FINAL REPORT

EVOLUTION, PATHOBIOLOGY, AND BREEDING ECOLOGY OF LARGE GULLS (LARUS) IN THE NORTHEAST GULF OF ALASKA

AND

EFFECTS OF PETROLEUM EXPOSURE ON THE BREEDING ECOLOGY OF GULLS AND KITTIWAKES

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SUMMARY OF OBJECTIVES, CONCLUSIONS, AND IMPLICATIONS WITH RESPECT TO OCS GAS AND OIL DEVELOPMENT:

This final report of Research Unit #96 is addressed to the following tasks:

TASK A-4 -- Summarize and evaluate existing literature and unpublished data on the distribution, abundance, behavior, and food dependencies of marine birds.

TASK A-5 -- Determine the seasonal density, distribution, critical habitats, migratory routes, and breeding locales for the principal marine bird species in the study area. Identify critical species particularly in regard to possible effects of oil and gas development.

TASK A-6 -- Describe dynamics and trophic relationships of selected species at offshore and coastal study sites.

TASK A-28 -- Determine by field and laboratory studies the incidence of diseases presently existing in fish, shellfish, birds, and mammals for use in evaluating future impacts of petroleum-related activity.

This report provides information on the evolution, breeding ecology, disease aspects, and effects of petroleum exposure on the breeding ecology of the Gulf of Alaska Herring Gull group (Larus argentatus x Larus glaucescens), with supporting information on the effects of petroleum exposure on the reproductive productivity of Black-legged Kittiwakes (Rissa tridactyla).

There are six known large gull colonies along the northeast Gulf of Alaska between Cordova and Juneau in an area potentially impacted by the development of oil resources. These colonies are located at Egg Island, Copper Sands, Strawberry Reef, Haenke Island, Dry Bay, and North Marble Island. There is little information known about these colonies prior to this investigation. One of the goals of this study has been to assess the reproductive health of these gull populations. Reproductive indices are now available fcr three of these colonies over a multi-year time span. Additional information of comparative value is available for an interior Herring Gull colony near Glenallen.

This information indicates coastal gull populations have the potential for rapid increase with access to human garbage, sewage and refuse associated with increased oil operations, but their colonies are sensitive to disturbance during the breeding season. Gulls are associated with canneries, fish-processing houses, garbage dumps, sewer outfalls, and municipal water supplies along the coast of Alaska, and are clearly implicated with the spread of human disease in Alaska.

Large gulls are an excellent example of vertebrate "weedy" species, adapted to man-disturbed environments and to utilize artifical food. Future development in coastal Alaska, particularly in fisheries and petrochemical industries, will increase genetic 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 be increased in future years as a secondary consequence of human activities, and may lead to a new adaptive peak in these commensal forms, with consequences for municipal health and sanitation.

Gulls are opportunistic, efficient predators on other seabird species, and increased gull populations potentially threaten the population stability of other Alaskan seabird species.

Very small amounts (20 micro liters) of North Slope Crude Oil exposure to gull eggs in the field, at early stages of incubation, lead to high embryonic mortality. Embryonic resistance to petroleum exposure increases with the duration of incubation.

GuI? behavior is altered by continued incubation of eggs killed by petroleum exposure. Adult gulls fail to respond with the normal production of replacement clutches, which usually follow clutch loss to natural causes. The combination of high egg mortality and alteration of adult behavior virtually elminates gull reproduction in experimental areas .

Weathered as well as "raw" North Slope Crude Oil significantly depress gull egg matchability, but Black-legged Kittiwakes are apparently more resistant than gulls to the effects of oil exposure on egg surfaces.

Thus, while oil spills have a potentially depressing effect on gull reproduction, the net result of. increased human development in coastal Alaska will be expanding populations of large gulls, with distinctly negative implications.

(Part I)

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure page

(Part I)

ABSTRACT

Two large white-headed gulls, *Larus argentatus* and *L. glaucescens*, exist in a zone of overlap and hybridization along the southern Alaskan coastline. Mixed pairs, parental phenotypes, and intermediates are found within single colonies. The gulls inhabit geologically dynamic environments, ranging from recently deglaciated fjords, to earthquake-influenced sandbar barrier islands, to river deltas. Nesting habitat selection is flexible, and includes flat gravel bars, sloping grassy hillsides, and nearly vertical cliff faces. Onset of breeding is flexible within an individual colony. A mixed colony at the south of the Alsek River, which connects West Coast marine with boreal interior environments, exhibits most flexibility in timing of breeding.

Analysis of adult morphology and pairing indicates individuals of mixed genetic background survive to breed. The complete range of variability in primary feather pigmentation is expressed by the offspring of hybrid x *glaucescens* backcrosses. Mating patterns, however, are assortative, and include individuals of intermediate phenotype selecting mates of similar phenotypes (Chi-square = 102.64, 36 d.f., $P < .00001$), although exceptions do occur.

Adult gulls are not significantly different in morphological dimensions from population to population with the following exception: males from two Copper River Delta colonies are significantly different ($p < .01$) from all other colonies in bill depth at posterior nares. "Pure" types of *argentatus* and *glaucescens* do not differ significantly in any dimension except wing length, which is significantly greater in *argentatus* ($p < .01$). This may relate to the longer migration pattern

of argentatus, which breeds on boreal lakes and rivers and winters offshore from the Gulf of Alaska to southern California.

Mean wing hybrid indices become progressively darker' along a northwest to southeast axis within the study area between Prince William Sound and Glacier Bay. Individual gulls within the study area are highly variable in primary feather pigmentation. The complete range of primary feather pigmentation is found within the colony at the mouth of the Alsek River at Dry Bay. As a general trend, mean wing hybrid indices increase in value from coastal populations most like glaucescens through intermediate populations in fjords and bays to an interior population of argentatus on a freshwater lake. Individual gulls in the Cordova City area show a slightly larger range of body measurements, primaries lighter than the mantle, and light irides, suggesting hyperboreus genes are present in the summer non-breeding Larus population.

There is an uninterrupted continuum of the categories of iris color within the study area, from populations most like glaucescens (dark brown irides) to populations clearly identifiable as phenotypic argentatus [bright yellow irides), with intermediate populations that have irides of light brown to light yellow. Neighboring colonies on the Copper River Delta sandbar barrier islands have strikingly similar distributions of iris hues. The mixed colonies of North Marble Island and Dry Bay share similar, although not identical distributions of iris hues and values. More kinds of iris color were found in the mixed colony at Dry Bay than in any other group examined.

Iris color is highly linked with primary feather pigmentation in gull populations in southern Alaska (Chi-square = 81.4, 36 d.f., p <.001). Light-eyed gulls tend to have dark primaries, dark-eyed gulls tend to have light primaries, and gulls with intermediate amounts of melanin in the primaries have irides of intermediate shades.

Gulls in southern Alaskan populations have orbital rings ranging from dark pink to bright yellow, with six intermediate hues connecting the extremes with increasing amounts of yellow pigment. Each population examined had a different composite orbital ring unlike those of other populations (Chi-square = 151.02, 77 d.f., p < .001). Some orbital rings in individual gulls were uniformly pigmented, while others were composed of as many as three hues. The mixed colony 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 composite hybrid index, which unifies characters of primary feather pigmentation, orbital ring and iris color, indicates that gull populations show increasing *argentatus* influence along an axis extending from Prince William Sound southeast towards Glacier Bay. The major source of *argentatus* genes along the North Gulf Coast of Alaska is the mixed colony at Dry Bay, which serves as a partial bridge between coastal and interior populations. Gene flow is more in the direction of *argentatus* into *glaucescens* populations.

Clutch size of "pure" versus mixed pairs is not statistically different (2.89 - 2.93; p < .05), although there are significant differences in clutch size between *glaucescens* populations along the southern Alaskan coastline (2.05 - 2.93; $p < .01$). Comparative hatching success is highest (93%) in a mixed colony due to low rates of egg inviability and low rates of egg predation. Hybrid, F_2, and aparent backcross zygotes are not reduced in viability and demonstrate slightly enhanced fledging success (1.47 vs. 1.40 chicks per nest).

The summary comparison of the mean clutch size and the mean number of fledglings produced per nest provides the clearest picture of reproductive success in *Larus* colonies in southern Alaska. The colonies where interbreeding is occuring have a higher mean clutch size (2.9 versus 2.7 - 2.5) and net productivity (1.44 to 1.77) than colonies of either *glaucescens* (1.08) or *argentatus* (0.95) phenotypes. Although clutch size and fledging success of mixed versus "pure" pairs within the individual colony at Dry Bay are not statistically different ($p < .05$), the hybrid pairs are reproducing slightly better than the *glaucescens* phenotypes (1.47 vs. 1.40). In addition, southern Alaskan colonies with mixed populations are reproducing considerably more offspring per pair than colonies of either *argentatus* or *glaucescens* parental types.

L. argentatus and *glaucescens* are proposed as semispecies, since parental phenotypes as well as mixed pairs and intermediates are found within single colonies, and assortative mating is occurring even though hybrids are viable. The Pacific Coast *argentatus* complex, including *hyperboreus*, *glaucescens* and *occidentals* is not usually included with the rest of the circumpolar *Formenkreis*, but recent information indicates that a chain of interbreeding groups extends up and down the Pacific Coast of North America and that members of this group are members of the Holarctic Herring Gull <u>Formenkreis</u>. The Glaucous-winged Gull is apparently the ‘key’ species in the Pacific Coast gull complex because it interbreeds with every other large white-headed gull with which it comes into contact.

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DEFINITIONS

allele
An alternative form of a gene at the same locus on the chromosome.

allopatric
Populations distributed in different dimensions of space, occupying mutually exclusive but usually adjacent geographical areas.

allopatric speciation
The separation of a population into two or more evolutionary units as a result of reproductive isolation caused by geographical separation of two subpopulations.

allozyme
A protein with an amino acid substitution but a similar enzymatic function to another such protein.

Artenkreis
A group of closely related species distributed as a partially overlapping mosaic within a given geographic zone. A zoogeographic species.

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

backcross
An individual of the F_1 or subsequent generations mating to an individual of the parental type.

chick
A young bird from time of hatching until full-grown and flying: technically a 'pullus'.

chroma
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.

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 a good species, that is, non-interbreeding. As exemplified by a ‘ring’ species.

cline
A geographic gradient in a measurable character, or gradient in gene, genotype, or phenotype frequency.

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

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

dispersal
The roughly random and nondirectional 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 main portion 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.

ethnological
Behavioral, particularly with reference to species-specific behavior elements, the phenotype of which is largely determined genetically.

F_1
The first offspring generation of a cross.

F_2
The second offspring generation of a cross.

F-ratio
The statistic appropriate to the analysis of variance.

fitness
The ability of an organism to survive and reproduce; the survival value and reproductive capacity of a given genotype relative to other genotypes 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.’

Formenkreis
Kleinschmidt's (1900) term for an aggregate of geographically representative (allopatric) species and subspecies.

founder principle

The principle that the founders of a new colony 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 is 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 isolation

The separation by geographical barriers of a population from the main body of the species.

hue

The notation of a color in the Munsell system which indicates its relation 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; those differing in alleles at one or more loci.

hybrid index

A method for analyzing variation in dissimilar yet interbreeding populations of plants and animals, using numerical scores for the characters which differ between the two populations.

hybrid zone

Narrow belts (clines) with greatly increased variability in fitness and morphology compared to that expected from random mixing, separating distinct groups of relatively uniform sets of populations.

incubation period

The time between the onset of incubation of an egg and the date of hatching.

intergradation

Character gradients between groups of populations. Often refers to two or more clines for different characters in the same organism, and going in the same geographic direction.

intergrade

An individual which is the product of a cross between different parental types and which displays characters intermediate between those of the parental types.

introgression

The incorporation of genes of one species into the gene pool of another.

iris

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

isolating mechanism

A property or properties of individuals that prevent successful interbreeding with individuals belonging to different populations.

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 wing covers of a gull, together presenting an area of distinctive color which extends from the primaries across the rest of the wings and the back.

melanin

A protein forming dark pigments, resulting from the interaction of the enzymes tyrosin and tyrosinase.

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

Having onlyone subspecies or form.

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 <u>does,</u> instead of where it <u>lives</u> (the habitat).

orbital ring

The fleshy portion of the eyelid of a gull visible when the eye is completely open, which forms a circle around the opened eye, and which 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 (the appearance) which results from the interaction of genotype and environment.
philopatry	The tendency, or drive of an individual to return to its home area, especially for breeding. In German, <u>Ortstreue</u> (true to district).
polytypic	Having more than one subspecies or form.
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. Usually ten in number, and borne on the manus (carpometacarpus and distal phalanges).
range	The geographic distribution of a species.
<u>Rassenkreis</u>	A group of subspecies connected by clines. Some of its subspecies may be sexually or genetically isolated from each other.
remige	The main flight feathers of a bird (see 'primaries' above).
secondary contact	The rejunction of partially diverged populations derived from a common ancestor.
secondary intergradation	Intergradation between two geographic forms that at one time diverged in isolation.
selection pressure	The environmental resistance leading to differential survival and reproduction of genotypes.
Sewall Wright Effect	The tendency in small isolated populations for greater 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

A group of closely related species, usually with partially overlapping ranges (see '<u>Artenkreis</u>' above).

stepped cline

A cline with a very rapid change in gene frequency separating two regions with a relatively small change of gene frequency with distance.

subspecies

An aggregate of local populations of a species, inhabiting a geographical subdivision of the range of the species, and differing taxonomically from other populations of the species.

substrate

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

subterminal

'-AS applied to gulls, that portion of the main flight feathers (the' primaries] prior to the tips.

sympatry

The occurrence of 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.

synchrony

The tendency of a population of colonial birds to reproduce within a short period of time of each other. It is an adaptive anti-predator strategy.

