmann, 1934). These ancestral populations spread in both easterly and westerly directions across the Eurasian land mass, and crossed the Bering Land Bridge into the North American continent (Stresemann and Timofeeff-Ressovsky, 1947; Hopkins, 1962; Haag; 1962). Expanding ice masses of the late Pleistocene subsequently separated the ancestral Larus argentatus populations, forcing them into refugia in Europe, Asia, and North America during successive glaciations (Geyr von Schweppenburg, 1938). One group was pushed back by the continental glaciation to an interior refugium known as Greater Beringia (Chukotka, Bering Land Bridge, Yukon-Tanana uplands, and western Yukon Territory). The other group was forced to retreat southward along the Pacific Coastline to the Puget Sound region.

During their long period of separation, morphological differences evolved between the coastal population, and the population in the northern interior. The interior Alaskan gull population remained essentially connected to Eurasian populations during the glaciation period. This population was flexible and adapted to a wide variety of ecological niches, being an obligatory migrant to marine environments during the winters.

While a land-bridge connected Alaska and Siberia and Alaska and western Yukon Territory were environmentally more a part of Asia than North America, the ancestors of the northern-interior gene pool (proto-argentatus), though marginally located, maintained gene exchange with related Eurasian populations (vegae, taimyrensis).

By contrast, the isolated, coastal-southern gull population (proto-glaucescens) evolved and differentiated as it adapted to marine regions near glacier fronts. The Puget Sound lowland of Washington and southwestern British Columbia became ice-free about 13,500 to 11,500 years ago and more northerly areas only slightly later (Borden, 1979). The contraction of coastal glaciers was followed by a rapid range expansion of proto-glaucescens northward along the Pacific Coast, similar to the situation today in Glacier Bay, as breeding gull populations colonize recently deglaciated areas.

In the interior of British Columbia and in southwestern Yukon Territory, as well as in the passes through the Coast Mountains, glaciers remained longer. By about 10,000 years ago, Cordilleran ice had vanished from the southern Canadian plateau. Access from unglaciated areas of the northern interior to deglaciated parts of the intermontaine region may have developed about 9500 to 10,000 years ago. In early Holocene times, an ancestral argentatus population, adapted to boreal lakes and rivers, but possessing the capacity to colonize marine regions, expanded as soon as deglaciation would allow into the subarctic interior of British Columbia and moved southeast along the retreating base of the Wisconsin glaciers, across southern Canada, to the Great Lakes region, and eventually colonized the Eastern Seaboard.

The two gull populations which expanded into newly available territory during the late Pleistocene and early Holocene times, had evolved certain morphological (colorimetric) differences and habitat preferences during their period of separation, but they appear to have been derived from a common ancestral group before the main Wisconsin glaciation. During early post-glacial time, proto-argentatus moved southward through the interior, and proto-glaucescens moved northward along the coast. These two populations eventually encountered each other where the major geographical barrier dividing the coastal and interior environments was incomplete. Genetic contact was probably established when the argentatus populations followed one or more recently deglaciated river valleys through the coastal mountain ranges to reach to northern Pacific coast and returned.

6.7 Alternative Hypotheses for the Narrow Hybrid Zone Between argentatus and glaucescens

This description of the two forms and the environment in which they meet presents the basis of the argentatus - glaucescens interaction. The two colorimetrically different but interfertile taxa, which evolved in dissimilar natural environments, are interbreeding in a zone of contact in southern Alaska. In addition to the rapid geological and successional changes in coastal southern Alaska, certain aspects of the environment are becoming progressively altered by human influence, notably by the development of intensive fisheries, producing increasing amounts of fish offal and similar garbage.

Four alternative theoretical hypotheses for the existence of a narrow hybrid zone between argentatus and glaucescens were explored in search of the best explanation for the data collected. These hypotheses are not mutually exclusive, and the "best fit" for the southern Alaskan Larus situation appears to involve a combination of elements of two of them (see below). The four hypotheses are known as the (1) ephemeral-zone, (2) the dynamic equilibrium, (3) the hybrid superiority, and (4) the ecotone-disclimax hypotheses.

The ephemeral-zone hypothesis states that hybridization will end either in speciation or fusion of the hybridizing taxa by means of introgression (Dobzhansky, 1940, 1951; Sibley, 1957, 1959, 1961; Wilson, 1965; Remington, 1968; Moore, 1977). This hypothesis is inappropriate to the argentatus - glaucescens contact for several reasons. Speciation requires selective pressure against those individuals which form mixed pairs, and is to be expected if the populations have diverged to the extent that the hybrids are less fit than the parental phenotypes; otherwise the hybrids would serve as a bridge for introgressive hybridization. Historical data on the duration and extent of the contact are not available, other than from Williamson and Peyton (1963) in Cook Inlet. This study reveals that natural selection was apparently not acting against hybrids in the coastal environment, at least through the fledging stage (cf. Results, Section 5.10). Further, analysis of adult morphology indicates intermediate adults are common and reproduce as well as "pure" types within the contact zone (cf. Results, Sections 5.1 - 5.6). The viable and fertile hybrids could serve as a bridge for introgressive hybridization. However, evidence suggests that coastal glaucescens genes are not penetrating interior argentatus populations to the degree that the converse is occurring. Therefore, rapid speciation or fusion of these two forms is not occurring, although the glaucescens population are increasing in variability (cf. Discussion, Section 6.2).

The dynamic equilibrium hypothesis, as postulated by Bigelow (1965) and discussed by Moore (1977), requires influxes of genes from both parental populations. The hypothesis has aspects which apply to the southern Alaskan *Larus* contact zone. The spring migration pattern of *argentatus* from offshore wintering areas, which extend from the Gulf of Alaska to southern California (Sanger, 1973; Harrington, 1975), towards breeding localities in interior Alaska and the Yukon, includes river valleys such as those of the Alsek and Susitna. These rivers pass through major mountain barriers, such as the Alaska and St. Elias Ranges. Local *glaucescens* populations at colonies near river mouths may receive substantial influxes of *argentatus* genes, as well as *glaucescens* genes from other colonies. Continued immigration of "naive" individuals could swamp evolution of isolating mechanisms. Hoffman *et al*. (1978), using computer simulation techniques, suggested that the continued immigration of both parental types is assisting in maintenance of the apparently stable *glaucescens* - *occidentalis* contact zone in western Washington State. Bigelow (1965) proposed that stable hybrid zones might result from a dynamic balance between gene flow and selection against hybrids. He suggested that steep selection gradients on either side of the contact zone might inhibit introgression, and that the evolution of antihybridization mechanisms in the restricted zone of contact might be disrupted by migrants moving into the restricted zone from more extensive areas of allopatry. To some extent this does occur in southern Alaska, where *argentatus* move through the study area during spring migration.

The hybrid superiority hypothesis states that hybrids are actually more fit than the parental phenotypes in the restricted regions in which they occur (Anderson, 1949; Muller, 1952; Hagen, 1967; Short, 1969, 1970, 1972; Littlejohn and Watson, 1973; Moore, 1977). Data from the southern Alaskan _Larus_ contact zone indicate evidence of hybrid fertility, backcrossing, morphological intermediacy, and hybrid viability (cf. Results), but these do not imply superiority. Hybrids which select like types as mating partners could theoretically increase their reproductive fitness by production of offspring adapted to the intermediate environment.

The concept that ecological factors are most important in determining the fitness of these hybrids is central to the development of the hybrid superiority hypothesis (Moore, 1977). The extent of a contact zone could be determined by the range of ecological conditions to which the parental types are less well adapted. It has also been stated that most hybrid zones are narrow and occur at the juxtaposition of the ranges of the parental populations (Moore, 1977). The _argentatus_ - _glaucescens_ contact zone within this study area is clearly narrow and at the interface between the two parental populations (see also Short, 1969; Fig. 1). However, the extent of the _glaucescens_ - _argentatus_ contact zone is apparently determined by geographical rather than ecological conditions, and there is no evidence that the intermediates are better adapted to this zone than are the parental types.

The _ecotone-disclimax hypothesis_ is based on the observation that most stable hybrid zones appear to occur in ecological conditions that are ecotones, disclimax, or perpetually disturbed habitats (Moore, 1977). This explanation has aspects which apply to the _argentatus_ - _glaucescens_ contact zone. The mixed populations of gulls are found when _argentatus_ of the interior boreal lakes and rivers meet the coastal _glaucescens_ at the mouths of rivers and in recently deglaciated fjords. The occurrence of the zone of overlap and hybridization also appears to correlate with a change in climatic conditions from west coast marine to boreal interior, or in the case of the recently deglaciated fjords, from west coast marine to circumstances which mimic arctic conditions.

River valleys are among the most variable of environments (Anderson, 1949). River action may drastically alter previously existing conditions within a short time. The relationship between disturbed environments and hybridization is typical of many cases of hybridization (Anderson, 1949; Grant, 1971; Moore, 1977, Corbin and Sibley, 1977). The greater the number of gene differences between the parental types, the greater will be the number of special new habitats (in a broad sense, including time-energy budget and feeding preferences) necessary for the segregants. Presumably, the genetic differences between argentatus and glaucescens are not especially great. Theoretically, if F_2 and subsequent generations are to survive and reproduce, there must be environments not only with intermediate habitats, but also environments which present possible recombinations of the contrasting differences of the parental environments. The theoretical expected intermediate habitat for these two gull forms would be a fresh water / salt water mosaic within a mixed west coast marine - boreal forest environment. This is precisely the environment near the mouth of the Alsek and Susitna Rivers in southern Alaska.

Zones of contact (cf. Mayr, 1963) usually involved only a small portion of the complete ranges of the participating populations. The vast majority of both glaucescens and argentatus populations breed outside this particular contact zone, although glaucescens is in genetic contact with two other forms, hyperboreus (Strang, 1977), and occidentalis (Hoffman et al., 1978), to the north and south, respectively. The continuation of hybridization in the southern Alaskan contact zone may result from the very sharp boundary between the two environments in which argentatus and glaucescens usually breed, in this case the radical separation of interior Alaska and northwestern Canada from coastal Alaska by very high mountain ranges. The abrupt separation allows such a small fraction of each form to be sympatric with the other at river mouths, bays, and recently deglaciated fjordlands, that gene flow to these ecotones may swamp development of complete ethological pre-mating isolating mechanisms (Jackson, 1973). L. glaucescens and argentatus are not in contact over a broad area. If they were, then theoretical requirements would be present for rapid evolution of antihybridization mechanisms and the end of introgression.

Pioneering gull populations in recently deglaciated fjordlands are within a partially different selective framework, even though the environment is a dynamic ecotone. Whenever retreat of ice masses is rapid, as within the last 200 years in Glacier Bay, large areas are opened for colonization. Tinbergen (1953) noted that hybridization is characteristic of pioneering populations. When the pioneering individuals, for example, argentatus phenotypes, arrive in the recently deglaciated environment, they are unable to find conspecific mates. Thus, even though their pre-mating isolating mechanisms could be as completely developed as those in the eastern Canadian arctic (Smith, 1966b), the threshold of the pioneering argentatus may eventually diminish to a low enough level that they hybridize with glaucescens rather than not reproduce at all (cf. pp. 82 - 86, in Blair, 1961). L. argentatus is distinctly less common than glaucescens within the fjordlands of Glacier Bay. Individual argentatus may not find conspecific mates, and the instinctive mating drive may eventually overcome the inhibitory restraint of differing species-specific recognition signals and mixed *argentatus* x *glaucescens* pairs are formed. The viable offspring, with recombinant genomes, may have a selective advantage in the rapidly changing environment.

Man, in addition to catastrophic natural forces, creates new, artificial ecological niches in which hybrid segregants might survive and reproduce (Anderson, 1949; Sibley, 1950, 1954; Sibley and West, 1958, Sibley and Sibley, 1954, Corbin and Sibley, 1977). Some of these artificial niches are of definite types. For instance, natural plant hybrids are often restricted to man-disturbed environments, i.e., they are weeds in an ecological sense (Anderson, 1949; Grant, 1971, Moore, 1977). Most stable hybrid zones appear to occur in ecological conditions which conform to Wright and Lowe's (1968) definition of "weed" habitat (*in* Moore, 1977). Some of the most important artificial feeding niches for *Larus* gulls are garbage dumps, sewage outfalls, and concentrations of fish offal around canneries and fish processing plants. *L. argentatus* in particular is an excellent example of a vertebrate "weedy" species, rapidly increasing in numbers and expanding its range on the East Coast of North America, in Britain and Europe, *L. argentatus* is pre-adapted to man-disturbed environments and to use artificial food (Drury, pers. comm.). Continued rapid development in coastal Alaska, particularly of fisheries and petrochemical industries, will lead to increased contact between *Larus* populations, assist in the survival of hybrid forms, facilitate gene flow between colonies, and after a period of enhanced variability, may even lead to a new adaptive peak in these commensal gulls (cf. Discussion, Secton 6.5).