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., <u>argentatus</u>), in which the head is moved rapidly up and to the rear through an arc extending over the back, from a low, nearly horizontal position.

value (Munsell)

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

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.

CHAPTER 1: INTRODUCTION

The evolution and systematic of the Herring Gull group (Larus argentatus and relatives) are complex. A circle of interbreeding races (Formenkreis) extends around the Northern Hemisphere (Stresemann and Timofeeff, 1947). Where the presumed terminal populations on the circle overlap in Western Europe. extreme varient races (L. argentatus and L. fuscus) may act as good species (Paludan, 1951; Goethe, 1955). The critical linking populations occur in areas difficult to visit (e.g., Canadian arctic, east-central Siberia, sub-arctic Alaska), and fundamental questions remain concerning the distribution, intergradation, or isolation among these circumpolar populations. This section of the report concerns the evolutionary dynamics of the western North American portion of the circumpolar Larus complex, more specifically with the large white-headed gulls of the Pacific Northwest, L. hyperboreus, L. glaucescens, L. argentatus, and L. occidentals.

Spatial isolation, genetic divergence, and subsequent rejunction of populations that may or may not have attained reproductive isolation is regarded as classical speciation theory (Sibley, 1961; Mayr, 1963; Short, 1969). Concurrent with the development of genetic divergence is the evolution of attributes which may, if fully formed, reduce the potential for interbreeding. These attributes have been termed reproductive isolating mechanisms (Dobzhansky, 1937, 1951).

One of the major examples used by Mayr (1963) to support the importance of spatial isolation and the evolution of isolating mechanisms in the speciation process is that of the large white-headed gulls

(<u>Larus</u>) of the Northern Hemisphere. The data on gulls have been interpreted as providing a good example of a dynamic evolutionary system in which gulls may act as distinct species in one region while hybridizing extensively in another (Ingolfsson, 1970). Zones of hybridization can be observed in a breakdown of interspecific isolation in such factors as nest site selection, timing of breeding, and morphological or behavioral characters concerned with or influencing mate selection (Smith, 1966b).

The Larinae (gulls) as a group may have evolved in the North Atlantic Or North Pacific regions. Gulls currently have a world-wide distribution of 42 species (Fisher and Lockley, 1954), with 16 species of gulls now found in the North Pacific (Vermeer, 1970). At least 6 species of North Pacific gulls overlap in narrow zones of sympatry along the North Pacific rim (Williamson, ?966) but the question of reproductive isolation in western North American gull populations remains only partially explored. Smith (1966b) focused his study on gull evolution in the eastern Canadian arctic, where he found four sympatric species reproductively isolated by pre-mating mechanisms. Evidence has accumulated since his study suggesting that pre-mating isolating mechanisms are incompletely formed or have broken down in the western North American large white-headed gull populations.

In search of answers to questions of reproductive isolation among these gulls, I have studied gull morphology and breeding biology in Alaska for seven field seasons (1971-1977). Results of this study relate the Alaskan situation to the larger evolutionary history of northern gulls and the connection to the circumpolar <u>Formenkreis</u>.

With the advent of continental ice masses during the Pleistocene, large white-headed gull stock broke up into geographically isolated populations in refugia in Europe, Asia, and North America (Rand, 1947; McPherson, 1961). Some of these geographically isolated populations, for instance *Larus marinus*, a large dark-backed predatory species, and *L. argentatus*, a medium-sized grey-backed scavenger, evolved complete pre-mating isolating mechanisms in species recognition, timing of breeding, and nesting habitat selection. Hybrids between *marinus* and *argentatus* are rare except in artificial situations (Grey, 1958; Jehl, 1960; Andrle, 1972). A classic example of populations formerly in geographic isolation is the secondary contact between *L. fuscus* and *L. argentatus*, which are now sympatric in Europe at the terminal ends of the circumpolar *Formenkreis*. These gulls have evolved partial isolating mechanisms; however, these mechanisms were insufficient to prevent occasional hybridization after the post-glacial range expansion of *argentatus* to Europe from North America. The contact between *hyperboreus* and *argentatus* in Iceland since 1925 is an example of lack of pre-mating isolating mechanisms. Prior to 1925, *hyperboreus* was the only large white-headed gull breeding in Iceland, but a hybrid swarm with *argentatus* has been formed as *argentatus* populations colonize Iceland from Britain (Ingolfsson, 1970).

Past workers on northern gulls (e.g., Smith, 1966b; Ingolfsson, 1970) did not directly attempt to relate their results to the concept of the *Formenkreis* as developed by Stresemann and Timofeeff (1947). Recent studies of gulls in western North America (Strang, 1977; Hoffman et al., 1978) have not linked the Pacific Coast *Larus* populations to the circumpolar chain of interbreeding races. I have developed the hypothesis during the course of my studies on Pacific Coast gulls which states, in brief, that gull populations other than *argentatus* (already known to be an important link) are part of the *argentatus-fuscus Formenkreis*. There is good evidence that a chain of interbreeding groups extends down the Pacific Coast and that members of this chain are part of the circumpolar Herring Gull *Formenkreis* (Fig. 1).

The Pacific Coast *argentatus* complex has not been previously included with the rest of the circumpolar chain of interbreeding races due to the lack of sufficient knowledge of *Larus* populations in the area. Recent investigations, however, have partially clarified the situation. Strang (1977) found a high proportion of intermediates on the Yukon-Kuskokwim Delta, indicating gene flow between *hyperboreus* and *glaucescens* in western Alaska. Williamson and Peyton (1963) and Patten and Weisbrod (1974) found intermediates and mixed pairs between *argentatus* and *glaucescens* in southern Alaska. Scott (1971) and Hoffman et al. (1978) have examined mixed pairs, intermediate adults, and mating behavior between *glaucescens* and *occidentals* in western Washington.

I focused my investigation most intensively on two members of the genus *Larus* in the Pacific Northwest and the results of this study form the substance of my dissertation. The Glaucous-winged Gull (*L. glaucescens*) which breeds along the coast from Washington state to the Aleutians, is quite closely related to the Herring Gull (*L. argentatus*), a common, widely distributed species. Herring Gulls make up a low proportion of the breeding gulls in the northeast Gulf of Alaska, but occur more frequently in migration, in winter, and offshore. The Herring Gull subspecies *smithsonianus* breeds on boreal lakes in interior Alaska, British Columbia, and the Yukon, while *glaucescens* is confined

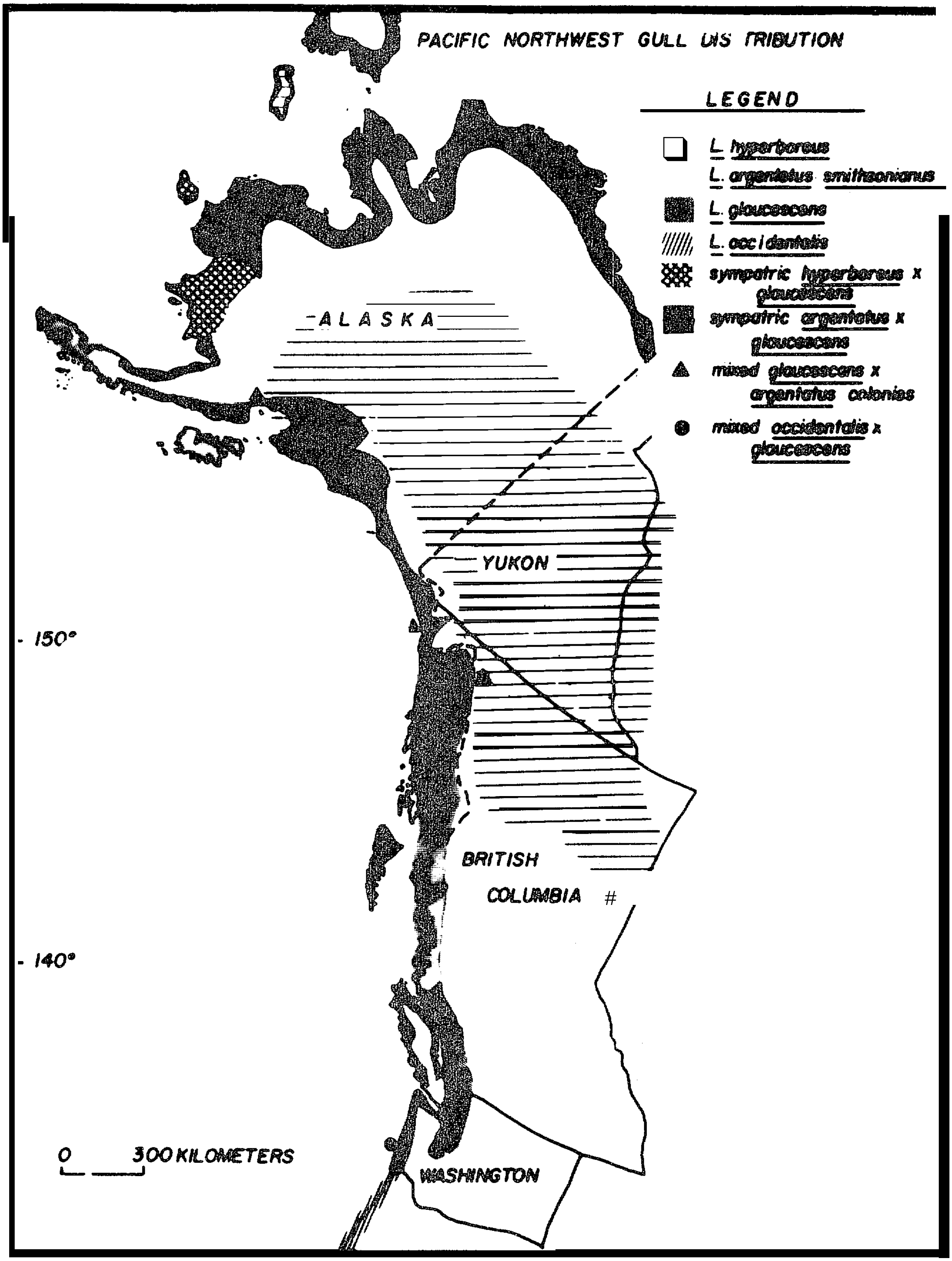

PACIFIC NORTHWEST GULL DIS TRIBUTION
LEGEND
L. hyperboreus
L. argentatus smithsonianus
L. glaucescens
L. occidentalis
sympatric hyperboreus x glaucescens
sympatric argentatus x glaucescens
mixed glaucescens x argentatus colonies
mixed occidentalis x glaucescens
ALASKA
YUKON
BRITISH COLUMBIA
WASHINGTON
150°
140°
0 300 KILOMETERS

Figure 1

to coastal areas. L. glaucescens resembles L. a. smithsonianus in plumage characters, except that the black pigment on the distal ends of the primaries in smithsonianus is replaced in glaucescens by a light grey matching the rest of the mantle. The iris of glaucescens is dark brown while that of argentatus is yellow. These two forms are considered separate species in the A.O.U. Checklist of North American Birds (1957) but the existence and extent of hybridization between the two were unknown in 1957 and thus their taxonomic and ecological relationships were unclear. In some areas hybrids are common, notably where rivers such as the Susitna and Alsek break through the high range of mountains separating the south coast of Alaska with the interior (Fig. 1).

My previous studies of breeding biology of glaucescens and argentatus indicated the possibility of tracing gull eggs and chicks of known hybrid or apparent backcross ancestry through the breeding season to the fledging stage (Patten, 1974; Patten and Patten, 1975, 1976, 1977, 1978). In the current studies, I have examined allopatric and sympatric populations of argentatus and glaucescens in southern Alaska in search of answers to several sets of questions. The first series of questions concerns aspects of breeding biology:

(1) Are there pre-mating or pre-zygotic mechanisms preventing the formation of hybrid zygotes through differences in nesting habitat selection, timing of breeding, or species recognition?

(2) Is mutual attraction between the sexes of argentatus and glaucescens weak or absent?

(3) Are post-mating or zygotic isolating mechanisms reducing the viability or fertility of hybrid zygotes (e.g., are the eggs fertile)?

(4) Are hybrid zygotes reduced in viability or inviable (indicated by reduced clutch size, reduced hatching or fledging success)?

(5) Are the F_2 or backcross hybrids reduced in viability or fertility?

The second series of questions concerns aspects of morphology:

(1) Are the adult gulls different in morphological dimensions from population to population in southern Alaska?

(2) What is the distribution of primary feather pigmentation and soft part colors (orbital ring, iris, feet and legs) among the different populations?

(3) Are the soft part colors and primary feather pigmentation genetically linked?

(4) What are the mating patterns among these gulls?

My intent in answering these questions is to clarify the taxonomic and ecological relationships between *glaucescens* and *argentatus*; relate the southern Alaskan situation to the larger *Formenkreis*; and aid in further understanding the complex systematic of the Herring Gull group.

Ethnological analysis of relationships between gulls in the pacific Northwest has not been a major focus of this study for the following reasons. Tinbergen (1972) has demonstrated that the complete series of postures associated with the "Long Call" in *argentatus* involves a motion (the "Throwback") in which the head is moved rapidly up and backwards through an arc, from a low, nearly horizontal position. As the head is lowered from the "Throwback" position, a series of loud calls is given by the gull, combining vocally elements of both sexual display and aggressive defense of territory. L. occidentals and L. glaucescens make the "Long Call" but lack the throwback posture. All other displays, such as "Choking," "Mew Call," and "Aggressive Threat," are identical in the two species (Tinbergen, 1972; underlining mine).

A study of vocalization in the large gulls of the Pacific Northwest, including argentatus and glaucescens calls recorded in southern Alaska, is being conducted by J. L. Hand (pers. comm.). Analysis of glaucescens and argentatus "Long Calls" is Incomplete, but sonagrams of "pure" glaucescens and occidentalis are quite different, yet the gulls interbreed. Clearly different vocalizations are not functioning as pre-mating isolating mechanisms in this case.

The purposes of this research, therefore, are threefold. First, I examined morphology, plumage characters, and breeding biology of large gulls in southern Alaska for the status of characters which may act as" isolating mechanisms. Second, I explored theoretical alternative hypotheses for the existence of a narrow hybrid zone between argentatus and glaucescens in south coastal Alaska. Finally, I related the information gathered during this study to the larger problem of gull relationships within the Formenkreis. The nature of this study is thus to examine morphology, reproductive biology, and fledging success in colonies of glaucescens and argentatus in southern Alaska (Fig. 2). These colonies have been selected for research because of the unknown character of the populations inhabiting the sites, and the potential for sympatry between species.

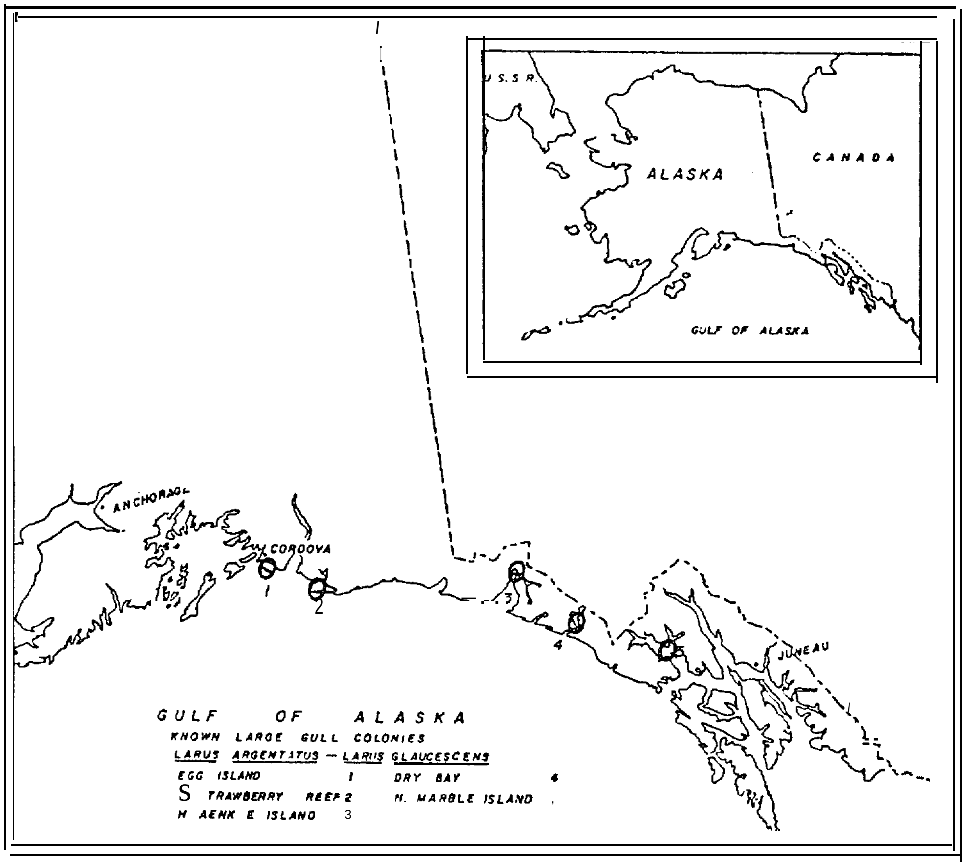


Figure 2. Map of the northeast Gulf of Alaska, showing known large gull colonies of *Larus argentatus* - *Larus glaucescens* (Inset: map of Alaska and northwest Canada showing Gulf of Alaska.)

CHAPTER 2: CURRENT STATE OF KNOWLEDGE

I. Palearctic

The morphology of Eurasian *Larus* has been studied over an extended period of time by various authors. Hartert (1921), Pleske (1928), Stegman (1934), Meinertzhagen (1935, 1950, 1954), Geyr (1938), Stresemann and Timofeeff-Ressovsky (?947), Witherby (1949), Witherby et al,, (1958), Voipio (1954), Voous (1959, 1961, 1962, 1963), Portenko (1963), Tinbergen (1960), Goethe (1960, 1961), Bianki (1967), Brown (1967), Barth (1967a,b, 1968, 1975), Harris (1970), and Verbeek (1977) have analyzed aspects of the Palearctic *Larus argentatus* - *Larus fuscus* complex. Conflicting interpretations of morphology and behavior at times have inhibited attempts to resolve dynamic, highly complicated evolutionary problems of variation in foot and mantle coloration and in ecological and ethnological segregation.

Geyr (1938), Stresemann (1947), Voipio {?954), Voous (1959), and Kist (1961) have studied the problem of the origin of yellow-footed (*L. argentatus cachinnans* and *fuscus* group) and pink-footed (*L. argentatus* group) gulls. These authors agree that during the Pleistocene an ancestral *Larus* population was divided into two refugia by the East Siberian Ice Barrier, with the populations that evolved into the pink-footed *argentatus* grouped on the east side of the barrier, and the populations that evolved into the yellow-footed *cachinnans* on the west side in the Aralo-caspian area. Ancestral *argentatus* dispersed in interglacial times over North America, leading to gradual development of the pink-footed american group, which includes *glaucescens* and *occidentals* among others (see below). Post-glacially, L. a. smithsonianus emigrated to Europe from eastern North America, coming into contact with the westward-expanding cachinnans-fuscus group, to which argentatus is partially isolated, and forming the classic overlap of a “ring” species. However, after the Pleistocene, L. argentatus also spread into interior Siberia, forming the subspecies vegae and birulai. The pink-footed populations of birulai, moving west, met the populations of the yellow-footed L. a. antelius, moving east. Large-scale hybridization took place in central Siberia, where no geographical barriers exist, thereby forging the connecting link in the Palearctic chain of races of the Formenkreis. Indeed, Jungfer (1956) reported on the occasional arrival of the siberian Herring Gulls (birulai) in the North Sea, indicating that westward' movement is still occuring.

The Formenkreis, as developed by European authors, is now best regarded as somewhat of an over-simplification. This is due to previous lack of information concerning the western North American populations. These can also can be linked to the Formenkreis, as demonstrated below.

II. Nearctic

The morphology of large white-headed gulls of the Nearctic argentatus group has been studied since the last century with virtually continuous debate over aspects of species status. Research has focused on two major geographical areas: the high arctic, and more recently, the West Coast. The status of the arctic forms of hyperboreus, thayeri, kumlieni, and argentatus has been examined by Henshaw (1884), Ridgway (1886), Dwight (1906, 1919, 1925), Oberholser (1918), Bishop (1927), Stemann (1934), Portenko (1939), Rand (1942, 1948), Bailey (1948), Salomonsen (1950), Manning et al. (1956), Johansen (1958), McPherson (1956, 1961), Jehl and Frohling (1965), Smith (1966a,b, 1967), Ingolfsson (1970) and Knudsen (1976). Research interest in Nearctic *Larus* has been in aspects of primary feather, iris, and orbital ring coloration, rather than in foot and mantle pigmentation as in Eurasian large gulls. Studies have demonstrated that *hyperboreus* and *argentatus* are reproductively isolated in the eastern Canadian arctic, but they interbreed in Iceland. The taxonomic positions of *kumlieni* and *thayeri* remain unclear pending results of ongoing research (cf. Knudsen, 1976).

The West Coast forms, *occidentalis*, *glaucescens*, *argentatus* and *hyperboreus*, have been studied by Dawson (1909), Swarth (1934), Shortt (1939), Pearse (1945), Vermeer (1963), Williamson and Peyton (1963), Williamson (1966), Scott (1971), Patten and Weisbrod (1974), Hoffman (1976), Patten (1976), LeValley (1976), Strang (1977) and Hoffman et al. (1978). A literature review of the evolutionary status of these West Coast gulls, together with the North Pacific *vegae* and *schistisagus*, suggests none of these populations are reproductively isolated by premating mechanisms, since they interbreed in narrow zones of sympatry (Williamson, 1966). The contact between these forms clearly bears further study.

III. Narrow Hybrid Zones in Vertebrates

Moore (1977) recently reviewed the literature on vertebrate hybridization and discussed the existence of narrow hybrid zones in vertebrates other than *Larus*. I will briefly describe the four hypotheses presented by Moore as explanations for these zones in order that I may explore the theoretical aspects of interbreeding in the contact zone between argentatus and glaucescens in southern Alaska.

The ephermeral-zone hypothesis states that hybridization will end either in speciation or fusion of the hybridizing taxa by means of introgression (Dobzhansky, 1940; Sibley, 1957; Wilson, 1965; Remington, 1968). Known examples of stabile hybrid zones, such as the contact between Corvus corone and C. cornix in central Europe, and the situation between Colaptes auratus auratus and C. a. cafer on the Great Plains, provide evidence against this hypothesis (Mayr, 1963; Short, 1965, 1969, 1970; Moore, 1977).

The dynamic equilibrium hypothesis allows for stabile hybrid zones. Where hybrids are confined to a small area by steep selection gradients, “crystallization” of antihybridization mechanisms might be prevented by “naive” immigrants from the parental populations even though hybrids are selected against. This hypothesis reconciles the existence of narrow hybrid zones with the concept of co-adapted gene complexes, and states that if two populations have diverged to the point where the hybrids suffer depressed fitness, gene flow through the hybrid zone into the parental populations should be inhibited by selection (Bigelow, 1965). Where selection gradients are steep, intergradation should be restricted to a narrow zone between the parental populations. Although hybrids might be less fit than parental phenotypes, only a few individuals in or near the zone of secondary contact would be exposed to selection against hybridization, while a much larger proportion of the parental phenotypes would never experience this selection pressure. 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 stabile zone.

A third hypothesis, which could also account for a stabile hybrid zone, is that hybrids are actually more fit than the parental phenotypes in the narrow zones in which they occur. This hypothesis has been put forward by botanists for some time {Anderson, 1949; Muller, 1953; Grant, 1971) but until recently has not been given serious consideration as an alternative to the ephemeral hybrid zone and the dynamic-equilibrium hypothesis for animals (Moore, 1977). Short (1970) pointed out that ephemeral hybrid zones are the exception rather than the rule in avian hybrids, and concluded that these hybrids are actually more fit than parental phenotypes in stabile hybrid zones, although strong selection may occur in parental populations against immigrant genes (Short, 1972). 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. Most vertebrate hybrid zones are, in fact, narrow {Moore, 1977).

The fourth hypothesis explored to account for the narrow contact zone between _argentatus_ and _glaucescens_ is based upon the following logic: hybrids, in some cases, can succeed in environments where competition from parental phenotypes is weak (Anderson, 1949). Ecotones are one such area, and Moore (1977) suggested that stabile hybrid zones are narrow because they tend to occur in ecotones which are themselves narrow.

Exploration of the data collected in the narrow contact zone between argentatus and glaucescens in southern Alaska may provide sufficient insight to allow discrimination among the various hypotheses stated above. I believe they are not mutually exclusive, however, and the "best fit" of the southern Alaskan Larus situation may involve combinations of one or more hypotheses.

IV. The Breeding Biology of Large Gulls

A review of allopatric breeding biology of large gulls aids in understanding selective forces which may operate upon interbreeding forms discussed in the following chapters. The breeding biology of argentatus in Europe and eastern North America has been studied in detail by Goethe (1937), Paynter (1949), Paludan (1951), Tinbergen (1960), Harris (1964), Ludwig (1966), Keith (1966), Brown (1967 b), Kadlec and Drury (1968), Drury and Smith (1968), Kadlec et al. (1969), Parsons (1971, 1975), Drury and Nisbet (1972), and Hunt (1972). Nesting habitat selection is flexible (Drury and Nisbet, 1972) and includes marshes (Burger, 1977), sand dunes (Tinbergen, 1960), and cliff faces (Emlen, 1963; Goethe, 1960). Average clutch size in argentatus is nearly always three, and variations are small. Most egg loss is due to predation, and infertility rate is low. Hatching success is usually 60 to 80 percent. Herring Gulls raise an average of one young per pair per year to fledging. Critical factors affecting hatching and fledging rate are egg and chick loss through cannibalism, chick mortality due to aggressive behavior of adults, and weather conditions during the breeding season.

In contrast to the intensive investigations of North Atlantic argentatus, few researchers have studied large gulls along the Pacific Coast of North America. The breeding biology of the Western Gull (L. occidentals) has been studied by Coulter (1969), Schreiber (1970), Harpur (1971), Coulter et al. (1971), Hunt and Hunt (1973, 1975, 1977), Hunt and McLoon (1975). Most aspects of the breeding biology of occidentals are similar to East Coast argentatus, or North Pacific glaucescens (see below) but nesting habitat selection differs due to drier conditions on nesting islands (Hoffman et al., 1978). Hunt's (1977) studies have demonstrated the apparent failure of sex recognition in the formation of female-female pairs in occidentals.

The breeding biology of the Glaucous-winged Gull (L. glaucescens) in the Pacific Northwest 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 investigations indicate glaucescens is quite similar to argentatus in nesting habitat flexibility, average clutch size, low infertility rate, moderate to good hatching success, arid variable chick mortality and fledging success, often related to availability of food. The Glaucous-winged Gull has the same plumage sequences as the Herring Gull (Schultz, unpub. ins.) and similar adaptability to urban environments (Ward, 1973).