In summary, it is apparent that the hypotheses discussed above are not mutually exclusive. In the study area, the "best fit" appears to include elements of the dynamic equilibrium and ecotone-disclimax hypotheses. L. glaucescens colonies at mouths of rivers providing migration routes to interior Alaska receive regular influxes of argentatus genes. Mixed populations of gulls are also found in rapidly changing environments such as recently deglaciated fjords. The occurrence of the zone of overlap and hybridization also appears to correlate with a change in climatic conditions from west coast marine to boreal interior, or to circumstances which mimic arctic conditions. The geographically restricted narrow zone of overlap and hybridization appears potentially stable in its present configuration, although rapid resource development in coastal Alaska may increase gene flow between gulls in environments disturbed by the availability of fish offal and similar refuse.

6.8 Relationship of the Findings of this Study to the Circumpolar Formenkreis through Eastern Siberia

Dr. Alexander A. Kistchinski of the Soviet Academy of Sciences (pers. comm.) reports a Larus situation on the eastern side of the Bering Strait similar to that in Alaska. Species composition differs slightly. L. glaucescens breeds on the Aleutian chain and extends into Soviet territory only on the Commander Islands[1], where Ludmila V. Firsova of the Ornithology Department, Zoological Institute, Leningrad, has been studying the breeding biology of glaucescens (Fig. 38). She also reports a mixed pair, which produced viable offspring, of L. glaucescens and L. schistisagus, the Slaty-backed Gull[2], breeding at Korf Bay, on the northern Kamchatka Peninsula (Kistchinski, pers. comm.).

The Slaty-backed Gull occupies the coastal niche of glaucescens

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[1]Reference specimens are AMNH 745216, 745218, 745221, 745223, 745228.

[2]The type specimen is Larus schistisagus Stejneger, USNM 92885.

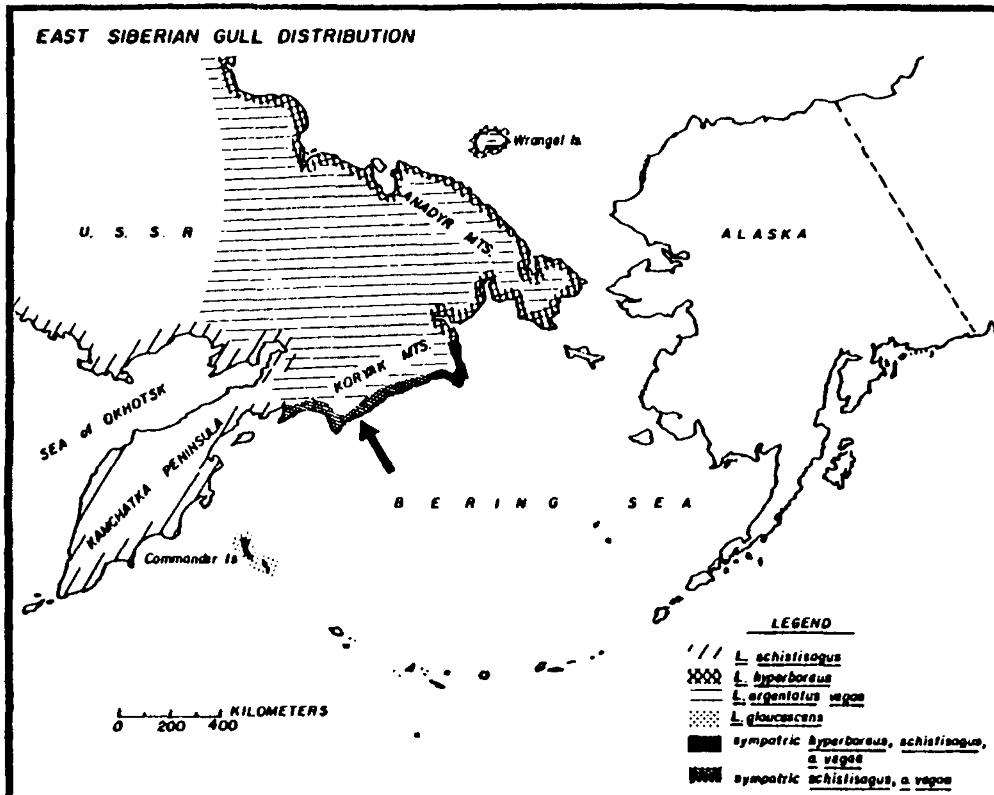

Fig. 38. East Siberian gull distribution. L. schistisagus breeds on the eastern shore of the Sea of Okhotsk and the Kamchatka Peninsula. L. a. vegae breeds in interior northeastern Siberia. A zone of overlap and hybridization between vegae and schistisagus exists on the coast of Siberia.

on the eastern shore of the Sea of Okhotsk and the Kamchatka Peninsula. L. argentatus vegae inhabits interior northeastern Siberia, as L.a. smithsonianus occupies interior Alaska. A zone of overlap and probable hybridization exists between schistisagus and vegae where rivers descend from the northern Koryak Highlands and enter the Bering Sea (Fig. 38). L. schistisagus typically nests on cliffs facing the Bering Sea, and vegae usually nests in scattered pairs on subarctic rivers and lakes. However, Portenko (1963; cf. Vaurie, 1965) and Kistchinski (pers. comm.) found vegae and schistisagus breeding sympatrically on sea cliffs of the Northern Bering Sea from Cape Barykov to the mouth of the Khatyrka River and in the river deltas of the southern Koryak Highlands. Birds breeding in these river deltas may serve as a partial gene bridge connecting coastal with interior populations, forging another link in the circumpolar Formenkreis. These settings are remarkably similar to those found in Alaska, e.g., the Alsek River Delta at Dry Bay, and the Susitna River Delta near Anchorage, where interior - coastal populations hybridize.

The following species composition serves as an example of those gulls breeding on sea cliffs in the northern Koryak Highlands: about 5% hyperboreus, 70% schistisagus, 5% vegae, and 20% probable intermediates exhibiting a wide variety of characteristics of both vegae and schistisagus. Portenko (1963) believed that schistisagus and vegae should be regarded as conspecific, Firsova and Kistchinski (pers. comm.) now believe that the binomial nomenclature should be retained, since parental types are present in the mixed colonies. L.a. vegae and L. schistisagus coexist in a narrow zone of overlap and hybridization, and should be treated as semispecies.

L. hyperboreus breeds northward from the Anadyr Ridge on the coastal lowlands of Siberia, where it is in sympatry with vegae on the subarctic and arctic lakes and offshore islands. L. hyperboreus pallidissimus[1] nests on arctic coastal cliffs and lowland shores westward across Northern Siberia, and on the periphery of Wrangel Island. Mixed colonies of vegae and hyperboreus are found in many locations on the Arctic Coast of Siberia, with no interbreeding. L. hyperboreus also nests on low shores and coastal cliffs southwards to the northern Koryak Highlands, where it coexists with L.a. vegae and L. schistisagus. Small numbers of L.a. vegae breed in U.S. territory on St. Lawrence Island, where they nest on cliffs (Fay and Cade, 1959; Searing, 1976; Drury, pers. comm.). St. Lawrence Island is a fragment of the former Bering Land Bridge that the ancestral populations of argentatus moved from eastern Siberia into North America during the early Pleistocene. From St. Lawrence Island, or the Siberian coastline, L. argentatus vegae may move to coastal Alaska[2] since Drury (pers. comm.) recently reported a mixed pair of L. hyperboreus barrovianus and L.a. vegae on the Seward Peninsula of Alaska. Ingolfsson (1970) considered aberrant hyperboreus from western Alaska result from hybridization with vegae which are known to stray over to the Alaskan mainland[3] (Gabrielson and Lincoln, 1959).

In addition to the generally E - W or circumpolar connection of the

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[1]USNM 589394 is an example of this form, collected at St. Matthews Island, Alaska, by I. Gabrielson.

[2]L.a. vegae appear regularly in fall migration in the western Aleutians (Gibson, pers. comm.). UAM 3568 is an example collected at Shemya Island.

[3]The type of "Larus nelsoni Henshaw" (USNM 97253), collected at St. Michaels, Alaska, by E.W. Nelson, on June 20, 1880, had in fact been identified as a hyperboreus x vegae hybrid by Dwight (1925).

Formenkreis in the subarctic and arctic regions, there is a N - S connection along the Pacific Coast of North America, at least along the Alaskan, western Canadian, and northwestern U.S. coasts, as exemplified by the *glaucescens* - *hyperboreus*, *glaucescens* - *argentatus*, and *glaucescens* - *occidentalis* contacts, as outlined below with a discussion of their taxonomy.

6.9 Taxonomy of Large White-headed Gulls of the North Pacific Rim

The effects of glaciation, as discussed above, are particularly apparent where pairs of "semispecies" are formed (Rand, 1948). These are cases in which two forms, or groups of forms, meet in a narrow zone of overlap. The relationships of the forms to each other are neither those of species, nor of subspecies, but combine characteristics of both, in a stage of evolution between species and of subspecies, called semispecies. Gene exchange would still be possible among semispecies, but not as free as among conspecific populations (Amadon, 1966). Mayr (1969) considered semispecies as transient intermediate steps in the evolution of full species. Hoffman, Weins, and Scott (1978) suggested that the semispecies concept should be further expanded to include such apparently stable zones of overlap and hybridization as the *glaucescens* - *occidentalis* contact in Western Washington State[1] (Fig. 1).

Data gathered in southern Alaska during research for this dissertation support the concept developed by Hoffman *et al.* (1978). Similar to the *glaucescens* - *occidentalis* contact, the morphology and mating patterns of *glaucescens* and *argentatus* demonstrate that Short's (1969) and Mayr's

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[1]A number of *glaucescens* x *occidentalis* specimens are housed in the Washington State Museum under accession numbers 11605, 12866, 12295, 12299, 13402, 13441, and 13444.

(1963) criteria for conspecificity, i.e., that the zone of contact should be characterized by random mating, complete intergradation, absence of pure parental types, with introgression into adjacent parental populations, are not met in southern Alaska. Short (1969) first suggested that glaucescens and argentatus are semispecies. The results of my study confirm that suggestion.

However, evidence from western Alaska suggests that the hyperboreus - glaucescens contact[1] may meet the criteria for conspecificity. L. hyperboreus barrovianus[2], breeding in northern and western Alaska, as well as in the western Canadian arctic to the MacKenzie Delta, is characterized by smaller size and darker mantle than other hyperboreus subspecies (Rand, 1952; Manning et al., 1956; Macpherson, 1961). Johansen (1958) suggested that barrovianus showed a probable glaucescens influence. Swarth (1938) found gulls on Nunivak Island off western Alaska to be nearly completely intermediate between glaucescens and barrovianus. Strang (1977) found a uniform level of glaucescens characters in populations of barrovianus on the Yukon - Kuskokwim Delta of western Alaska (Fig. 1). However, a character gradient has not been demonstrated between these two forms, nor have mixed colonies or mixed pairs been located. The contact between barrovianus and glaucescens clearly bears further investigation. The available evidence does suggest that the contact between barrovianus and glaucescens has not been restricted by geographical

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[1] A reference specimen from this contact zone is USNM 589396.

[2] The type specimen of this form is Larus barrovianus Ridgway (USNM 88913).

barriers, and is of considerable antiquity, especially as compared to that of the glaucescens - argentatus zone of southern Alaska. Further, argentatus, glaucescens, and occidentalis apparently form a chain of semispecies. L. glaucescens is the "key" link in this chain, since it interbreeds with every other large white-headed gull with which it comes in contact, including hyperboreus.[1] This chain is in turn linked through L. argentatus vegae and L. schistisagus of the Siberian coastline with the circumpolar argentatus, cachinnans - fuscus Formenkreis (Table 1).

This study designates the Glaucous-winged Gull as a semispecies to the circumpolar Herring Gull superspecies. Thus, the appropriate taxonomic treatment for the Glaucous-winged Gull is Larus [argentatus] glaucescens (cf. Amadon, 1966)

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[1] Ingolfsson (1970) reported extensive interbreeding between hyperboreus and argentatus on Iceland. See Current State of Knowledge, Section 2.22.

7.0 SUMMARY

This study investigated plumage and soft part colors, nesting habitat selection, mating patterns and hatching and fledging success of large gulls (*Larus*) in colonies in southern Alaska. The research was approached through a comparative field study of allopatric and sympatric gull populations.

The evolution and systematics of the Herring Gull group were introduced in Chapter 1, after two Alaskan members of the genus *Larus* were described. Questions were posed in search of answers to pre- and post-mating isolating mechanisms between the Herring Gull (*Larus argentatus*) and the Glaucous-winged Gull (*Larus glaucescens*). The intent in answering these questions was to clarify the taxonomic and ecological relationships between *argentatus* and *glaucescens*, relate the Alaskan situation to the larger circumpolar *Formenkreis*, and aid in further understanding the complex systematics of the Herring Gull group.

The literature on the morphology and evolution of Palearctic and Nearctic *Larus* gulls was summarized in Chapter 2. There was general agreement in the literature on the origin of yellow-footed and pink-footed gulls. An ancestral *Larus* population was divided by the East Siberian Ice Barrier into two major refugia. Populations that evolved into the pink-footed *argentatus* group were forced to the east side of the barrier, and the populations that evolved into the yellow-footed *cachinnans-fuscus* group were displaced to the west side in the Aral-Caspian area. The ancestral *argentatus* dispersed in interglacial times over North America, leading to gradual development of the pink-footed American group, which includes *glaucescens* and *occidentalis*, among others.

Post-glacially, argentatus emigrated to Europe from eastern North America, coming into contact with the westward expanding cachinnans-fuscus group, to which argentatus was, in general, reproductively isolated. The classic overlap of a "ring" species (Formenkreis) was thus formed. The connecting links in the Formenkreis were the sympatric populations of Larus gulls in central Siberia, which hybridize on a large scale[1].

Evidence was presented linking the western North American Larus populations with the circumpolar Formenkreis. A review of the evolutionary status of large white-headed gulls of the West Coast suggested none of these Larus populations were completely reproductively isolated by pre-mating mechanisms, since they interbreed in narrow zones of sympatry. Breeding biology of large white-headed gulls was reviewed to assist in understanding the dynamics of the interbreeding forms. Four hypotheses, which were pertinent to the theoretical aspects of interbreeding between argentatus and glaucescens in southern Alaska, were presented in a brief section on narrow hybrid zones in vertebrates.

The study areas were discussed in Chapter 3. After an introduction to the general environmental conditions on the south coast of Alaska and adjoining interior regions, eight individual study sites were described. These sites consisted of six coastal colonies located between Juneau and Prince William Sound, an offshore island in the Gulf of Alaska, and a colony on a fresh-water lake in interior Alaska, north of Valdez. The geology of the coastal and offshore sites was changing rapidly because of recent deglaciation, major earthquakes, and floods. Slope and substrate of the study colonies varied from horizontal gravel bars to nearly vertical cliff faces. Two coastal colonies supported interbreeding

[1] Cf. L.a. taimyrensis, Table 1.

argentatus and *glaucescens*. The interior colony at Lake Louise was composed of only *argentatus*, and only *glaucescens* nested on the offshore Middleton Island. Principal periods of study for these colonies were given.

Materials and methods were presented in Chapter 4. Techniques used to study nesting habitat selection, mating patterns, and reproductive productivity of Glaucous-winged, Herring Gull, and intermediate forms were described. The Hybrid Index was discussed as a method for analyzing hybridization. Numerical scores were assigned to the variation exhibited by the parental types and intermediate forms. Colors analyzed in the study were identified and recorded by the Munsell System of Color Notation.

Chapter 5 contained the results of the research. The study included such colorimetric characters as primary feather pigmentation, iris, and orbital ring colors. The primary feather pigmentation (WHI) of southern Alaskan gulls was analyzed in detail. Individual gulls within the study area were highly variable, and the variation included primaries the same shade as the mantle, with no observable pattern of melanin deposition, to a distinctly delimited and extensive black pattern including much of the outermost primaries. The complete range of variation in primary feather pigmentation between *glaucescens* and *argentatus* types was found within an individual colony located at Dry Bay, southeast of Yakutat, Alaska.

The range of iris coloration in gulls within the study area included very dark brown, dark brown, brown, light yellow, and bright yellow, forming an uninterrupted continuum from populations most like *glaucescens* to populations clearly identifiable as *argentatus*.

Qualitative comparisons of the frequencies of the individual Munsell categories of iris hue, value, and chroma, and the combinations thereof, revealed that neighboring colonies on the Copper River Delta had strikingly similar distributions of iris hues. The mixed populations at North Marble and Dry Bay shared similar, although not identical distributions of iris hues and values. The distribution of iris values in the irides of the Strawberry Reef population resembled that of the population inhabiting Dry Bay. The Copper Sands and Strawberry Reef populations were closely related, although Strawberry Reef additionally resembled the hybrid population at Dry Bay.

The relationship between gull iris color and primary feather pigmentation in southern Alaska was statistically significant. Light-eyed gulls had dark primaries, dark-eyed gulls had light primaries, and gulls with intermediate shades of melanin in the primaries had irides of various intermediate shades. However, exceptions were common. The variation and distribution of iris color, although related to primary feather pigmentation, were not likely to function in species recognition between the light-eyed argentatus and the dark-eyed glaucescens, since the two forms were linked by a complete range of intermediates.

The extreme pigments in orbital rings of glaucescens and argentatus in southern Alaska were dark pink and bright yellow, but six intermediate hues existed, and more than one hue may occur in an individual eye-ring. Each colony examined had a different mean composite orbital ring, but statistical tests confirmed that the orbital ring colors of the populations at ends of the spectrum were connected by increasing amounts of yellow pigment. Orbital rings of some individual gulls in the study area were uniformly pigmented. Other gulls possessed orbital rings with two or three hues. The population at Dry Bay had the greatest distribution of uniformly pigmented orbital rings, as well as the most even distribution of orbital rings with combination hues. The function of orbital ring pigmentation as a species-specific recognition character was unlikely, because of the spectrum of variation. However, the variability may function as a character for individual or population recognition.

Hybrid indices demonstrated three partially independent clines of increasing *argentatus* influence extending from the offshore Middleton Island to the interior Lake Louise. Primary feathers became darker and yellow pigments increased in the irides and orbital rings in gull populations along this axis. The major source of *argentatus* genes along the North Gulf Coast of Alaska was the hybrid colony at Dry Bay, which served as a bridge between coastal and interior *Larus* populations.

Three statistical tests were conducted on the mating patterns of gulls in 112 pairs at Dry Bay as additional evidence for the hypothesis. These tests indicated that mating patterns were significantly assortative; i.e., the gulls tended to choose mates similar to themselves, but in some cases selected mates of widely different phenotypes, forming mixed pairs and apparent backcrosses. The combination of both iris color and primary feather pigmentation was considerably more important than iris color in mate selection.

Both allopatric and sympatric *argentatus* and *glaucescens* were flexible in nesting habitat selection in southern Alaska. Nest site substrate ranged from gravel bars to cliff faces, including from 0% to over 50%

slope. Favored sites for both forms were grassy island slopes.

Clutch size, hatching success, and fledging success of Larus gulls in southern Alaska were examined for evidence of post-mating isolating mechanisms. While there were statistically significant annual and geographical differences in clutch size between Larus colonies in southern Alaska, populations of argentatus were not significantly different from mixed or glaucescens populations.

Rates of egg inviability (failure to hatch) in all colonies were low, and the differences between populations in frequencies of non-hatching eggs were not significant. Clutch size and fledging success of mixed versus "pure" pairs were also not significantly different within the mixed colony at Dry Bay.

Chapter 6 contained a discussion of the research results, beginning with a section on the allopatric hybridization of Glaucous-winged and Herring Gulls. Nesting habitat preferences and assortative mating patterns were incompletely formed pre-mating isolating mechanisms in the study area. The relationships between breeding populations of Glaucous-winged and Herring Gulls along the North Gulf Coast of Alaska were explored. Mixed populations of argentatus and glaucescens displayed degrees of reproductive isolation ranging from occasional interbreeding between pioneering individuals, through intergrades selecting like types as mating partners, to absorption of argentatus into variable populations of glaucescens.

The geological and evolutionary history of the argentatus - glaucescens contact was discussed in detail.

An ancestral Pacific Northwest Larus population most resembling argentatus was separated into two groups about 25,000 years ago by the Cordilleran ice mass of the main Wisconsin glaciation. The isolated coastal form (proto-glaucescens), displaced south to the Puget Sound region, evolved on marine headlands resembling arctic environments in proximity to glacier fronts. This isolated form developed pale primaries characteristic of arctic Larus populations. The second gull population, displaced north to the Greater Beringia refugium in interior Alaska and the Yukon, bred on boreal lakes, migrated along river valleys, and wintered offshore in the Pacific from the Gulf of Alaska to southern California. This population remained in genetic contact with related Siberian populations of argentatus across the Bering Land Bridge until the world-wide rise in sea level approximately 10,000 years ago, which submerged the Bridge.[1] The retreat of the Cordilleran ice mass allowed both northern and southern gull populations to expand, but coastal mountains, broken only by major river systems, still separated the two gull populations as the glaucescens moved north along the coast. Small numbers of pioneers of the argentatus form colonized the southern Alaskan coast at river mouths and in recently deglaciated fjords. Hybridization occurred with glaucescens in these rapidly changing habitats, thus permitting one-way gene flow from the northern interior to the coastal southern gull population. Gene flow was primarily one-way for a variety of reasons. First, glaucescens with few exceptions did not breed in the interior. The interior environment, with restricted food availability

[1]Rausch (1963) considers the term "bridge" for this connection is perhaps unfortunate, since by connotation it implies a narrow corridor. At the time of maximum exposure of the Bering-Chukchi platform, this isthmus was approximately equal in width to the present north-south dimension of Alaska.

and limited nesting space, could support only small populations of large gulls adapted to that specific environment. Second, the coastal environment, rich in food, provided little motivation to occupy the interior. Third, annual migration was normally obligatory for boreal argentatus and optional for coastal glaucescens. Interior lakes and rivers freeze, while the south coast of Alaska remains ice-free through the winter. The lack of a fully developed instinct for migration could be a strong selective pressure against glaucescens in interior environments. Recently fledged glaucescens or glaucescens x hybrids could not survive in the interior following failure to migrate from boreal lakes in the autumn.

This one-way gene flow in allopatric hybridization of argentatus and glaucescens led to increasing variability of the coastal glaucescens in iris, orbital ring, and primary feather pigmentation. The interior argentatus, by contrast, remained relatively monomorphic.

Glaucous-winged and Herring Gulls are still largely allopatric except in restricted areas where intermediate habitat meets the preferences of both taxa. They are semispecies (in the amended definition of Lorkovic, 1958), displaying some of the characteristics of species, and some of subspecies (cf. Mayr, 1963; Amadon, 1966). The fact that they hybridize to a greater or lesser extent proves that they did not acquire complete reproductive isolation during their period of geographic separation.

The glaucescens - argentatus contact thus led to an unusual situation between the extremes of reinforcement of isolating mechanisms as when hybrids are selected against, and swamping of both parental populations when hybrids are not selected against (cf. Sibley, 1957). Selection on hybrid genomes was at least neutral in the coastal environment, but potentially severe in the interior environment. The post-glacial coastal environment was severely disturbed by the 1964 earthquake, and is still subject to rapid geological changes, while the interior environment is relatively stable. The increased variability of coastal populations is thus potentially a selective advantage. Future development in coastal Alaska, particularly in fisheries and petrochemical industries, will increase contact between *Larus* populations and assist in the survival of hybrid forms in disturbed environments. The gene flow between large white-headed gull populations will likely increase in future years as a secondary consequence of human activities, and may even lead to a new adaptive peak in these commensal forms.