Strang's studies (1972a,b, 1973, 1974, 1977) of the breeding biology of hyperboreus in western Alaska are the only works available on the reproductive productivity of this species. Nesting habitat includes both coastal and marshy sites, clutch size approaches three, infertility rate is very low, hatching success varies around 50%, and mean productivity is slightly over one chick per pair per year.

Philopatry has been documented for several gulls, including argentatus and glaucescens (Gross, 1940; Paynter, 1949; Tinbergen, 1953, 1961; Drost et al., 1961; Ludwig, 1963; Vermeer, 1963). There is a strong tendency for adult gulls to return to natal colonies for breeding. Voous (1961) showed that mantle coloration in L. a. argenteus was related to colony of origin, and that the relationships to neighboring colonies were not gradual in minor details, although apparently gradual on a larger geographical scale. This suggests a degree of isolation between members of adjoining colonies, which in turn leads to rapid evolutionary potential (Sewall Wright Effect).

In summary, studies of the breeding biology of allopatric large gulls indicate that nesting habitat selection is flexible, clutch size approaches three, infertility rate is low, and normal productivity is one chick per pair per year. Adult gulls tend to return to colonies of origin for breeding, suggesting a degree of isolation between neighboring colonies.

CHAPTER 3: DESCRIPTION OF STUDY AREAS

I. The General Milieu

The location of this study is the south coast of Alaska between Juneau and Prince William Sound, including a fresh water lake in the interior, north of Valdez (Fig. 2). The south coast of Alaska is a wild, relatively uninhabitated stretch of North Temperate shoreline, exhibiting dramatic changes in relief, with high mountain ranges in close proximity to marine environments. Fjords, bays, river deltas, and occasional sandy beaches indent the coastline. The basic factors affecting climate are similar at practically all points along the coastal study area (USDC, 1963). The climate is basically maritime, with nearby ocean areas modifying daily and seasonal temperatures at sea level to within rather narrow limits. The area is exposed to frequent low pressure systems moving out of the Gulf of Alaska, providing abundant precipitation. The high, rugged Fairweather, St. Elias, and Chugach Mountain Ranges (to 5800 m) intensify precipitation from onshore movement of moisture-laden air. Glacier Bay Ranger Station receives 225 cm of precipitation annually (Streveler and Paige, 1971), Yakutat 338 cm (Alaska Geographic, 1975), and the Copper River Delta 250 cm (usDC, 7963). Maximum precipitation over the entire area usually occurs from August through November. Average annual snowfall occurs mainly from November through March and ranges 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, which may be massive. The Malaspina Glacier northwest of Yakutat is larger than the State of Rhode Island.

The sky is rather persistently cloudy, averaging 80% coverage. Summer days are often characterized by overcast skies, rain, and cool temperatures. The mean annual number of clear days near Cordova is only 52 (USDC, 1963). High temperatures, usually encountered in early July, rarely climb above +27°C, while winter extreme low temperatures, reaching -35°C, are usually of short duration (USDC, 1963). The following is a description of the conditions at the large white-headed gull colonies along the Alaskan coastline between Glacier Bay and Prince William Sound (Fig. 2).

II. 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 ?792, uncovering large terrestrial and marine areas. North Marble Island lies in the middle of Glacier Bay and supports the largest (500 pairs) gull colony in the bay (Fig. 3). North Marble is about 600 m long and 300 m wide, and is surrounded by cold, highly oxygenated waters and strong tidal currents. - The island emerged from glaciation about 120 years ago (Streveler, pers. comm.). The resistant meadow barley (*Hordeum brachyantherum*) forms nearly 70 percent of the ground cover in the gull nesting areas on the east, west, and north sides of the island, which are sloping meadows above shallow (5-25 m) cliffs (Fig 4). For a complete description see Patten (1974). Gene flow between previously isolated *Larus* populations in the area may be as recent as the deglaciation.

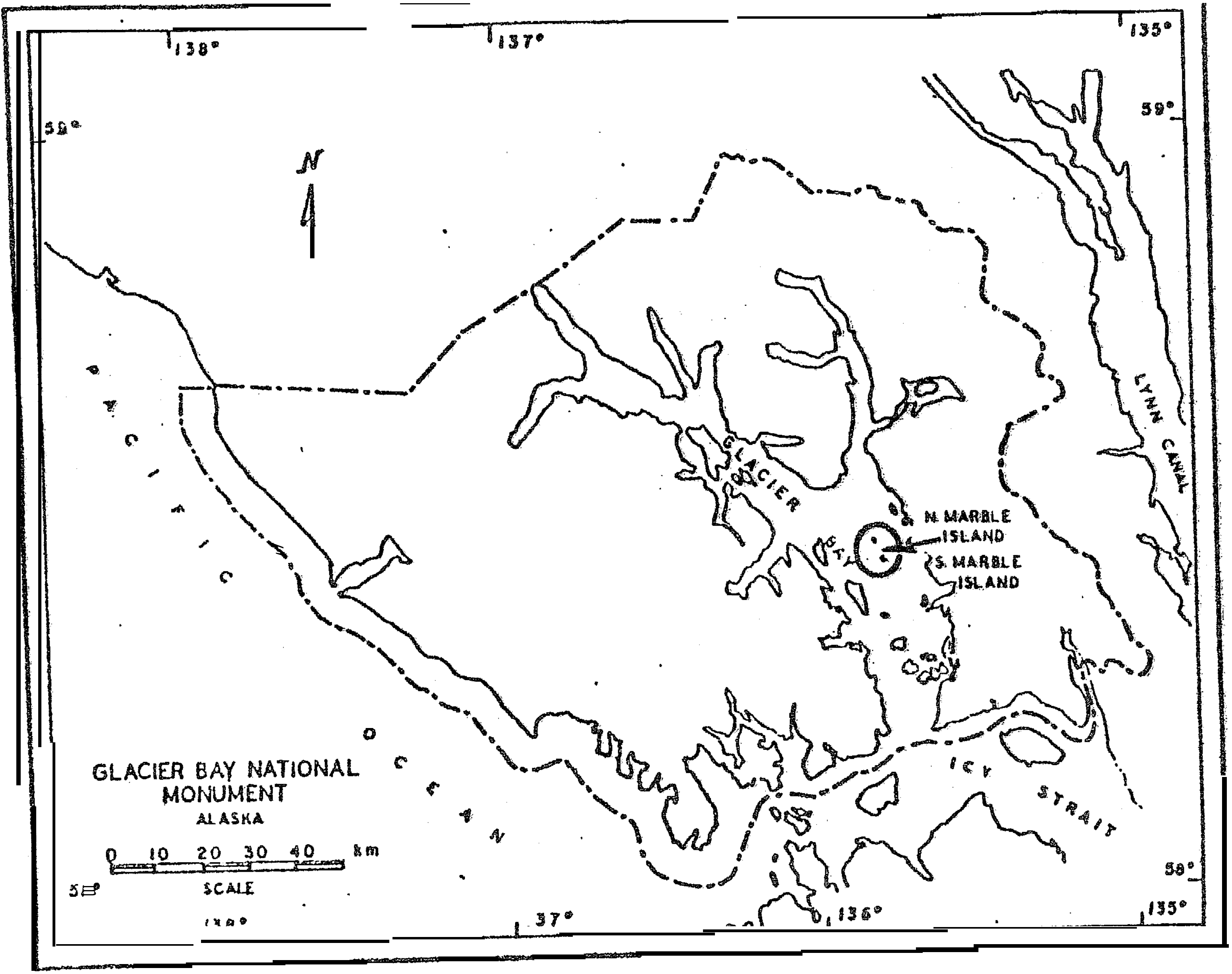


Figure 3. North Marble Island lies in the middle of Glacier Bay and contains large marine bird nesting areas. North and South Marble Islands, 2 km apart, are surrounded by cold, highly oxygenated waters and strong tidal currents.

Figure 4 , North Marble Island is about 600 m long and 300 m wide. Substrate is Willoughby limestone covered with scrubby Sitka Spruce and *Hordeum* meadows.

III. Dry"Bay

The gull colony (500 pairs) at Dry Bay, 75 km S of Yakutat, is located 4.8 km from the mouth of the Alsek River on flat gravel bars (Fig. 5,6). The Alsek River, rising in the Yukon and partially draining the. Fairweather Range, changes in level relative to rainfall and snow melt. Water surrounding the gull colony is fresh although silty, and carries ice floes from the Alsek Glacier, 28 km from the coast. Some years late summer' high water stages wash completely over the gravel islands (Mork, pers. comm.). In other seasons, powerful southeast storms cover the delta with heavy rains or snow. Winter winds over 160 kph drive ocean waves over 20 m high onto the outer beaches, occasionally inundating and washing overmuch of the delta. Japanese glass fishing floats are found on the gravel bars 4 km from the mouth of the river.

Dry Bay has apparently not been glaciated but may have been the location of catastrophic flooding within the last thousand years from glacially dammed lakes in the interior Yukon (Brogle, pers. comm.). Dry Bay is a geologically active, earthquake-prone area. A minor earthquake caused the mouth of the Alsek River to shift 1 km to the west in 197'5 (Alaska Geographic, 1975). The gravel islands of the Alsek River Delta at Dry Bay are subject to considerable repositioning due to river action. Vegetation on the gravel bars is a sparse mixture of alluvial and maritime forms. For a complete description of the area see Patten and Patten (1978).

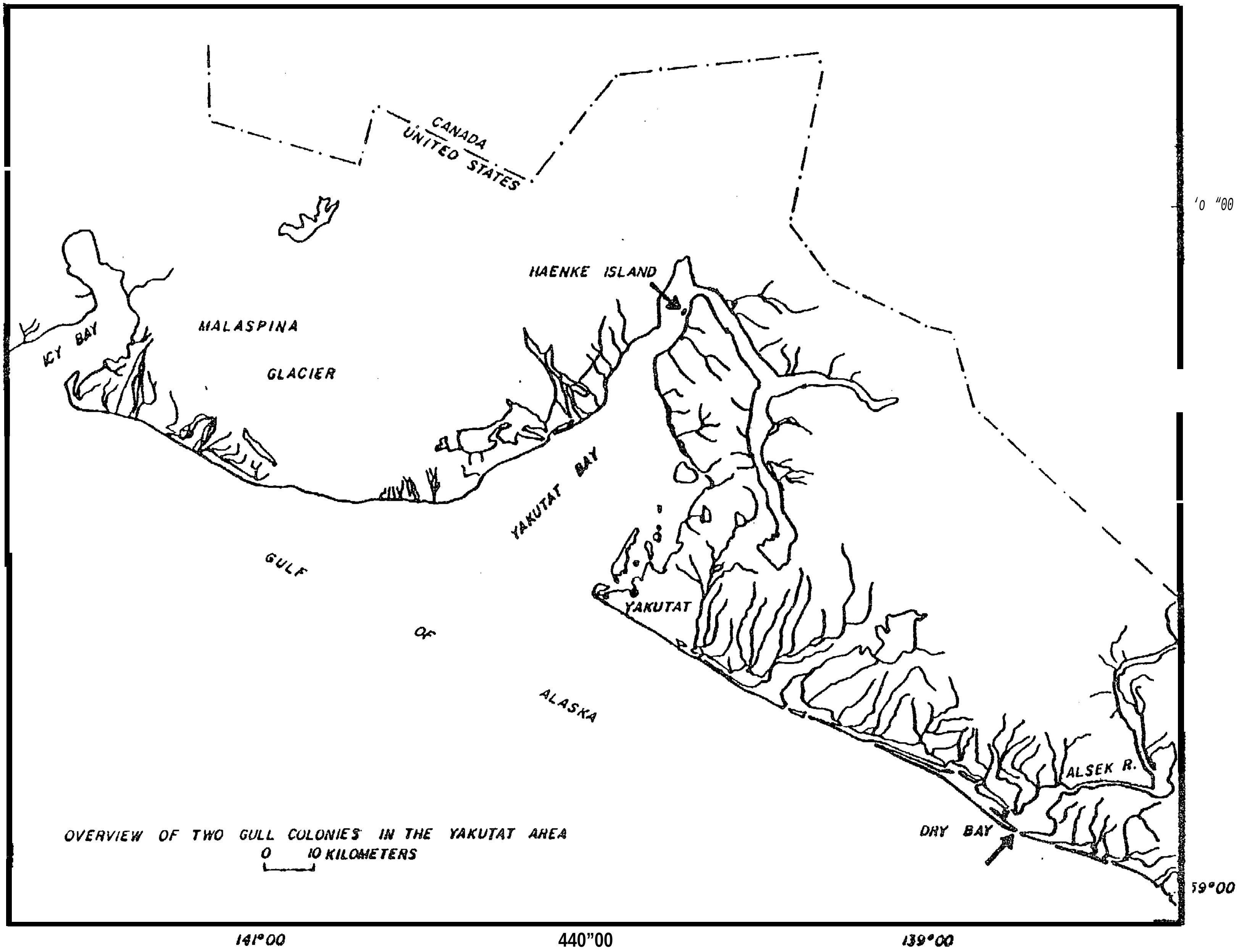

CANADA
UNITED STATES
'0 "00
HAENKE ISLAND
MALASPINA
GLACIER
ICY BAY
YAKUTAT BAY
GULF
OF
ALASKA
YAKUTAT
ALSEK R.
DRY BAY
59°00
OVERVIEW OF TWO GULL COLONIES IN THE YAKUTAT AREA
0 10 KILOMETERS
141°00
440"00
139°00

Fig. 5.