In the concluding section of the Discussion, the interbreeding between *Larus* gulls in southern Alaska was found to resemble that occurring between *Larus* gulls on the Pacific coast of Siberia, and the relationship to the circumpolar *Formenkreis* was indicated.

8.0 APPENDICES

8.1 APPENDIX I

National Oceanic Data Format 035

RECORD FORMAT DESCRIPTION

RECORD NAME CLUTCH - BIRD COLONY DATA

14. Field Name	15. Position from 1 measured in Bytes	16. Length		17. Attributes	18. Use and Meaning
		Number	Units		
File Type	1	3	Bytes	A3	Always '035'
File Identifier	4	6	Bytes	A6	
Record Type	10	1	Bytes	A1	Always 'F'
Station Number	11	5	Bytes	A5	Nest or ledge no.
Sample Date-Time					
Year	16	2	Bytes	I2	00-99) GMT
Month	18	2	Bytes	I2	01-12) GMT
Day	20	2	Bytes	I2	01-31) GMT
Hour	22	2	Bytes	I2	00-23) GMT
Taxonomic Code	24	12	Bytes	I12	

8.1 APPENDIX I (Continued)

14. Field Name	15. Position from 1 measured in Bytes	16. Length		17. Attributes	18. Use and Meaning
		Number	Units		
Station Type Code	36	1	Bytes	I1	'1' = nest '2' = nests '3' = ledge '4' = subcolony '5' = colony
Number of Eggs	37	3	Bytes	I3	Whole number
Number of Chicks	40	3	Bytes	I3	Whole number
Egg Mortality	43	3	Bytes	I3	Whole number
Chick Mortality	46	3	Bytes	I3	Whole number
Number of Incubators	49	3	Bytes	I3	Whole number
Number of Adult Birds	52	4	Bytes	I4	Whole Number
Number of Nests	56	3	Bytes	I3	Whole Number
Egg Mortality					
Cause Code (I)	59	1	Bytes	A1	
Cause Code (II)	60	1	Bytes	A1	
Cause Code (III)	61	1	Bytes	A1	

8.1 APPENDIX I (Continued)

14. Field Name	15. Position from 1 measured in Bytes	16. Length		17. Attributes	18. Use and Meaning
		Number	Units		
Chick Mortality					
Cause Code (I)	62	1	Bytes	A1	
Cause Code (II)	63	1	Bytes	A1	
Cause Code (III)	64	1	Bytes	A1	
Adult Activity Code	65	1	Bytes	A1	
Nest Condition Code	66	1	Bytes	A1	
Number of Adult Pairs	67	2	Bytes	I2	Whole number
Number of Non-Breeding Birds	69	2	Bytes	I2	Whole number
Number of adults	71	6	Bytes	I6	Whole number
Sequence Number	77	4	Bytes	I4	

8.2 APPENDIX II

GULL DATA FORM

Larus argentatus - Larus glaucescens

1. Date_____________ 2. Collected--Released Same date or ________
   Day-Month-Year D /M /Yr
3. Map Ref. #_____________ Location______________________________

   Nearest Town______________County____________State_____________

   Country____________Coordinates: Lat.________Long.____________
4. FWS band#__________________(L. Tarsus-known age)______________
   (Rt. Tarsus-unknown age______________
5. Tarsus Color Band: White/Yellow/Green/Red(Orange)/Blue/Black;

   Ref. #____________L or R Tarsus. 6. Plumage: 1 2 3 4+ or Specify
7. Age: L/HY/SY/TY/ATH (4th yr +).
8. Iris:____
9. Eye Ring:____
10. Primary Color:____
11. Wing Hybrid Index:________________12. Feet & Legs______________
13. Inside of Mouth:____________14. Weight:______________________gms
15. Sex: M or F . 16. Flattered Wing:____mm 17. Tarus:__________mm
18. Culmen:________mm. 19. Bill: Anterior Nares to Tip:___________mm
20. Bill: Depth at Posterior Nares:__________mm
21. Blood Smear Ref.#_________. 22. Serum Sample Ref. #____________
23. Parasites: Internal ________________External_______________
24. Crop/Stomach Contents:____

    ____
25. Photo: Yes/No--Date taken_________ by whom_____________________

26. Dye: Complete; Front ½ body; Rear ½ body; Left Side; Right Side;
    Other________________. Picric; nyansol; Rhod. B; Other______

27. Other markings: (Specify):______________ Sketch: see Reverse

28. Remarks: behavior of bird when released; location of release if different from site of capture, etc.

    ____

    ____

8.3 APPENDIX III

Munsell System of Color Notation

The following explanation is taken from Munsell Color, a private publication printed by Macbeth, a division of Kollmorgen Corporation, and is used with permission.

> The Munsell notation system of equally spaced color scales provides a tool for expressing perceived color of an object and the color differences observed among a group of objects. The system of color notation identifies color in terms of three attributes, hue, value, and chroma. This method of color notation arranges the three attributes of color into orderly scales of equal visual steps: the scales are used as parameters for accurate specification and description of color under standard conditions of illumination and viewing.
>
> The hue (H) notation of color indicates its relation to a visually equally-spaced scale of 100 hues.

The hue notation in this study is based upon three major hue names: Red (R), Yellow-Red (YR) and Yellow (Y), since these cover the range of pigmentation in orbital rings and irides.

> The value (V) notation indicates the degree of lightness or darkness of a color in relation to a neutral grey scale, extending from absolute black to absolute white. The value symbol 0/ is used for absolute black, the symbol 10/ for absolute white.
>
> The chroma (C) notation indicates the degree of departure of a given hue from a neutral grey of the same value. Chroma scales depend upon the strength (saturation) of the sample evaluated.
>
> The complete Munsell Notation for a chromatic color is written symbolically: H V/C.

The complete notation for a sample of "vermillion" would be 5 R 6/14, while the notation for a sample of "rose" would be 5 R 5/4.

The notation for a neutral (achromatic) color, such as found in primary feather pigmentation of gulls, is written N V/. The notation of black, a very dark neutral, would be N2; the notation of white, a very light neutral, would be N9/; while the notation for grey, visually half-way between these two, would be N5/.

8.4 APPENDIX IV

Mensural Characters

Mensural characters were ascertained for 138 gulls in eight different populations which ranged from "pure" types *glaucescens* through various grades of "mixed" populations to "pure" type *argentatus*. The measurements, descriptive statistics, and analysis of variance for these populations are present in Tables 29, 30.

Populations of "pure" types and "mixed" populations of *argentatus* and *glaucescens* did not differ significantly in any dimension ($p > .05$) with one exception. The one exception in this study was that male *glaucescens* collected at Copper Sands and Strawberry Reef, neighboring colonies on the Copper River Delta, had significantly enlarged bill depth at posterior nares ($p < .05$) compared to any other colonies. The deeper bills common to males at both colonies suggested a closer relationship between these two populations than to any other groups. This finding is similar to that obtained by analysis of colorimetric characters. See Discussion, Section 6.4, for a further elaboration of these findings.

Comparison of Measurements

The standard morphological measurements of 138 adult gulls in eight populations are presented in an exploratory univariate analysis in Tables 29, 30. Since gulls are sexually dimorphic in body size and mensural characters, the sexes were analyzed separately. In spite of the small sample sizes, it is clear that there is a great deal of overlap in means, ranges, and standard deviations (Table 29). For

Table 29. Comparison of the Measurements (in Millimeters) of Sympatric and Allopatric _Larus_ Gulls in Southern Alaska -- Males

Measurement	Colony	Composition	Mean	Range	S.D.
Culmen	North Marble	_arg._ x _glauc._	59.8	57-62	2.06
	Dry Bay	_arg._ x _glauc._	59.7	56-64	2.36
	Haenke Island	_glauc._	60.6	59-63	1.81
	Strawberry Reef	_glauc._	59.2	55-64	2.31
	Copper Sands	_glauc._	60.5	58-61	1.46
	Egg Island	_glauc._	59.1	55-64	2.57
	Cordova	_glauc._/_hyperbor._	59.9	57-63	1.97
	Lake Louise	_arg._	60.5	58-63	2.50
Bill: Anterior Nares to Tip	North Marble		27.8	27.5-28.5	0.50
	Dry Bay		28.0	24.5-31	1.58
	Haenke Island		28.4	26-30	1.46
	Strawberry Reef		28.8	27-31	1.09
	Copper Sands		30.2	28.5-33	1.99
	Egg Island		28.2	25-31	1.56
	Cordova		29.3	27-32	1.39
	Lake Louise		28.5	28-29	0.50
Bill: Depth at Posterior Nares	North Marble		19.7	18.7-20	0.65
	Dry Bay		19.9	18-22	1.04
	Haenke Island		19.8	19-21	0.75
	Strawberry Reef		21.4	27-31	1.13
	Copper Sands		21.6	21-22.5	0.73
	Egg Island		20.3	18-23	1.24
	Cordova		20.1	19-25	1.45
	Lake Louise		20.5	20-21	0.50

Table 29 continued.

Measurement	Colony	Composition	Mean	Range	S.D.
Tarsus	North Marble	_arg_. x _glauc_.	69.1	67-72	2.19
	Dry Bay	_arg_. x _glauc_.	68.0	61-73	2.58
	Haenke Island	_glauc_.	65.6	61-69	2.88
	Strawberry Reef	_glauc_.	67.9	63-72	2.61
	Copper Sands	_glauc_.	68.9	64-73.5	3.38
	Egg Island	_glauc_.	67.2	63-72	2.41
	Cordova	_glauc_./_hyperbor_.	68.2	62-72	3.37
	Lake Louise	_arg_.	70.3	66.5-74	5.30
Wing	North Marble		434.8	420-451	12.79
	Dry Bay		433.5	414-463	13.80
	Haenke Island		432.4	430-435	2.30
	Strawberry Reef		437.4	418-463	13.95
	Copper Sands		433.0	422-445	8.78
	Egg Island		435.4	419-455	9.25
	Cordova		434.1	417-450	9.49
	Lake Louise		455.0	450-360	7.07

Table 30. Comparison of the Measurements (in Millimeters) of Sympatric and Allopatric *Larus* Gulls in Southern Alaska -- Females

Measurement	Colony	Composition	Mean	Range	S.D.
Culmen	Dry Bay	*arg.* x *glauc.*	53.6	50-57.5	2.09
	Haenke Island	*glauc.*	53.2	50-57	2.78
	Strawberry Reef	*glauc.*	52.8	50-55	1.80
	Copper Sands	*glauc.*	53.1	52-53.5	1.24
	Egg Island	*glauc.*	54.2	51-60	2.33
	Cordova	*glauc.*/*hyperbor.*	54.6	50-58	2.65
Bill: Anterior Nares to Tip	Dry Bay		26.6	24-31	1.83
	Haenke Island		26.5	22-29	2.42
	Strawberry Reef		24.9	22-27	1.64
	Copper Sands		26.7	26-28	0.83
	Egg Island		25.8	23-29	1.48
	Cordova		26.8	24-29	2.32
Bill: Depth at Posterior Nares	Dry Bay		18.5	17-22	1.30
	Haenke Island		18.1	17-20.5	1.28
	Strawberry Reef		19.5	18.5-21	0.76
	Copper Sands		19.1	18-20	0.89
	Egg Island		18.2	17-20	1.08
	Cordova		19.0	17-23	2.19
Tarsus	Dry Bay		65.6	62-70	2.24
	Haenke Island		62.9	60-66	1.12
	Strawberry Reef		61.4	57-67	1.37
	Copper Sands		62.9	61-64.5	1.44
	Egg Island		62.3	56-69	3.29
	Cordova		62.0	58-64	2.83

Table 30 continued.

Measurement	Colony	Composition	Mean	Range	S.D.
Wing	Dry Bay	_arg_. x _glauc_.	419.7	400-450	12.38
	Haenke Island	_glauc_.	412.2	403-424	9.44
	Strawberry Reef	_glauc_.	421.3	410-435	9.81
	Copper Sands	_glauc_.	414.8	412-418	2.50
	Egg Island	_glauc_.	416.9	400-445	11.91
	Cordova	_glauc_./_hyperbor_.	410.5	400-425	10.85

example, the mean culmen measurements of the males from eight colonies were less than 1.5 mm apart; similarly, the mean culmen measurements for females from six colonies were less than 1.5 mm apart. By comparison, the difference of means of males as compared to female specimens in culmen length was greater than 5 mm.