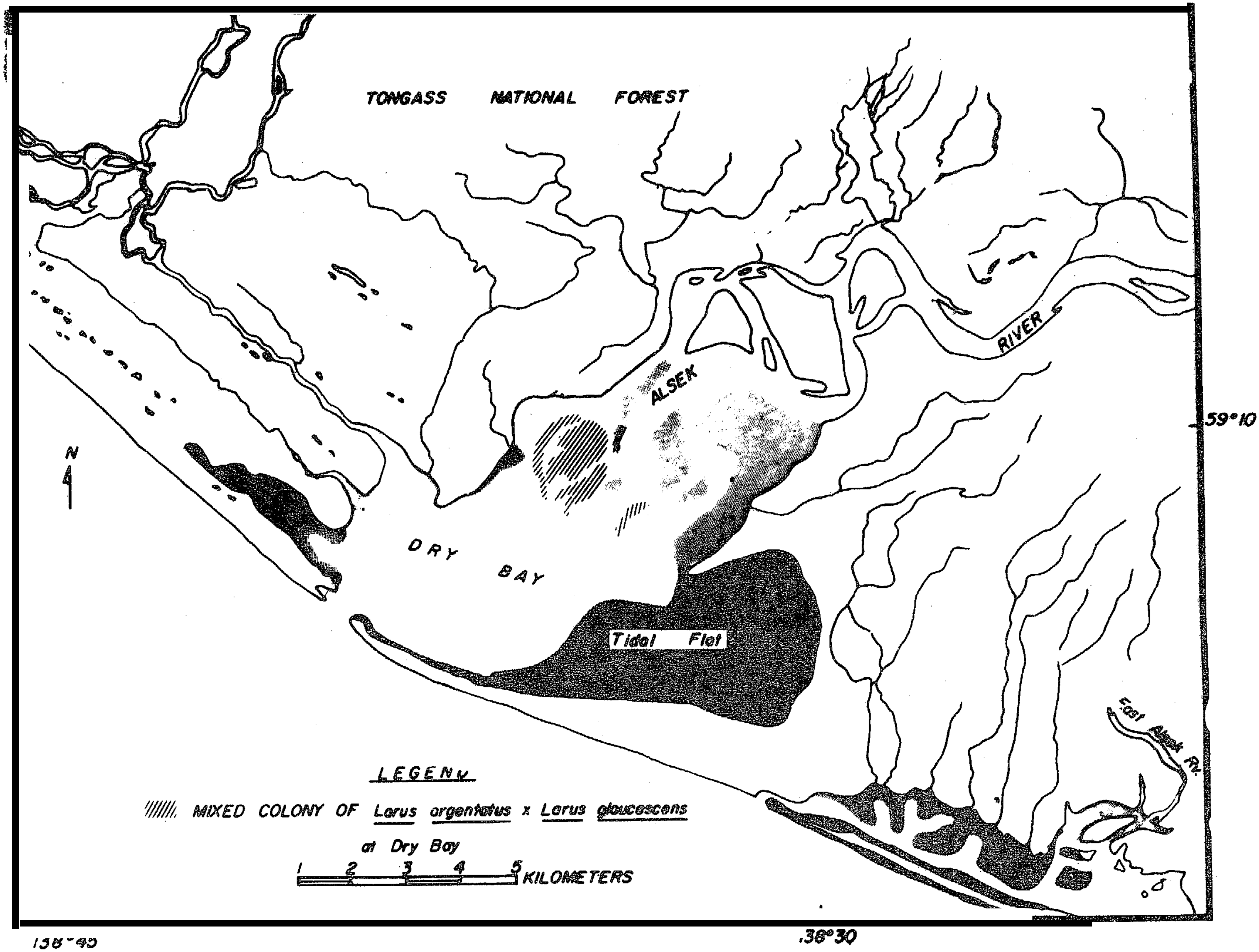

TONGASS NATIONAL FOREST
ALSEK
RIVER
59°10'
N
DRY BAY
Tidal Flat
East Alsek Rv.
LEGEND
MIXED COLONY OF Larus argentatus x Larus glaucescens at Dry Bay
1 2 3 4 5 KILOMETERS
138°45
38°30

Fig. 6.

IV. Haenke Island

Haenke Island, located in Disenchantment Bay, 75 km NE of Yakutat, and less than 1 km from the mainland, is often completely surrounded by pack ice from the nearby Hubbard Glacier (Figs. 7, 8). The island, with little level ground, is covered with low brushy vegetation dominated by alders, suggesting relatively recent deglaciation. The east side of the island, facing the Hubbard Glacier, gradually slopes to an elevation of 75 m, and then drops precipitously, forming a large westward-facing cliff, where 500 pairs of glaucescens breed on a series of narrow terraces.

The glacier once filling Yakutat Bay reached its maximum extent sometime in the Middle Ages and began to retreat about 600 years ago (Alaska Geographic, 1975). The retreat went far behind the branches of the Yakutat Bay Glacier, now the tidewater glaciers of Disenchantment Bay (Fig. 7). The ice then readvanced, reaching its largest extent during the 1700's. The Yakutat Bay glacier, best regarded as an expanded Hubbard Glacier, probably extended slightly beyond Latouche Point, 10 km past Haenke Island. The glacier again retreated to the vicinity of Haenke Island by the time of Malaspina and Vancouver, the early white explorers of the 1790's. Haenke Island, similar to North Marble, is thus recently deglaciated, but the exact date is uncertain due to the sporadic advances and retreats of the Hubbard Glacier. The gull colony at Haenke Island probably dates from the most recent deglaciation. For a complete description of conditions at Haenke Island see Patten and Patten (1978). This colony is the most geographically isolated of the sites examined.

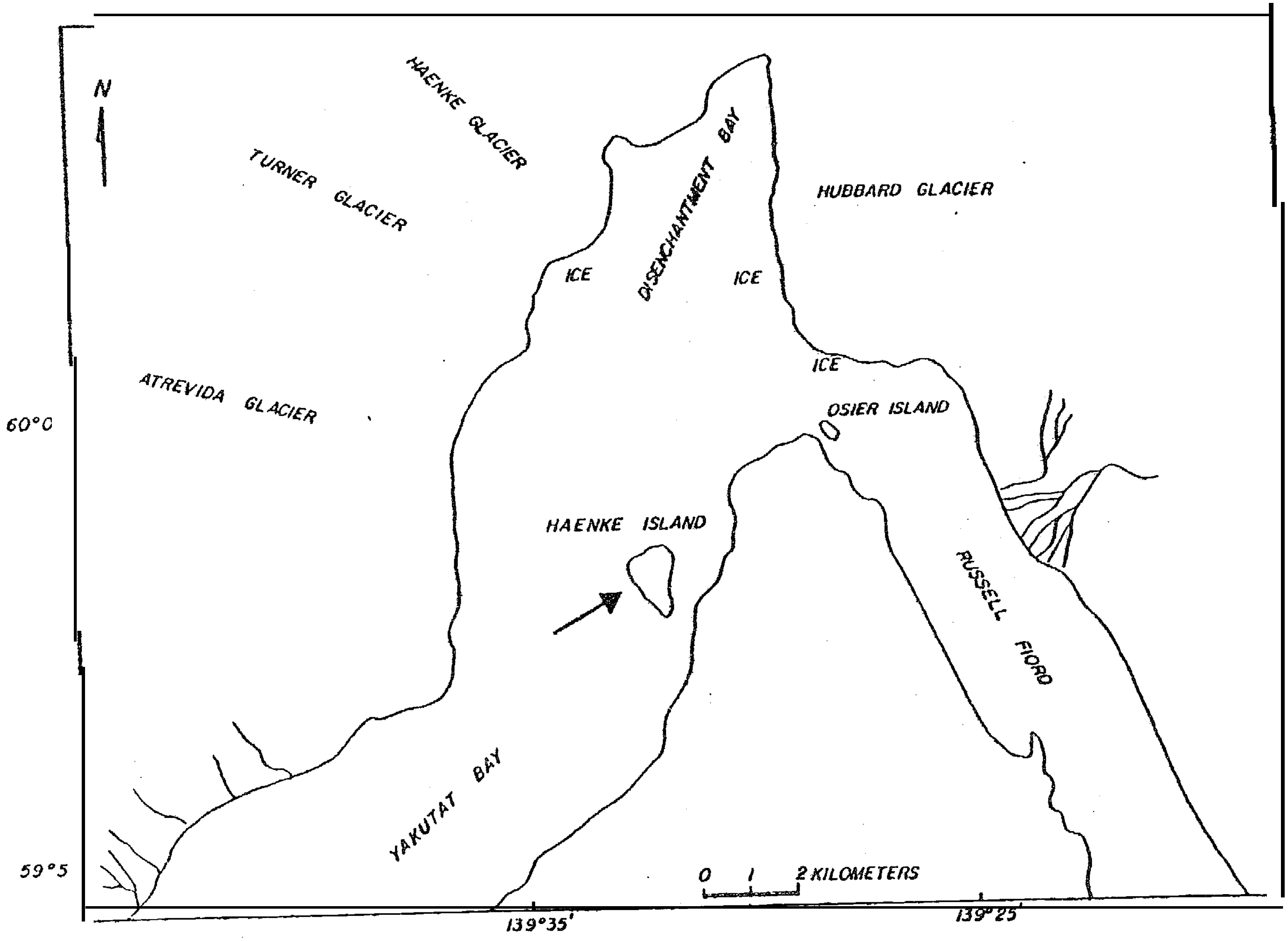


Fig. 7. Map of Haenke Island and surroundings in Disenchantment Bay, near Yakutat Bay, 50 km NE of Yakutat, Alaska. Note the proximity of four major glaciers. The advancing Hubbard Glacier threatens to close Russell Fjord and form a freshwater lake. Haenke Island is located less than 1 km from the mainland.

Fig. 8. HAENKE ISLAND

V. 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. South of Cordova the Copper River and the confluent Martin River have deposited sand and mud where they meet the sea, forming a 50 km wide delta. A few kilometers off the mouth of the Copper River' a series of low sandbar-dune islands forms a partial barrier to ocean storms. These islands have been formed by the deposition of sand and mud, and have been shaped by the counter-clockwise onshore currents- of the Pacific Ocean (Fig. 9).

Constant change is characteristic of the interface between land and sea, especially where rivers enter the ocean. Sandy islands are built up and eroded away in a relatively uninterrupted process. However, the Copper River Delta and surrounding areas have been marked by sudden geological changes that have been extremely important in affecting local biota. Janson (1975) wrote of major earthquakes in the Copper River Delta occurring 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 (USFS, 1975). The abrupt uplift disrupted the complex delta ecosystem and altered the balance between fresh water and saltwater. Nutrient input from saltwater to the delta appreciably diminished; several species of intertidal invertebrates and nesting populations of ducks declined in numbers. Willows and alders began to replace grass and sedge marshes in areas of the delta. Certain tidal sloughs dried out (Scheierl and Meyer, 1976).

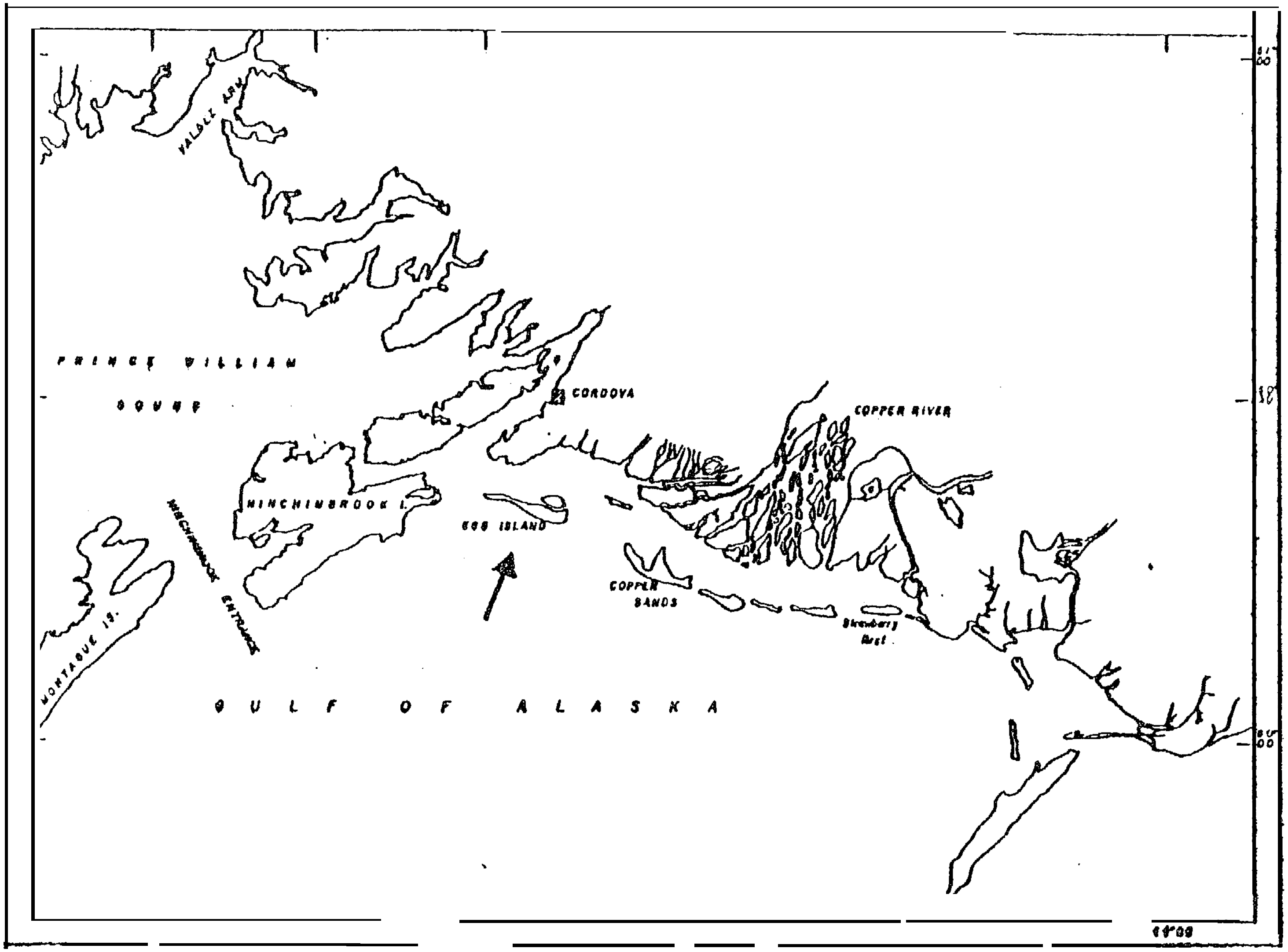


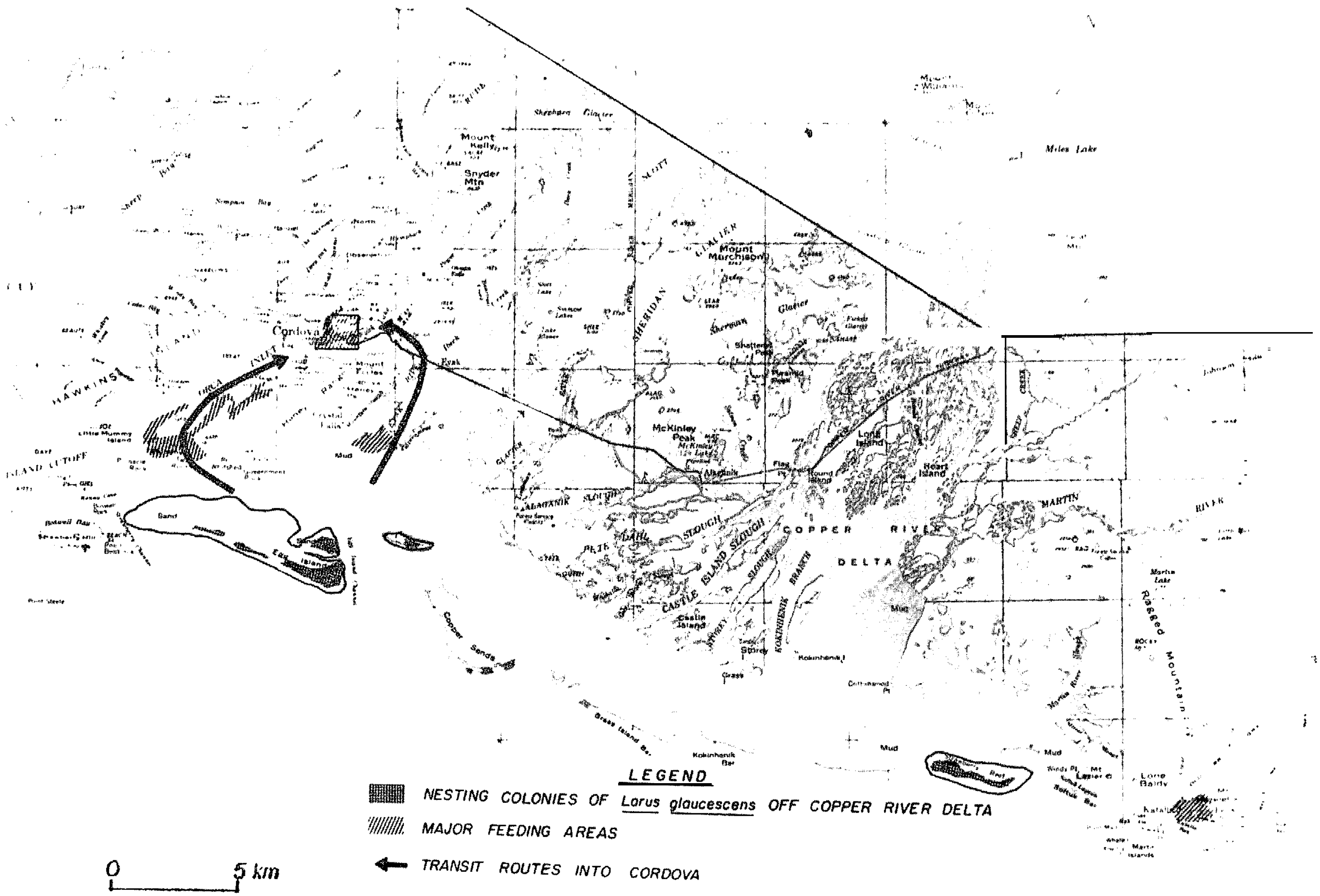
Figure 9. Map of the Copper River Delta region and Prince William Sound, showing location of Cordova, the Copper River, Egg Island (arrow), Copper Sands (S), and Strawberry Reef. Tanker traffic from Valdez will pass through Hinchinbrook Entrance. The area is highly vulnerable to oil spills.

The sandbar barrier islands at the mouth of the Copper River underwent the same sharp geological forces as the delta itself, but due to 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 formed, joining islets together. The actual land area of the barrier islands increased due to the uplift. Plant succession began on newly formed dunes, with beach rye (Elymus arenarius mollis) forming scattered tufts on the sandy surface. Meadows encroach on dunes as succession continues.

Large colonies of gulls nest on these meadow-covered dunes. The actual area upon which gulls can nest is increasing, and at the moment there are large areas of unoccupied meadows capable of supporting nesting gulls due to the earthquake uplift and subsequent plan succession on newly formed areas (Fig. 10).

Overlying the vegetation 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 (Fig. 10). Gulls also feed at the open municipal dump at the edge of the harbor.

The potent' al for discarded human food and industrial waste increases daily in coastal Alaska. Isleib (pers. comm. sees an increasing gull population in the Cordova area to date. Our NOAA


LEGEND
▦ NESTING COLONIES OF Larus glaucescens OFF COPPER RIVER DELTA
▨ MAJOR FEEDING AREAS
← TRANSIT ROUTES INTO CORDOVA
0 5 km
Cordova
ORCA INLET
HAWKINS ISLAND
ISLAND CUTOFF
Little Mummy Island
Mount Kelly
Snyder Mtn
Shepherd Glacier
SHERIDAN GLACIER
SCOTT GLACIER
Mount Murchison
McKinley Peak
Alaganik
ALAGANIK SLOUGH
PETE DAHL SLOUGH
CASTLE ISLAND SLOUGH
Castle Island
KOKINHENIK BRANCH
COPPER RIVER DELTA
Long Island
Heart Island
MARTIN RIVER
Ragged Mountain
Martin Lake
Lone Baldy
Katalla
Miles Lake
Copper Sands
Grass Island Bar
Kokinhenik Bar
Eyak
Mud
Egg Island Channel
Egg Island
Point Steele

F· o-l . · 0"

helicopter survey indicated 13,225 gull pairs nested on the sandbar barrier islands off the Copper River Delta in 1976 (Table 1). 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.

The discussion of study areas will now focus on four sandbar barrier islands off the Copper River Delta.

VI. Egg Island

Egg Island lies off the south coast. of Alaska 20 km S of Cordova. Prior to the 1964 earthquake, Egg Island was a series of sand dunes and bars, but since the earthquake the sandbars and dunes have coalesced and built up one basic island, with a tremendous increase in surface area, which is undergoing colonization by the beach rye *Elymus* (Fig. 11). Driftwood, remains of fishing vessels, and other debris are scattered along the former storm-tide line, now at least a kilometer from the nearest saltwater (Michelson, 1973). Egg island currently extends for 10 km along a series of dunes arranged on an east-west axis, containing the largest gull colony in the northeast Gulf of Alaska, approximately 10,000 pairs of nesting *glaucescens*. Changes on this island are nothing less than dramatic over the last dozen years. Quite recent earthquake activity (1964) is important in determining the structure of the island and the plant communities upon which the gulls nest. For complete analysis of the gull colony at Egg Island see Patten and Patten (1975, 1976, 1977, 1978). This is apparently the largest *glaucescens* colony in the world.

Table 1. Nesting Gull Populations

on Copper River Delta Sandbar Islands

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

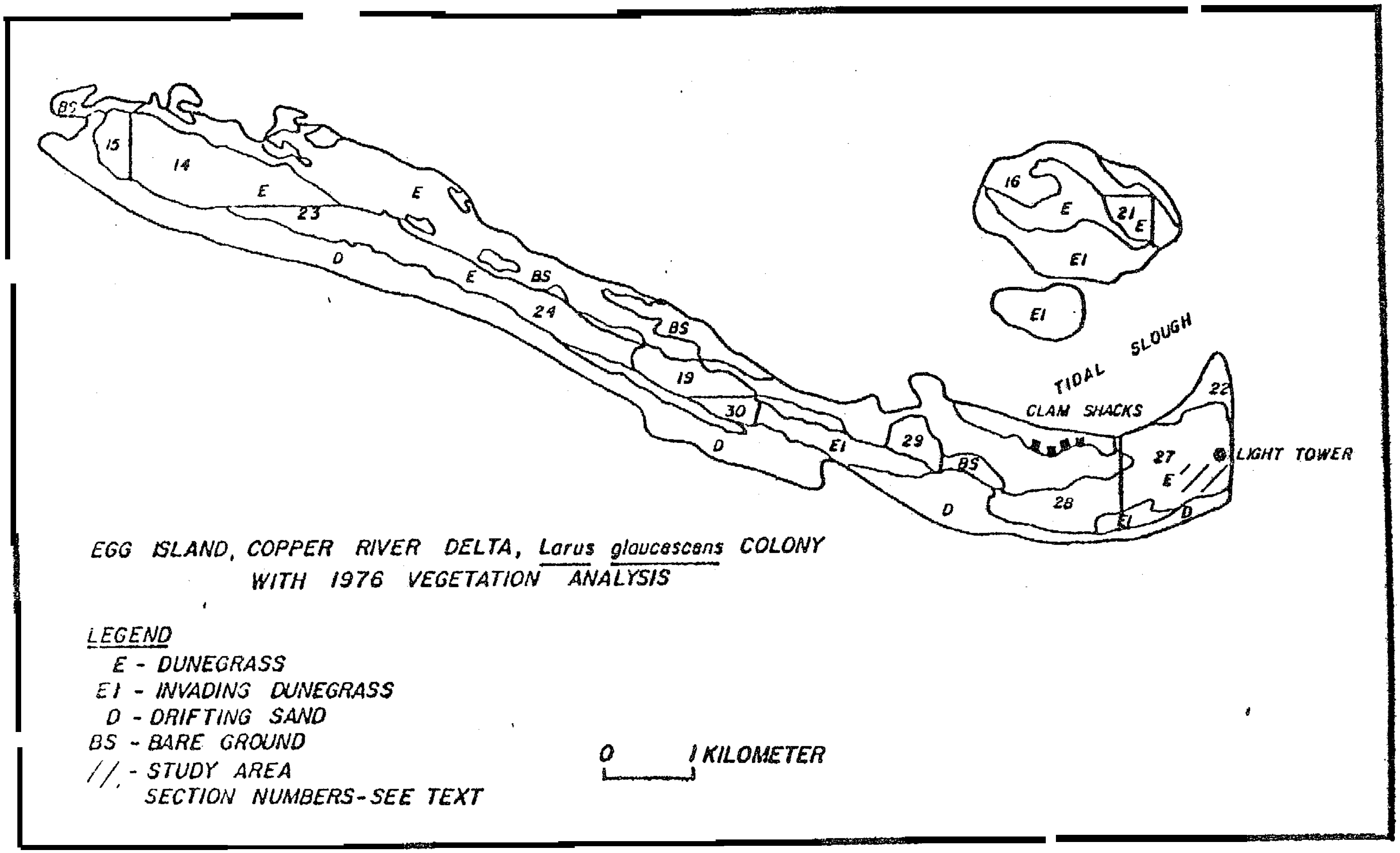

EGG ISLAND, COPPER RIVER DELTA, Larus glaucescens COLONY
WITH 1976 VEGETATION ANALYSIS
LEGEND
E - DUNEGRASS
EI - INVADING DUNEGRASS
D - DRIFTING SAND
BS - BARE GROUND
// - STUDY AREA
SECTION NUMBERS-SEE TEXT
0 1 KILOMETER
TIDAL SLOUGH
CLAM SHACKS
LIGHT TOWER
BS
15
14
E
23
E
D
E
BS
24
BS
19
30
D
EI
29
BS
D
28
EI
D
27
E
22
16
E
21
E
EI
EI

Fig 1.

VII. Copper Sands and Strawberry Reef

Copper Sands (S.), a bar 12 km long, one of a series of barrier islands at the mouth of the Copper River, lies 5 km ESE of Egg Island and 24 km SE of Cordova (Fig. 10). Copper Sands, consisting of a series of unstabilized dunes extending from southeast to northwest, has risen in elevation since the 1964 earthquake, but shows much less vegetation than Egg Island. The gull colony of 800 pairs is located on three dunes covered with Elymus at the SE tip of Copper Sands (Fig. 10).

CopperSands (N), a small, newly formed island less than a kilometer long, 2.5 km ENE of Egg Island off the mouth of the Eyak River, did not exist before the 1964 earthquake, but now contains several dunes with 150 pairs of glaucescens nesting in the Elymus (Fig. 10). Other barrier islands between Copper Sands and Strawberry Reef at the east end of the delta support few nesting gulls due to lack of suitable vegetation, a result of intense sand scouring during winter high pressure systems (Michelson, 1975; Isleib and Kessel, 1973). Gulls use unvegetated islands such as. Kokinhenik, Softuk, and Grass Island Bar as resting areas (Fig. 10).