However, in the interests of completeness, F-ratios, the statistic appropriate to the analysis of variance, were computed on these data, using the SPSS-10 ONEWAY program. The program provides an analysis of variance that tests for significant differences in means between groups, and takes into account differences in sample sizes and degrees of freedom by groups. The F-test may require some qualification if the means are skewed. Since observed gull body measurements appear to approximate a normal distribution, the F-test should give a valid measurement of whether the differences are real.

The F-ratios for the measurements of female adult gulls indicated no significant differences between any of the populations examined ($p > .05$)(Table 31). However, for male gulls, the comparison first yielded a significant F-ratio at the 5 percent level for bill depth (at posterior nares) and bill length (anterior nares to tip) (Table 32). Using Tukey's (1977) methods for exploratory data analysis, two populations were selected for additional analysis, since they formed "detached points." This further exploration of the data revealed that the males in two colonies, Copper Sands and Strawberry Reef (neighboring colonies on the Copper River Delta) were the source of the significant variation. If the males from Copper Sands and Strawberry Reef were eliminated from the analysis, the F-ratio indicated no significant differences among the remaining six populations (Tables 33,34). Males

Table 31. Analysis of Variance (SPSS-10 ONEWAY) of Morphological Measurements For Adult Gulls (Female)

Captured/Collected at: Dry Bay, Haenke Island, Strawberry Reef, Copper Sands (S), Egg Island, Cordova.

Body Part	Degrees of Freedom		F-ratio	Significance
	Between Groups	Within Groups		
Wing	5	41	0.741	n.s.*
Tarsus	5	41	2.515	n.s.
Culmen	5	41	0.483	n.s.
Bill: Anterior Nares to Tip	5	42	1.015	n.s.
Bill: Depth at Posterior Nares	5	42	1.079	n.s.

*n.s. = not significant at $p < .01$ or $p < .05$

Table 32. Analysis of Variance (SPSS-10 ONEWAY) of Morphological Measurements For Adult Gulls (Male)

Captured/Collected at: North Marble, Dry Bay, Haenke Island, Strawberry Reef, Copper Sands (S), Egg Island, Cordova, Lake Louise.

Body Part	Degrees of Freedom Between Groups	Degrees of Freedom Within Groups	F-ratio	Significance
Wing	7	94	1.143	n.s.*
Tarsus	7	94	1.197	n.s.
Culmen	7	94	0.593	n.s.
Bill: Anterior Nares to Tip	7	94	2.320	significant at $p < .05$ n.s. at $p < .01$
Bill: Depth at Posterior Nares	7	94	3.526	significant at $p < .01$

*n.s. = not significant at $p < .01$ or $p < .05$

(Since analysis of variance has given a significant F-ratio at two variables, further analysis is needed.)

Table 33. Analysis of Variance (SPSS-10 ONEWAY) of Morphological Measurements For Adult Gulls (Male)

Captured/Collected at: North Marble, Dry Bay, Haenke Island, Egg Island, Cordova, Lake Louise; WITHOUT Copper Sands, Strawberry Reef

Body Part	Degrees of Freedom Between Groups	Degrees of Freedom Within Groups	F-ratio	Significance
Wing	5	76	1.554	n.s.*
Tarsus	5	76	1.503	n.s.
Culmen	5	76	0.565	n.s.
Bill: Anterior Nares to Tip	5	76	1.593	n.s.
Bill: Depth at Posterior Nares	5	76	0.456	n.s.

*n.s. = not significant at $p < .01$ or $p < .05$

Table 34. Analysis of Variance (SPSS-10 ONEWAY) of Morphological Measurements For Adult Gulls (Male)

Captured/Collected at: Strawberry Reef, Copper Sands.

Body Part	Degrees of Freedom Between Groups	Degrees of Freedom Within Groups	F-ratio	Significance
Wing	1	18	0.431	n.s.*
Tarsus	1	18	0.510	n.s.
Culmen	1	18	1.431	n.s.
Bill: Anterior Nares to Tip	1	18	3.442	n.s.
Bill: Depth at Posterior Nares	1	18	0.130	n.s.

*n.s. = not significant at $p < .01$ or $p < .05$

from Copper Sands (n = 11) and Strawberry Reef (n = 19), compared to each other, showed no significant differences (Table 34). Further, the difference between the sample means in the measurement of bill length (anterior nares to tip) was of marginal significance ($p \geq .04$).

Since the F-ratio was at least marginally significant for these two dimensions, further comparisons were necessary. They required a rank-ordering approach. Duncan's Multiple Range Test (DMRT) (Steel and Torrie, 1960) was well suited for this type of analysis (cf. Statistical Procedures, Section 4.6). The DMRT confirmed that the differences between male populations in bill length (anterior nares to tip) were of marginal significance (n.s at $p > .01$). However, the next test indicated that males from the two neighboring colonies on the Copper River Delta, Strawberry Reef and Copper Sands, were significantly larger ($p < .01$) in bill depth (at posterior nares) than all other colonies examined. As before, the two colonies were not significantly different from each other in this measurement.

After testing the significance of differences in measurements among various populations, "pure types" were selected from the data base on the basis of iris color and primary feather pigmentation. "Pure types" of argentatus were considered as those with an iris hue of Munsell 5 Y (bright yellow) and a wing hybrid index of WHI 6 (black pigment deposited in a broad band across the subterminal portions of the primaries, and extending up the feather shafts of the 8th, 8th and 10th primaries). "Pure types" of glaucescens were considered as those with an iris hue of 7.5 YR (brown) and a wing hybrid index of WHI 1 (primaries the same shade as the mantle, with no observable pattern of melanin deposition).

The means of the body measurements of the "pure types" of _argentatus_ and _glaucescens_ were compared by t-test, appropriate for the small sample size (n=21). The "pure types" did not differ in any measurement ($p > .05$). The observed statistical differences in bill depth between the two Copper River Delta _glaucescens_ populations (Copper Sands and Strawberry Reef) and the other colonies cannot therefore, be used in taxonomic discrimination, since the "pure types" of _glaucescens_ and _argentatus_ do not differ statistically in this dimension. However, the difference in bill depth may have other genetic and evolutionary implications (cf. Discussion). Copper Sands and Strawberry Reef also resembled each other in colorimetric characters more than any other populations (cf. Results, Sections 5.1 Primary Feather Pigmentation; 5.2 Iris Pigmentation; 5.31 Iris Hue; and 5.34 Combined Iris Parameters (Hue, Value, and Chroma).

8.5 APPENDIX V

Superimposed upon the rapid vegetational and geological changes along the southern Alaskan coastline is the increasing human influence. Since the turn of the century successive tides of human influence have swept over Alaska. The most important developments for gulls have been the rise of intensive fisheries, open garbage dumps, and sewage outfalls. As an example, five seafood packing canneries and fish-processing houses in Cordova provide a major food source to gulls in the form of salmon and crab offal. Gulls also feed at the open municipal dump at the end of the harbor.

The potential for discarded human food and industrial waste increases daily in coastal Alaska. Isleib and Kessel (1973) have documented an increasing gull population in the Cordova area to date. Our NOAA helicopter survey indicated 13,224 gull pairs nested on the sandbar barrier islands off the Copper River Delta in 1976 (Table 35). This number is expected to increase with the development of offshore oil resources, since gull-associated problems of human waste and garbage disposal are not likely to decline.

Table 35. Nesting Gull Populations
on Copper River Delta Sandbar Island
29 June 1976 NOAA Helicopter Survey +

Sandbar Barrier Island	Population Estimate *
Egg Island	10,000 pairs
Copper Sands (N)	200 pairs
Copper Sands (S)	800 pairs
Kokinhenik Bar	a few pairs
Grass Island Bar	200 pairs
Softuk Island	25 pairs among driftwood
Strawberry Reef	2,000 pairs

* estimated by groups of 50 individuals

Other mudflats and islets serve as loafing areas for large populations of immatures and adults which may or may not be breeding.

+ observers: Pattens

8.6 APPENDIX VI

The Cordova Gull Population

Introduction

Huge flocks of gulls (≥ 10,000 individuals per hour) foraged in the effluent of the Cordova seafood processing plants during salmon-packing season (June - early August 1975 - 1978). The Cordova municipal dump provided an alternative food source when the canneries were not in operation. The origin of many of the adult gulls in the Cordova area was uncertain until this investigation, although interchange of some adult gulls between Cordova and the nesting colonies on the Copper River Delta was obvious.

Methods

To determine whether the Cordova gull population was qualitatively different in mensural and colorimetric characters from the breeding populations on the sandbar barrier islands (Egg Island, Copper Sands, and Strawberry Reef), and five other colonies in the study area, 23 adult gulls were live-trapped during June, July, and August 1975 - 1978 in the Cordova municipal dump. These individuals were analyzed by the same methods as were used in the investigation of collected adults from breeding populations, but the Cordova gulls were also banded, color-dyed and released in order to trace local movements (cf. Methods, Sections 4.43 Iris Pigmentation, 4.44 Orbital Ring Pigmentation, 4.45 Primary Feather Pigmentation, and 4.6 Statistical Procedures). (For analysis of mensural characters, see Appendix IV).

Results

The wing hybrid index (cf. Section 4.45) was revised when unusual gulls were trapped in the Cordova dump. These gulls had primaries lighter than the mantle (Munsell N7/ - N8/), as well as light-colored irides, and had slightly, although not statistically, larger body measurements than gulls collected from nearby breeding populations (Appendix IV, Tables 29 and 30). The wing hybrid index was modified to account for this variation, and the unusually light-primaried gulls given a score of "0" on the index.

Primary Feather Pigmentation

The mean wing hybrid index for the Cordova population (WHI 1.58) was the second lightest group sampled. Middleton Island gulls were the lightest (Table 36). The F-ratio for the analysis of variance of wing hybrid indices (including the Cordova population) was very highly significant (F = 28.9, 187 d.f., p < .001), indicating real differences among group means (Table 36). The data were further examined with the Duncan's Multiple Range Test (DMRT). However, the Cordova population, although lighter in primary feather pigmentation, was not statistically different from the Copper River Delta populations at the 5% level of significance (Table 37, Subset 1).

Iris Pigmentation

The mean index for the iris pigmentation of the Cordova population (IHI 7.26 - light brown) was the third lightest group sampled (Table 38). The F-ratio for the observed distribution of iris pigmentation for all populations was very highly significant (F = 10.52, 187 d.f., p < .001). (Table 38). The Cordova population was placed between the intermediate colonies of North Marble (light brown irides) and Dry Bay (light yellow irides) by the DMRT, but was not statistically different in iris pigmentation from the Copper River Delta populations at the 5% level of

Table 36. Hybrid Index of Primary Feather Pigmentation (WHI)* for *Larus* Populations in Southern Alaska (including Cordova)

Population	Mean	Range	Standard Deviation	Sample Size
Middleton Island	1.20	1.0-1.5	0.27	5
Cordova	1.59	0.0-3.0	0.87	23
Egg Island	1.91	0.0-4.0	0.69	56
Haenke Island	1.95	1.0-3.5	0.83	10
Copper Sands	2.03	1.0-3.0	0.67	16
Strawberry Reef	2.20	1.0-3.0	0.54	25
Dry Bay	3.10	1.0-6.0	1.56	38
North Marble	4.10	3.0-6.0	1.32	4
Lake Louise	5.90	5.0-6.0	0.30	11

Analysis of Variance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-ratio
Between Groups	88	207.14	25.89	28.91**
Within Groups	179	160.31	0.89	
Total	187	367.45		

*A Wing Hybrid Index of 1 = "pure" *glaucescens*; a WHI of 6 = "pure" *argentatus* (Fig. 37).

**Very highly significant ($p < .001$).

Table 37. Ranked Means for the Wing Hybrid Index* for *Larus* Populations in Southern Alaska (including Cordova) (Duncan's Multiple Range Test: $p < .05$ level)

Homogenous subsets (subsets of groups, whose highest and lowest means do not differ by more than the shortest significant range for a subset of that size). There is no significant difference between the means of groups underlined with a single dotted line.