Strawberry Reef, 8 km long, the easternmost barrier island at the mouth of the Copper River, contains the second largest glaucescens colony on the delta (Fig. 10). About 2000 gull pairs nest in the Elymus on Strawberry Reef, which is separated from the mainland by shallow tidal channels. The island is undergoing plant succession on recently uplifted areas, becoming more suitable to nesting gulls. Strawberry Reef, as Egg Island, consists of wide ocean beaches, unstabilized dunes, Elymus-covered dunes, and mud flats, but differs by expanding thickets of spruce and alder.

VIII. Lake Louise

Lake Louise, 8 x 12 km, lies 51.2 km NW of Glenallen, in the Copper River Basin on southcentral Alaska. Lake Louise drains through Susitna Lake and the Tyone and Susitna Rivers to Cook Inlet (Figs. 12, 13).

An island gull colony, readily observed due to disturbed vegetation, lies 1 km from the west shore of the lake on a steeply sloping rock known as "Bird Island." Bird Island, radically different in appearance from other spruce-covered islands in Lake Louise, shows evidence of heavy, long-term bird use. Vegetation, composed of lichens, mosses, grasses, resistant forbs, and woody vines, indicates disturbed conditions. Living plants are absent in the peat formation along the island crest, area of heaviest bird use. At least 77 pairs of _L. argentatus smithsonianus_ and 14 pair's of _Phalacrocorax auritus_ nest on the island (100 x 20 x 10 m, 0.36 hectare). Photographs taken by Hayes (pers. comm.) fifteen years ago show little change in island vegetation structure, in contrast to dynamic conditions in gull colonies previously examined. Hayes (pers. comm.) reports gulls and cormorants have inhabited Bird Island for as long as local residents can remember, probably centuries longer. . This invites comparison with the biology of gulls on the south coast of Alaska, where change is explosive.

IX. Summary of Study Areas

The study colonies are thus a series of islands in southern Alaska, extending over 4° latitude from Glacier Bay near Juneau, to Lake Louise in southcentral Alaska. Aquatic environments include the coast, tidal bays, river deltas, fjords, and a fresh-water lake.

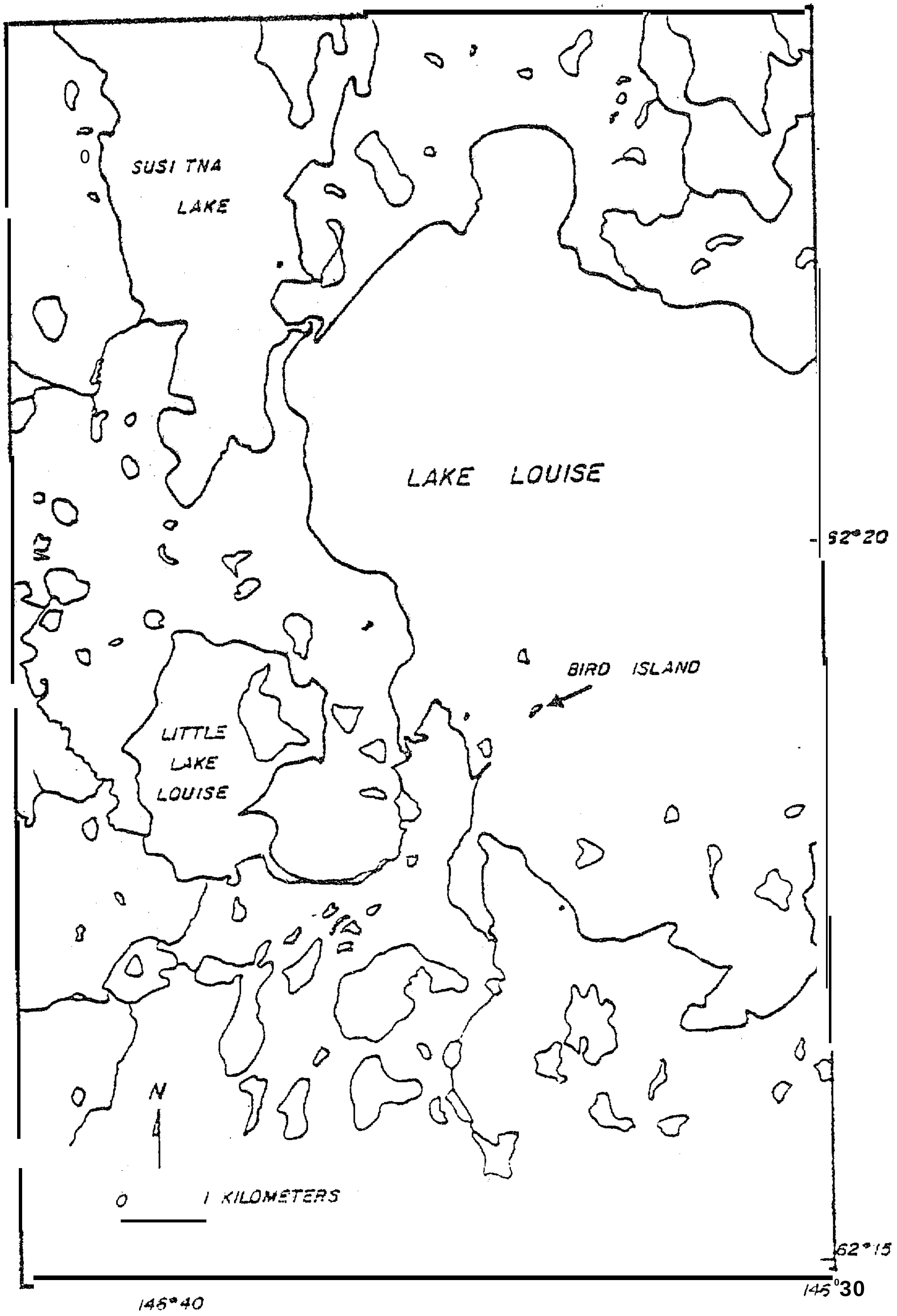


Fig. 13. Overview of the Lake Louise area, showing Susitna Lake and Little Lake Louise. Bird Island (arrow} lies 1 km from the west shore of the lake and contains 77 pairs of *Larus argentatus smithsonianus*.

The geology of the coastal sites is dynamic due to recent deglaciation, major earthquakes, and floods. Vegetation at 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).

Four coastal colonies, Egg Island, Strawberry Reef, Copper Sands, and Haenke Island, contain allopatric glaucescens. Two coastal colonies, North Marble and Dry Bay, support sympatric and interbreeding argentatus and glaucescens. The interior colony at Lake Louise is composed of allopatric argentatus. Cordova, a major feeding area, supports summering populations of glaucescens, low numbers of hyperboreus, and gulls showing intermediate characters between these two. Table 3 contains the principal periods of study for these Larus colonies in southern Alaska.

Table 2. Study Areas for *Larus* Colonies in Southern Alaska

colony	Coordinates N	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*
Cordova **	60°33'	145°45'	*glaucescens*, *hyperboreus*	tidal inlet	artificial urban environment	city dump
Lake Louise	62°20'	146°32'	*argentatus*	freshwater lake	slope lake islet	*Calamagrostris* meadows

* Large white-headed *Larus* populations during breeding season.
** Not a breeding colony but a major feeding area (see text).

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
Cordova City	1975	Intervals: June - August
Cordova City	? 976	Intervals: May - August
Cordova City	1977	Intervals: April - August

CHAPTER 4: MATERIALS ANO METHODS

I. Colony Selection and Investigation Dates

North Marble, Dry Bay, Egg Island, and Lake Louise were selected as principal locations for reproductive aspects of this study because they supported the largest gull colonies in southern Alaska. Each site has distinguishing features and represents the major colony for a large geographical area. North Marble, only recently deglaciated and thus available for nesting, is being colonized by pioneering populations of both argentatus and glaucescens. Dry Bay supports a coastal hybrid colony astride a major migration route to the Yukon. Egg Island contains the largest, still expanding, meadow-nesting glaucescens population in the northeast Gulf of Alaska. Lake Louise, "Bird Island," has long been inhabited by migratory interior argentatus.

II. Reproductive Cycle

All nests under study were marked with forestry survey stakes at the beginning of each colony investigation. Each heavy wire survey stake had a bright vinyl flag attached. Since vegetation growth tended to obscure the flags by mid-season, each survey stake was marked with an additional sequentially-numbered fluorescent streamer. A fiberglass meter tape was used to find the direct distance from every study nest to the center of' the nearest neighboring nest. The nest survey stakes were left in position for two field seasons in order to follow nests for two years where possible. Nest site slope was measured using a Brunton Survey Transit"

As part of each sequential visit through the gull colonies, numbers of eggs and chicks from each nest site inspected were recorded in National Oceanographic Data Center format 035, “Flat Colony Survey".

Visits at North Marble averaged once every three days during incubation. and once every six days during the chick stage. Visits at Egg Island averaged once every three days during incubation, and once every three days during the chick stage. The Dry Bay colony was visited every other day, and the Lake Louise colony at egg-laying, chick hatching, and at fledging time.

The plumage and soft-part colors of both parents at each nest site studied at Dry Bay were examined using a 25x telescope and comparing them to a Munsell color chart. Newly hatched chicks at Dry Bay were web-tagged with fingerling fish tags until large enough for banding with USF&WS rings. Young chicks in other colonies were counted in the nest upon hatching. Older chicks in study areas other than Dry Bay were presumed to have hatched in the nearest nest; such older chicks were marked at Egg Island with 2.5 cm aluminum bands bearing number codes which could be read vertically. The web-tagged chicks at Dry Bay, when nearly fledged, were banded with similar 2.5 cm aluminum bands, and an additional 2.5 cm lynply plastic band with engraved codes in black alphanumeric characters on the opposite leg. The parentage of fledged chicks at Dry Bay could be verified in this manner. At the end of the survey period each summer counts were made of fledged, banded chicks for entire study areas. The productivity of the hybrid colonies at Cry Bay and North Marble has been compared to the allopatric *glaucescens* at Egg Island and the *argentatus* at Lake Louise in search of evidence for pre- or post-mating isolating mechanisms.

III. Marking Methods: Banding

We banded 11,212 gulls during this study in order to answer questions of migration routes, wintering areas, and to permit individual recognition of chicks and adults. Outside of the main study areas we banded 1300 flightless. chicks in 1975, 2696 in 1976, 1200 in 1977, and 5546 in 1978. These young gulls were banded on their left tarsi with USF&WS butt-end aluminum, monel, or incoloy bands, size 6 (for *argentatus*) or 7A (*glaucescens* and hybrids).

All 1975 young *glaucescens* were captured at Egg Island. In 1976, we banded 2500 *glaucescens* chicks on Egg Island, 95 chicks at Strawberry Reef, and 101 at Copper Sands (S). In addition, within the 1975 study site (150 m x 150 m) southwest of Egg Island light tower, we captured every *glaucescens* chick which survived two weeks. These 222 individuals were banded on the left tarsus with 2.5 cm, butt-end aluminum bands, with the reference numbers twice repeated vertically (Sladen et al., 1968). We counted as fledged 157 of the 222 banded chicks in early August. We did not band until chicks were nearly fledged in 1976, in order to reduce disturbance to the study area. We then counted as fledged-those 208 *glaucescens* banded within the study in an intensive effort in late July.

At Dry Bay we banded 25 known hybrid chicks, 1 known *argentatus* chick, and 403 other chicks assigned to *glaucescens*. Study area chicks were marked with web-tags, 2.5 cm aluminum bands, and orange lynply 2.5 cmbands with engraved black alphanumeric codes (A001-A000), enabling individual recognition of the chicks.

U.S. Forest Service crews assisted by banding 700 additional *glaucescens* chicks on Egg Island in 1977. We banded 71 of the 73 argentatus chicks produced at Lake Louise in 1977, and 60 of the 75 produced there in 1978. In 1978 we banded 86 glaucescens chicks on Middleton Island, and with Forest Service assistance, 5400 gull chicks on Egg Island. All other gulls forming the combined total were trapped, banded and released in the municipality of Cordova.

IV. Morphological Measurements

In order to obtain morphological measurements from sympatric and allopatric Larus populations in southern Alaska, adult gull specimens were required. Gulls were collected with a shotgun, and live-trapped, since official permission to use drugs for capture of gulls (cf. Smith, 1966b) was denied. Collecting is less desirable since it invites non-random sampling (see Ingolfsson, 1970). Trapping was a more random method, since I took whatever birds entered the trap.

As soon as an adult gull was trapped or collected, standard measurements were taken (culmen chord length; bill length from the side of the anterior nares to tip; bill depth at posterior nares; diagonal tarsus length; chord of closed (flattened) wing; and weight) and the information was recorded on data sheets These same measurements have been used in previous gull studies and are of comparative value (Smith, 1966b).

The data was sorted into grouping by sex and colony. Only four gulls could be collected from Glacier Bay National Monument, all of which were males, due to permit restrictions. The Lake Louise colony was composed of only 77 pairs; therefore only two males were collected in addition to Williamson's earlier specimens. All birds obtained from Cordova were trapped, since discharge of firearms was not permitted within city limits. Sample size of females in all cases was less than males, suggesting that behavioral differences made them less likely to approach a trap or shotgun range. Both trapped and collected gulls have been included in the analysis of morphology, plumage characters, and soft part colors.

V. Hybrid Index Method

Initial perspective on the morphology 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 involving numerical scores for the characters which differ between the two populations (Anderson, 1949; Sibley, 1954). The two principal forms concerned in this dissertation, argentatus and glaucescens, differ in eye and orbital ring color, and in amount and pattern of melanin in the distal primaries. After a gull was captured or collected, I immediately photographed the orbital region of the head, with the primaries in juxtaposition, with a Pentax 35 mm camera and Kodachrome II color film. The iris, orbital ring, tarsi, and feet were verbally described, and then the colors were compared to the standard charts of the Munsell notation by holding the charts directly over the individual parts (Fig. 14; see below).