Subset 1 (subterminal primaries same shade as mantle to 1 shade darker)

Group	Middleton Island	Cordova	Egg Island	Haenke Is.	Copper Sands	Strawberry Reef
Mean	1.20	1.58	1.91	1.95	2.03	2.20

Subset 2 (primaries 2 shades darker than mantle; extensive melanin)

Group	Dry Bay
Mean	3.10

Subset 3 (primaries 3 shades darker than mantle; extensive melanin)

Group	North Marble
Mean	4.12

Subset 4 (primaries black; distinctly delimited and extensive black pattern)

Group	Lake Louise
Mean	5.90

*A Wing Hybrid Index of 1 = "pure" *glaucescens*; a WHI of 6 = "pure" *argentatus* (Fig. 37).

Table 38. Hybrid Index for Iris Color (IHI)* for *Larus* Populations in Southern Alaska

Population	Mean	Color	Range	Standard Deviation	Sample Size
Haenke Island	6.30	brown	6 - 7	0.48	10
Middleton Island	6.60	light brown	6 - 8	0.89	5
Egg Island	6.86	light brown	4 - 8	0.98	56
Strawberry Reef	7.08	light brown	6 - 8	0.95	25
Copper Sands	7.12	light brown	6 - 8	0.96	16
North Marble	7.25	light brown	6 - 9	1.50	4
Cordova	7.26	light brown	6 - 9	0.81	23
Dry Bay	7.79	light yellow	6 - 9	0.81	38
Lake Louise	9.00	yellow	9 - 9	0.00	11

Analysis of Variance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-ratio
Between Groups	8	65.49	8.19	10.52**
Within Groups	179	139.25	0.78	
Total	187	204.74		

*An Iris Hybrid Index (IHI) of 6 = "pure" *glaucescens*; an IHI of 9 = "pure" *argentatus* (Fig. 37).

**Very highly significant ($p < .001$).

significance (Table 39).

Iris Hue

This distribution of iris hues in the Cordova population was quite different from the distribution of iris hues in the Copper River Delta populations, although the means were statistically similar. The iris hues of the Cordova population were concentrated at 10 YR (light brown) and 2.5 Y (light yellow), and those of the Copper River Delta were concentrated bimodally at 7.5 YR (brown) and 2.5 Y (light yellow) (Fig. 39).

Iris Value

The value 8 in the Munsell System (quite light, indicating decreased melanin pigments) was present in the Cordova and Egg Island populations. The iris value 3 (quite dark, indicating abundant melanin pigments) was also present in the Cordova, Egg Island, and Copper Sands populations. In general, Cordova resembled Egg Island and Copper Sands in distribution of iris values (Fig. 40)

Iris Chroma

All populations except Cordova displayed a concentration of chroma 4 (Fig. 41). The Cordova population was quite different, with chroma rather evenly distributed among the classifications of C 2, C 3, C 4, with a smaller percentage of C 6 (cf. Results, Section 5.33). Since this study was conducted during the breeding season, the unexpected lack of a concentration at C 4 in the Cordova population suggested that the strength (saturation) of iris chroma in gulls may be related to breeding condition, and thus to endocrine physiology.

Combined Iris Parameters

The Cordova gull population displayed a wide distribution of combined iris parameters, extending from 5 YR 4/4 (chocolate brown) to

Table 39. Ranked Means for Iris Color Indices (IHI)* for *Larus* Populations in Southern Alaska (including Cordova) (Duncan's Multiple Range Test: $p < .05$ level)

Homogenous subsets (subsets of groups, whose highest and lowest means do not differ by more than the shortest significant range for a subset of that size). There is no significant difference between the means of groups underlined with a single dotted line.

Subset 1 (brown - light brown irides)

Group	Haenke Island	Middleton Is.	Egg Island	Strawberry Reef	Copper Sands	North Marble
Mean	6.30	6.60	6.85	7.08	7.12	7.25

Subset 2 (light brown irides)

Group	Middleton Is.	Egg Island	Strawberry Reef	Copper Sands	North Marble	Cordova
Mean	6.60	6.85	7.08	7.12	7.25	7.26

Subset 3 (light brown - light yellow irides)

Group	North Marble	Cordova	Dry Bay
Mean	7.25	7.26	7.79

Subset 4 (yellow irides)

Group	Lake Louise
Mean	9.00

*An IHI of 6.00 = "pure" *glaucescens*; an IHI of 9.00 = "pure" *argentatus*.

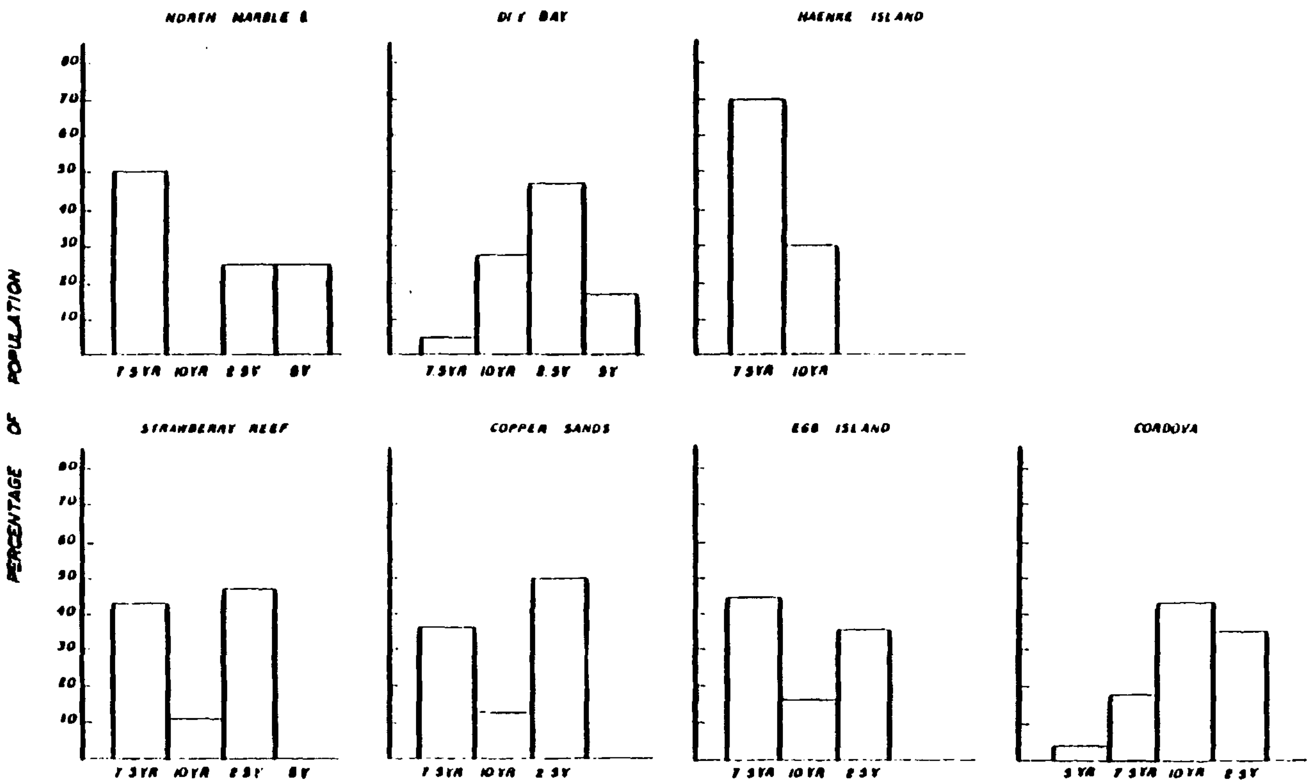

Fig. 39. IRIS HUE

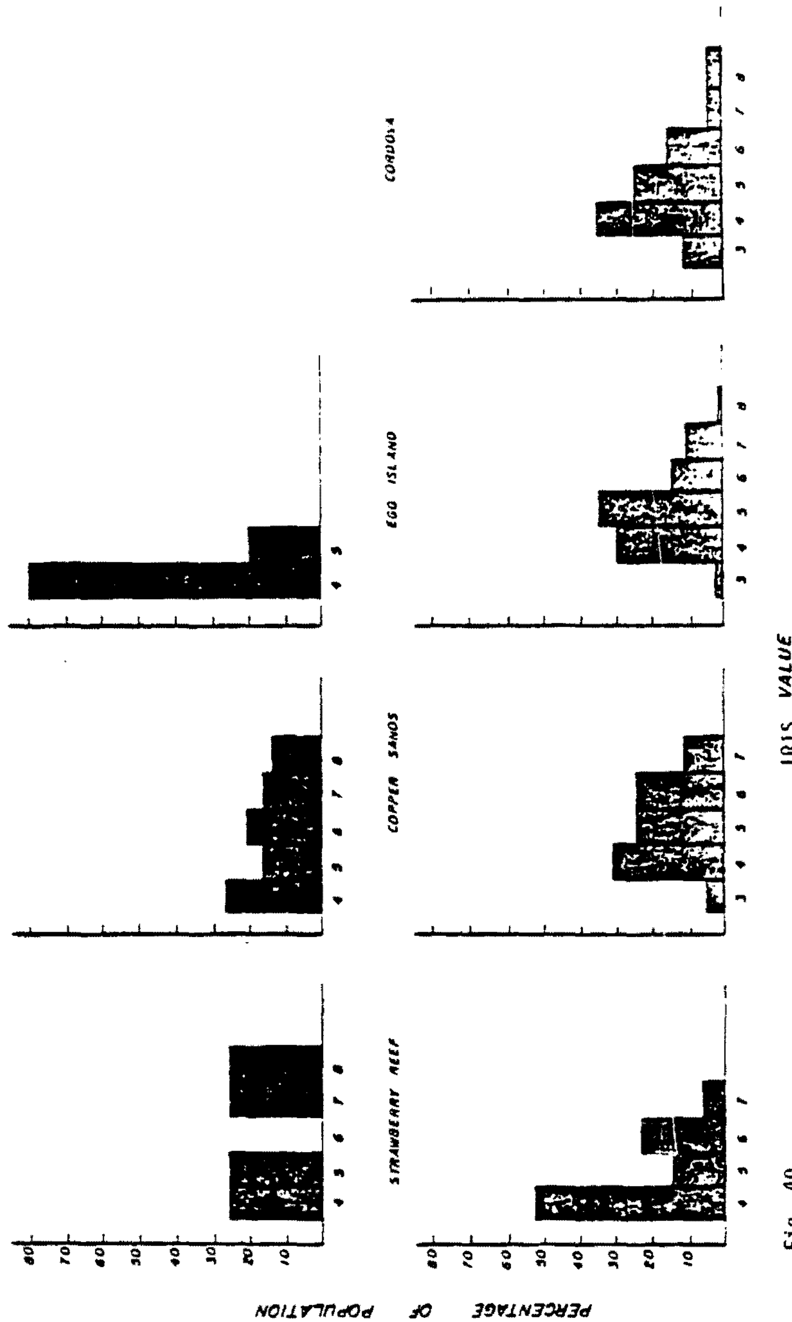
NORTH MARBLE I.
DRY BAY
HAENKE ISLAND
STRAWBERRY REEF
COPPER SANDS
EGG ISLAND
CORDOVA
PERCENTAGE OF POPULATION
IRIS VALUE

Fig. 40

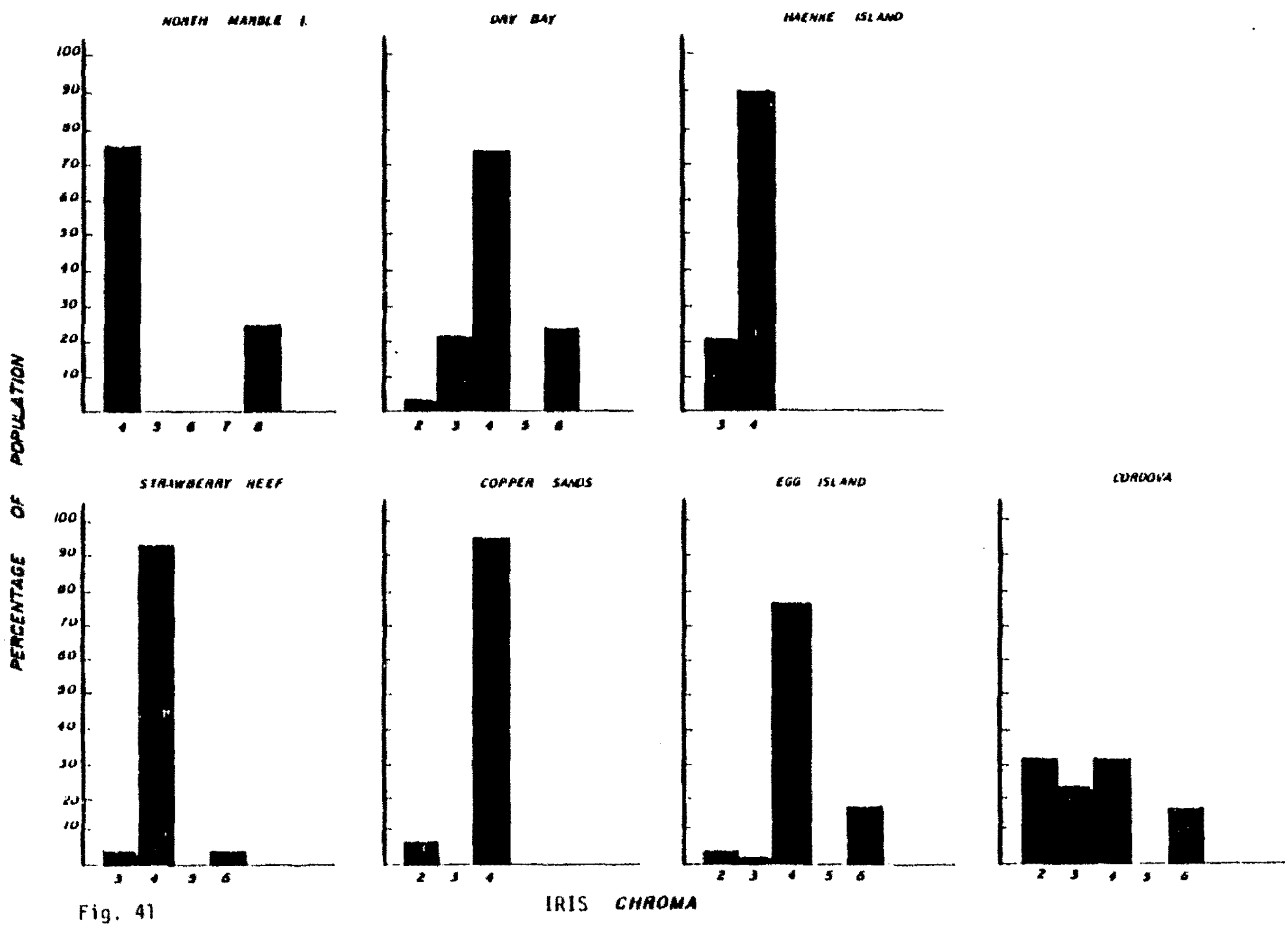
NORTH MARBLE I.
DRY BAY
HAENKE ISLAND
STRAWBERRY REEF
COPPER SANDS
EGG ISLAND
CORDOVA
PERCENTAGE OF POPULATION
IRIS CHROMA

Fig. 41

2.5 Y 6/6 (pale greyish yellow) (Fig. 42). The distribution was concentrated in the 10 YR hues, with highest concentration at 10 YR 4/2 (light greyish brown). By comparison, the distribution of the combined iris parameters for Egg Island, the nearest breeding population, extended from 2.5 YR 3/4 (dark brown) to 2.5 Y 7/6 (light yellow), but the concentration was notably highest at 7.5 YR 4/4 (brown) (Fig. 42).

Orbital Ring Pigmentation

The mean index for orbital ring pigmentation in the Cordova population was medium pink (OHI 1.83), the second darkest population examined, ranking after Haenke Island (OHI 1.3) (Table 40). The F-ratio for all populations was very highly significant ($F = 9.21$, 187 df., $p < .001$) (Table 40). The Cordova population was statistically different in orbital ring pigmentation from all the Copper River Delta colonies at the 5% level of significance in the DMRT, but not statistically different from the Cordova population at the 1% level of significance, with considerable more yellow pigment in the orbital ring (cf. Iris Value, Section 5.32) (Tables 41, 42).

Solo Hues

Dark pink (5 R) was the dominant solo hue in the Cordova population, as at Egg Island, Dry Bay, Haenke Island, and North Marble (Figs. 43, 34). Solo hues were not found in the Copper Sands and Strawberry Reef populations, which had admixtures of yellow and pink hues (Fig. 35).

Combination Hues

A pink orbital ring with areas of intensive reddish pigment (5 R - 5 R) formed 17% of the Cordova and 28% of the Egg Island samples

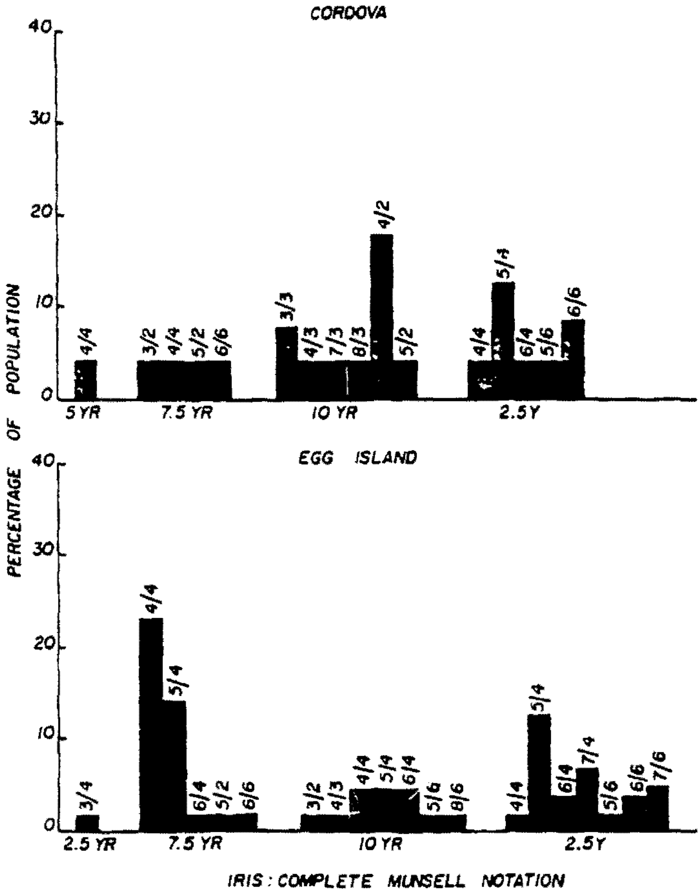

Fig. 42. Complete Munsell Notation for Iris Colors of Larus gulls at Egg Island, and Cordova, Alaska. Note the differences in the distributions of the 7.5 YR and 10 YR hues between Cordova and Egg Island

Table 40. Hybrid Index of Orbital Ring Pigmentation (OHI)* for *Larus* Populations in Southern Alaska

Colony	Mean	Munsell Hue	Color	Sample Size
Haenke Island	1.30	5 R	dark pink	10
Cordova	1.83	7.5 R	pink	23
Middleton Island	2.40	7.5 R	pink	5
North Marble	2.75	10 R	light pink	4
Egg Island	3.66	2.5 YR	yellowish pink	56
Copper Sands	4.00	2.5 YR	yellowish pink	16
Dry Bay	4.50	2.5 YR	yellowish pink	38
Strawberry Reef	4.60	5 YR	pinkish yellow	25
Lake Louise	8.91	5 Y	yellow	11

Analysis of Variance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-ratio
Between Groups	8	488.34	61.04	9.21**
Within Groups	179	1186.32	6.63	
Total	187	1674.66		

*A "pure" *glaucescens* has an Orbital Hybrid Index of 1 - 2; a "pure" *argentatus* has an OHI of 8 - 9.

**Very highly significant ($p < .001$).

Table 41. Ranked Means for Orbital Ring Indices (OHI)* for *Larus* Populations in Southern Alaska (including Cordova) (Duncan's Multiple Range Test: $p < .05$ level)

Homogenous subsets (subsets of groups, whose highest and lowest means do not differ by more than the shortest significant range for a subset of that size). There is no significant difference between the means of groups underlined with a single dotted line.

Subset 1 (dark pink - light pink orbital rings)

Group	Haenke Island	Cordova	Middleton Island	North Marble
Mean	1.30	1.86	2.40	2.75

Subset 2 (pink - pinkist yellow orbital rings)

Group	Middleton Is.	North Marble	Egg Island	Copper Sands	Dry Bay	Strawberry Reef
Mean	2.40	2.75	3.66	4.00	4.50	4.60

Subset 3 (yellow orbital rings)

Group	Lake Louise
Mean	8.90

*An OHI of 1 - 2 = "pure" *glaucescens*; an OHI of 8 - 9 = "pure" argentatus.

Table 42. Ranked Means for Orbital Ring Indices (OHI)* for *Larus* Populations in Southern Alaska (including Cordova) (Duncan's Multiple Range Test: $p < .01$ level)

Homogenous subsets (subsets of groups, whose highest and lowest means do not differ by more than the shortest significant range for a subset of that size). There is no significant difference between the means of groups underlined with a single dotted line.

Subset 1 (dark pink - yellowish pink orbital rings)

Group	Haenke Island	Cordova	Middleton Island	North Marble	Egg Island	Copper Sands
Mean	1.30	1.83	2.40	2.75	3.66	4.00

Subset 2 (pink - pinkish yellow orbital rings)

Group	Middleton Is.	North Marble	Egg Island	Copper Sands	Dry Bay	Strawberry Reef
Mean	2.40	2.75	3.66	4.00	4.50	4.60

Subset 3 (yellow orbital rings)

Group	Lake Louise
Mean	8.90

*An OHI of 1 - 2 = "pure" *glaucescens*; an OHI of 8 - 9 = "pure" *argentatus*.

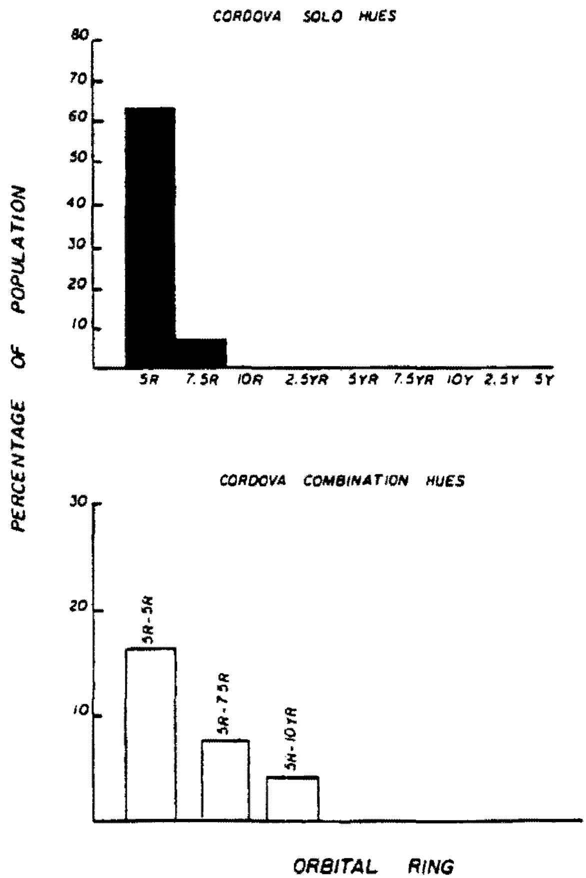

Fig. 43. Solo and combination hues of orbital rings pigmentation present in the Cordova, Alaska, Larus population.

(Figs. 43, 35). The combination of 5 R - 7.5 R (pink with areas of less intense pigmentation) was found in 8% of the Cordova population and 3% of the Egg Island population. The combination of 5 R - 10 YR (pink with light yellowish pink) appeared in 4% of the Cordova population, but this particular combination was not found on Egg Island. The Egg Island population had considerably more combination hues than that at Cordova and the distribution was extended in the direction of pink and yellow combinations. The Copper Sands and Strawberry Reef populations both had 100% combination pink and yellow hues in their orbital rings (Fig. 35).

Composite Hybrid Index

The composite hybrid index mean for the Cordova population was 10.02, i.e., most resembling *glaucescens* ("pure" *glaucescens* = 9.00) (Table 43). The F-ratio for the distribution of the composite hybrid indices for all populations was very highly significant (F - 60.52, 186 d.f., $p < .001$) (Table 43). The composite hybrid index for the Cordova population was placed between that of Haenke Island and Egg Island in the DMRT, but was not statistically different from the Copper River Delta gull populations at the 5% level of significance. (Table 44).

Discussion

Statistics based upon means indicated that the Cordova gulls were *glaucescens* and not significantly different from the Copper River Delta populations in primary feather, iris, and orbital ring pigmentation (with the exception of Strawberry Reef). However, qualitative comparisons demonstrated marked differences in the distribution of iris

Table 43. Composite Hybrid Index (CHI)* for *Larus* Populations in Southern Alaska (Iris + Orbital Ring + Primary Feather Pigmentation Indices)

Colony	Mean	Range	Standard Deviation	Sample Size
Middleton Island	9.40	8.00-11.00	1.29	5
Haenke Island	9.55	8.00-12.00	1.21	10
Cordova	10.02	8.00-13.00	1.32	23
Egg Island	10.39	6.00-16.00	1.76	56
Copper Sands	10.41	8.50-13.40	1.26	16
Strawberry Reef	11.40	8.50-17.00	2.33	25
Dry Bay	13.54	9.00-20.00	2.62	38
North Marble	14.12	10.00-23.00	6.00	4
Lake Louise	23.82	23.00-24.00	0.40	11

Analysis of Variance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-ratio
Between Groups	8	2018.63	252.33	60.52**
Within Groups	178	742.14	4.17	
Total	187	2760.77		

*A Composite Hybrid Index of 8 - 9 = "pure" *glaucescens*; a CHI of 23 - 24 = "pure" *argentatus*.

**Very highly significant ($p < .001$).

Table 44. Ranked Means for the Composite Hybrid Index (CHI)*
(Iris + Orbital Ring + Primary Feather Pigmentation Indices)
for *Larus* Populations (including Cordova) in Southern Alaska
(Duncan's Multiple Range Test: $p < .05$ level)

Homogenous subsets (subsets of groups, whose highest and lowest means do not differ by more than the shortest significant range for a subset of that size. There is no significant difference between the means of groups underlined with a single dotted line.

Subset 1 (most like *glaucescens*)

Group	Middleton Is.	Haenke Island	Cordova	Egg Island	Copper Sands	Strawberry Reef
Mean	9.40	9.55	10.02	10.39	10.41	11.40

Subset 2 (hybrid colonies with individual *argentatus* present)

Group	Dry Bay	North Marble
Mean	13.54	14.12

Subset 3 (interior *argentatus*)

Group	Lake Louise
Mean	23.82

*A "pure" *glaucescens* has a Composite Hybrid Index of 8 - 9; a "pure" *argentatus* has a CHI of 23 - 24.

hues as compared to the Copper River Delta populations. There was also a distinctly different distribution of the combined iris parameters as compared to Egg Island. In addition, qualitative comparisons of orbital ring hues and iris values suggest gulls from Copper Sands and Strawberry Reef were not represented in the population sampled from the Cordova municipal dump, although Egg Island gulls were clearly not excluded from this group. The distribution of iris chroma in the Cordova gulls was qualitatively different from all other (breeding) populations. The distribution of iris values indicated both dark-eyed and light-eyed gulls were present in the Cordova population. Primary feather and iris pigmentation indices reveal an unexpected percentage (12%) of individual gulls in Cordova with light eyes and primaries lighter than the mantle, a combination not found among any other populations examined in this study. Gulls breeding along the coastline of the northeast Gulf of Alaska usually had dark eyes and light primaries (glaucescens) or light eyes and black primaries (argentatus), although many argentatus x glaucescens hybrids have dark eyes and dark primaries (cf. Results, Section 5.4).

It is believed that the Cordova gull population at the time of this study was composed of an admixture of gulls from Egg Island and non-breeding individuals originating from a large area of Alaska, attracted by the availability of an artificial supply of food. L. argentatus x glaucescens hybrids were absent from the Cordova gull population during these summers, although they are more common during the winter (Isleib and Kessel, 1973). However, juvenile hyperboreus are present in the Cordova area during the entire year (Isleib and Kessel, 1973), and such individuals were trapped in the Cordova municipal dump during this investigation. Distinctly aberrant adult gulls, resembling _glaucescens_ in size and mantle coloration, but with white primaries, have been photographed in Cordova by Patten and Isleib. These individuals were probably _glaucescens_ x _hyperboreus_ hybrids. These observations support the conclusion that the Cordova summer non-breeding gull population, while not statistically different from adjacent breeding _glaucescens_ populations, displays qualitative color characters which suggest _hyperboreus_ influence, the nearest known breeding population of which is located on the Yukon-Kuskokwim Delta of western Alaska (cf. Strang, 1977).

8.7 APPENDIX VII

The following series of tables show dates on which I was physically present in the colonies proper for data collection.

Table 45

Schedule of Visits - North Marble Colonies

Year	Month	Day									
1972	May	15	16	19	21	22	23	27	29		
1972	June	1	2	4	8	10	12	18	20	21	25
		28	30								
1972	July	4	6	7	8	9	12	13	18	20	22
		25	28								
1972	August	1	2	3	10	11*					
1973	April	30									
1973	May	2	3	4	8	9	15	16	19	20	21
		23	28	30	31						
1973	June	1	3	7	8	10	11	12	14	15	17
		18	22	24	25	30					
1973	July	1	5	7	8	11	16	25	27	29	30
1973	August	1	3								

*Specimens collected.

Table 46

Schedule of Visits - Yakutat Colonies

a. Haenke Island

Year	Month	Day							
1974	June	14	15*						

b. Dry Bay

1974	June	17	18*						
1975	June	28	29	30*					
1975	July	1	2	3					
1977	May	9	13	14	15	17	19	21	23
1977	June	2	4	5	16	17	18	19	21
		23	25	26	27	29*			
1977	July	13	15	16	17	18	19	21	22
		23	25*						

*Specimens collected.

Table 47

Schedule of Visits - Copper River Delta Colonies

a. Egg Island Study Site

Year	Month	Day									
1975	June	18	19	20	21						
1975	July	7	9*	14	15	16*	21	23	26	27*	28
1975	August	1*+ (banding other sections)									
1976	May	21	22	25	26	30					
1976	June	3	7	11	18	24	27				
1976	July	5	11*	15	17	23*	24	25	28	29	
1976	August	4*+ (banding other sections)									
1977	July	24 (Forest Service Banding crew)									
1978	July	18-25 (Forest Service Banding crew)									

b. Strawberry Reef

1976	June	29*	30*

c. Copper Sands (S)

1976	July	1*

*Specimens collected.

Table 48

Schedule of Visits - Lake Louise "Bird Island"

Year	Month	Day		
1976	August	24		
1977	June	9	10	
1977	July	8	10	
1977	August	1	2	3*
1978	August	1	2	3

Table 49

Schedule of Visits - Middleton Island Colony

1978	May	19	21	22	26	28			
1978	June	1	5	9	13	17	21	25	29
1978	July	3	7*						

*Specimens collected.

8.8 APPENDIX VIII

Table 50. Hybrid Indices of Primary Feather Pigmentation of Males Against Females in 112 Pairs of *Larus* Gulls at Dry Bay, Alaska

	Same as Mantle	1 Shade Darker than Mantle	2 Shades Darker than Mantle	Black Primaries	Row Total
Same as Mantle	51 *	7	5	3	66
	77.3	10.6	7.6	4.5	58.9
	70.8	38.9	35.7	37.5	
	45.5	6.3	4.5	2.7	
1 Shade Darker than Mantle	11	8	4	1	24
	45.8	33.3	16.7	4.2	21.4
	15.3	44.4	28.6	12.5	
	9.8	7.1	3.6	0.9	
2 Shades Darker than Mantle	5	1	4	1	11
	45.5	9.1	36.4	9.1	9.8
	6.9	5.6	28.6	12.5	
	4.5	0.9	3.6	0.9	
Black Primaries	5	2	1	3	11
	45.5	18.2	9.1	27.3	9.8
	6.9	11.1	7.1	37.5	
	4.5	1.8	0.9	2.7	
Column Total	72	18	14	8	112
	64.3	16.1	12.5	7.1	100.0

* Each section contains: Count, Row %, Column %, Total %

(Raw Chi Square = 24.20370, 9 d.f., significance = $p < 0.0040$.)

8.9 APPENDIX IX

Table 51. Hybrid Indices of Eye Color (Equivalent to Munsell Hues) of Males Against Females in 112 Pairs of *Larus* Gulls at Dry Bay, Alaska

	7.5 YR	10 YR	2.5 Y	5 Y	Row Total
7.5 YR	100 * 95.2 96.2 89.3	2 1.9 100.0 1.8	1 1.0 100.0 0.9	2 1.9 40.0 1.8	105 93.5
10 YR	1 33.3 1.0 0.9	0 0.0 0.0 0.0	0 0.0 0.0 0.0	2 66.7 40.0 1.8	3 2.7
2.5 Y	1 100.0 1.0 0.9	0 0.0 0.0 0.0	0 0.0 0.0 0.0	0 0.0 0.0 0.0	1 0.9
5 Y	2 66.7 1.9 1.8	0 0.0 0.0 0.0	0 0.0 0.0 0.0	1 33.3 20.0 0.9	3 2.7
Column Total	104 92.9	2 1.8	1 0.9	5 4.5	112 100.0

* Each section contains: Count, Row %, Column %, Total % (Raw Chi Square = 34.82256, 9 d.f., significance = $p < 0.0001$.)

8.10 APPENDIX X

Table 52. Combined Indices of Primary Feather Pigmentation and Eye Color of Males Against Females in 112 Pairs of *Larus* Gulls at Dry Bay, Alaska

	Glaucescens Phenotypes	Female Intermediates					Argentatus Phenotypes	Row Total
"Pure"	51 *	6	3	2	2	0	0	64
Glaucescens	79.7	9.4	4.7	3.1	3.1	0.0	0.0	57.1
Primaries	71.8	33.3	27.3	66.7	40.0	0.0	0.0	
as Mantle	45.5	5.4	2.7	1.8	1.8	0.0	0.0	
Iris 7.5 YR								
Male Intermediates 8	10	7	4	1	1	1	0	24
	41.7	29.2	16.7	4.2	4.2	4.2	0.0	21.4
	14.1	38.9	36.4	33.3	20.0	100.0	0.0	
	8.9	6.3	3.6	0.9	0.9	0.9	0.0	
9	5	1	3	0	1	0	0	10
	50.0	10.0	30.0	0.0	10.0	0.0	0.0	8.9
	7.0	5.6	27.3	0.0	20.0	0.0	0.0	
	4.5	0.9	2.7	0.0	0.9	0.0	0.0	
10	0	2	0	0	0	0	1	3
	0.0	66.7	0.0	0.0	0.0	0.0	33.3	2.7
	0.0	11.1	0.0	0.0	0.0	0.0	33.3	
	0.0	1.8	0.0	0.0	0.0	0.0	0.9	

* Each section contains: Count
Row %
Column %
Total %

Table 52 continued.

	Glaucescens Phenotypes	Female Intermediates					Argentatus Phenotypes	Row Total
Male Intermediates 12	5	2	0	0	1	0	0	8
	62.5	25.0	0.0	0.0	12.5	0.0	0.0	7.1
	7.0	11.1	0.0	0.0	20.0	0.0	0.0	
	4.5	1.8	0.0	0.0	0.9	0.0	0.0	
Male Intermediates 13	0	0	0	0	0	0	1	1
	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.9
	0.0	0.0	0.0	0.0	0.0	0.0	33.3	
	0.0	0.0	0.0	0.0	0.0	C.0	0.9	
"Pure"	0	0	1	0	0	0	1	2
Argentatus	0.0	0.0	50.0	0.0	0.0	0.0	50.0	1.8
Primaries Black	0.0	0.0	9.1	0.0	0.0	0.0	33.3	
Yellow Eyes	0.0	0.0	0.9	0.0	0.0	0.0	0.9	
Column	71	18	11	3	5	1	3	112
Total	63.4	16.1	9.8	2.7	4.5	0.9	2.7	100.0

* Each section contains: Count (Raw Chi Square = 102.63608, 36 d.f., significance = $p < 0.00001$.)
Row %
Column %
Total %

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