Figure 14. Study of isolating mechanisms, Determination of adult *glaucescens* orbital ring and iris pigmentation using a Munsell chart of skin, hair and eye colors, based upon the Munsell Soil Color Chart, Note numbered tarsal band. Cordova, 1977,

Mantle and primary pigmentation were also recorded by direct comparison with the Munsell Neutral Value Scale (see below). Mantle, primary color, and a wing hybrid index derived from amount and pattern of melanin on the outer primaries, were included in this analysis. For the wing hybrid index, elements in the series were scored as essentially like one of the two species, or assigned to the spectrum of intermediate forms. The wing hybrid index and the corresponding Munsell notation are presented below (Fig. 15). The combination of amount and pattern of melanin on the distal portions of the five outermost primaries was classified into one of seven categories which were given the numerical notations or scores of 1 (typical glaucescens) to 6 (typical argentatus). The score of 0 was reserved for those atypical Cordova glaucescens in which the primaries were lighter than the mantle. The notation of the primaries in atypically light glaucescens was revised to account for the possibility of genetic interaction with a third species, hyperboreus.

The distribution of iris colors was scored in six grades from 1 (typical glaucescens, hue 2.5 YR) to 6 (typical argentatus, hue 5 Y). The observed range of pigmentation in orbital rings included all nine possible Munsell hues within the major hue names of Red, Yellow-Red, and Yellow (see Munsell System of Color Notation, below). Orbital rings were composed of all three major hues in some cases. The scores within the major hues were added tugether for the individual gull to form a "composite orbital ring." In similar fashion, the scores for the primaries, irides, and orbital rings were added together for each gull to produce a "composite hybrid index."

HYBRID INDEX OF PRIMARY FEATHER PIGMENTATION

MUNSELL NEUTRAL VALUE SCALE

Hybrid Index	Munsell Scale	Verbal Description
	N7/	primaries lighter than mantle
	N6/	primaries same shade as mantle
	N5/	primaries 1 shade darker than mantle
▨	N4/	primaries 2 shades darker than mantle
▨	N3.25/	primaries 3 shades darker than mantle
m	N2.5/	primaries blackish
■	N2/	primaries black

Fig. 15.

The scores are set in such a way that resemblance to _argentatus_ is always high in value, and resemblance to _glaucescens_ always low in value. The hybrid index obtained was of course an arbitrary indication of the "hybridness" (i.e., the relative number of _argentatus_, _glaucescens_, or in some cases, _hyperboreus_ genes), since the categories were arbitrarily defined. The definitions of the categories used are given in Fig. 15, and typical examples of wing patterns are shown in the Frontispiece. My main concern in defining the categories was to arrive at recognizable stages which could be differentiated from other stages.

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

VI. Munsell System of Color Notation

The colors discussed in this study, that of gull irides, orbital rings, primary and mantle feathers, required a rapid and precise method of identification and recording. The Munsell System of Color Notation (Munsell Skin, Hair and Eye Color Charts, Matte Finish Edition, Munsell Color Co., Baltimore, Maryland) was used in order to reduce subjective evaluation and because soft part colors quickly fade and may change colors after a specimen is taken. The following introduction is taken from Munsell Color, a privately printed publication of

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, Yellow-Red, and Yellow, 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, is written N V/. The notation of black, a very dark neutral, might be N2/; the notation of white, a very light neutral, might be N9/; while the notation for a grey, visually half-way between these two, would be N5/.

VII. Data Analysis

Numbers of eggs and chicks, recorded as part of sequential visits through the gull colonies, with distance to the nearest neighboring nest, were entered on 80-column sheets and key-punched following the NODC Format 035, “Flat Colony Survey.” A custom program written by Mr. Mark Miller of the University of Washington and modified by Mr. Galen Smith of the Johns Hopkins Computing Center was used to compute clutch size, egg loss, hatching success, and fledging success for North Marble, Dry Bay, and Egg Island, and to portray these variables graphically using the Cal-Comp system on the Johns Hopkins University DEC-system 10 computer.

VIII. Study Skins

During this study 174 adult gulls were collected from North Marble Island, Dry Bay, Haenke Island, Strawberry Reef, Copper Sands (S), Egg Island, and Lake Louise, for taxonomic verification, food habits, and serology. Representative series of study skins will be presented to the University of Washington, Seattle; National Museum of Natural History, Washington, DC; and the American Museum of Natural History, New York City.

CHAPTER 5: RESULTS

I. Comparison of Measurements

Although there are suggestions in the literature that argentatus and glaucescens populations are broadly overlapping in body dimensions (Dwight, 1925; Williamson and Peyton, 1963) I did not immediately dismiss the possibility that certain morphological features might be useful to discriminate between populations of gulls in southern Alaska. I formulated two null hypotheses, and examined the standard measurements of 174 gulls in search of evidence to accept or reject these null hypotheses:

(1) There are no significant differences in mensural characters between sympatric and allopatric populations of glaucescens and argentatus in southern Alaska;

(2) There are no significant differences in measurements between so-called "pure types," e.g., those exhibiting plumage and soft part colors characteristic of strictly parental types. (For descriptions of the parental types please see the Introduction.)

The morphological measurements of gulls in populations in southern Alaska are presented in Tables 4 and 5. Means, standard deviations, and ranges have been included in an exploratory univariate analysis of the body measurements. Since gulls are sexually dimorphic in body size and mensural characters, males were not compared against females. Inspection of the means, ranges, and standard deviations reveals that the magnitude of difference between colonies is not absolutely great (Tables 4 and 5).

Table 4. 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	I*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	}.24
	Cordova		20.1	19-25	1.45
	Lake Louise		20.5	20-21	0,50

Table 4, cent’d,

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	450-460	7.07

Table 5. 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 5, cent'd.

Measurement	Colony	Composition	Mean	Range	S.D.
Wing	Dry Bay	*arg*. x *glauc*.	418.7	400-450	2.38
	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	1.91
	Cordova	*glauc*./*hyperbor*.	410.5	400-425	0.85

F-ratios (the statistic appropriate to the Analysis of Variance), were then computed, using the S?SS-10 ONEWAY program. This program is an Analysis of Variance that takes into account differences in sample size and changes in degrees of freedom by groups. The F-test may require some qualification if the means are skewed. However, since gull body measurements (within sexes) are approximately normally distributed, the F-test should give a good approximation of the real differences between population means.

The F-ratios for the measurements of the female adult gulls indicated no significant differences between any of the populations examined at either level: $P < .01$ orp $< .05$ (Table 6). However, for male gulls, the comparison of body measurements first yielded a significant F-ratio at the 5 percent level for two measurements: bill depth at posterior nares; and bill length, anterior nares to tip (Table 7). Further exploration of the data revealed that the males in two colonies, Copper Sands (S) 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, then the F-ratio indicated no significant differences between the remaining populations (Table 8). Males from Copper Sands and Strawberry Reef, compared to each other, showed no significant difference {Table 9). Further, the difference between population means in the measurement of bill length (anterior nares to tip) was of marginal significance ($p < .04$).

Since the F-ratio was at least marginally significant for these two dimensions, further comparisons were necessary. Analysis now required a rank-ordering approach. Duncan's New Multiple Range Test

Table 6. 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	nos.
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 7. Analysis of Variance (SPSS-10 ONEMAY) 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 8. Analysis of Variance (SPSS-10 ONENAY) 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
Ming	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 9. 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	 Within Groups	F-ratio	Significance
Wing	1	18	0.431	I-I*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

(Steele and Torrie, 1960) is well suited to this sort of analysis. This test, and the t-test used below, are both robust (i.e., they assume a normal distribution of means, not samples, and therefore can be used without qualification).

The results of Duncan's Multiple Range Test confirmed that the differences between male populations in bill length (anterior nares to tip) were of marginal significance (not significant at $p < .01$). However, the next test showed that males from the two neighboring Copper River Delta colonies, Copper Sands (S) and Strawberry Reef, were significantly different ($p < .01$) in bill depth (at posterior nares) from all other colonies examined (Table 8). The two colonies were not significantly different from each other (Table 9).

After testing the significance of differences in measurements between various populations, "pure types" were selected from the data base, and the means of the body measurements of the "pure types" were compared by t-test, appropriate for the small sample size ($n=15$). The "pure types" did not differ except for wing measurement, which was significantly longer in _argentatus_ types ($t=3.20$, $p < .01$). The observed statistical difference in bill depth between the two Copper River Delta populations and the other colonies examined cannot, therefore, be used in taxonomic discrimination, since the "pure types" of _glaucescens_ and _argentatus_ do not differ statistically in this dimension. However, this difference may have other genetic and evolutionary implications (see discussion below).

Since no significant differences were found in measurements between female gull population examined, the first null hypothesis was accepted. This hypothesis was rejected for males, however, since there is a significant difference in bill depth between two Copper River Delta colonies and other populations examined. However, male gull populations examined do not differ significantly in any other dimension.

The, ''pure types" of *argentatus* and *glaucescens* do not differ significantly in any dimension except wing length, which is significantly longer in *argentatus*. However, the non-significant F-ratio for allopatric and sympatric populations indicates broad overlap in wing length (Table 7).

The conclusion was therefore drawn that a minor sex-linked difference in bill measurement exists among various populations of gulls in southern Alaska, but there is broad overlap in all other. mensural characters. As a result, the examination of morphology was extended to include an analysis of calorimetric characters, including primary feather pigmentation, iris and orbital ring coloration.

11. Primary Feather Pigmentation

The most obvious character which differed between individuals and populations of gulls in southern Alaska was the amount and pattern of melanin in the distal ends of the primaries. As the amount of melanin in the primaries intensified, the pattern of deposition expanded from the subterminal area to include progressively more of the distal portions of the outermost remiges. The melanin extended up the feather shafts of the three outermost primaries in very dark-primaried gulls. Initial field observations suggested that gulls could be sorted into groups by their primary feather pigmentation. As I inspected the primaries at close range in collected or captured specimens, I began to classify the patterns into categories.

This combination of amount and pattern of melanin deposition was used to construct a wing hybrid index (HI). The index ranged from 1 to 6. The range of the index included typical glaucescens, with primary tips the same shade of grey as the mantle (Munsell N6; a score of 1 on the hybrid index) and typical argentatus, with primaries of extensive black pigment (Munsell N2; an HI of 6) (Fig. 15).

When unusual gulls were trapped in the Cordova dump, this classification was revised. These birds had primaries one shade lighter than the mantle, as well as light-colored irides, and often had slightly, although not statistically larger body measurements than other populations (Tables 4, 5). The wing hybrid index was modified to account for this variation, with the unusually light-primaried gulls given a score of 0 on the index. The revised wing hybrid index for 174 gulls from populations between Glacier Bay and Lake Louise is presented in Table 10.

The mean hybrid index of the Cordova population was the lightest of the groups sampled, due to the presence of three light-primaried gulls (Table 10). Another gull with primaries lighter than the mantle was collected from Egg Island, and the range of the index for Egg Island includes this individual. Egg Island has the greatest upward range (to 4) of colonies where "pure" argentatus is absent. The means of the hybrid indices constructed for Cordova, Egg Island, Haenke Island, Copper Sands (S), and Strawberry Reef are grouped around the score of 2, i.e., the populations showed slight but noticeable darkening of the distal portions of the primaries. The hybrid indices for these colonies are within one standard deviation of each other. No colonies studied on this section of the Alaskan coastline exhibited a monomorphic, typically *glaucescens* characteristic of primaries the same shade as the mantle. Such colonies are found in the Aleutians (Williamson, pers. comm.; Strang, 1977).

The complete range of primary feather pigmentation, including forms most like *glaucescens* and *argentatus*, along with four intermediate types, is found in the gull colony at Dry Bay (Table 10). The means of the hybrid indices constructed for Dry Bay and North Marble are close to the middle of the range, with large standard deviations, reflecting the presence of many intermediate types. Gulls scoring 6 on the index, with black primaries, and melanin extending up the shafts of the three outer primaries, are present in the Dry Bay, North Marble, and Lake Louise populations. The means of the hybrid indices for Dry Bay and North Marble are beyond the standard deviations of all other colonies except Lake Louise-, but are within one standard deviation of each other. Gulls at Lake Louise, the darkest population examined, all scored 6 on the index

Inspection of Table 0 indicates that a very highly significant ($p< .001$) distribution exists for wing hybrid indices in *Larus* colonies in southern Alaska, including the complete spectrum of variation between the parental types of *argentatus* and *glaucescens*. The observed distribution of primary -feather pigmentation includes

Table 10. Hybrid Index of Primary Feather Pigmentation for *Larus* Colonies in Southern Alaska

Colony	Mean	Range	Standard Deviation
Cordova	1,58	0.0-3.0	0.87
Egg Island	1.91	0.0-4.0	0.69
Haenke Island	1.95	1.0-3.5	0.83
Copper Sands (S)	2.03	1.0-3.0	0.67
Strawberry Reef	2.20	1.0-3.0	0.54
Dry Bay	3.10	1.0-6.0	1.56
North Marble	4.12	3.0-6.0	1.32
Lake Louise	6.00	6.0-6.0	0.00

Analysis of Variance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-ratio
Between Groups	7	88.0957	12.5851	13.130 *
Within Groups	166	159.1055	0.9585	
Total	173	247.2011		

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

primaries lighter than the mantle, primaries the same shade as the mantle, primaries of various shades of grey, and primaries of extensive black pigment. Since the F-ratio for the wing hybrid indices was very highly significant, the data were explored further using Duncan's Multiple Range Test. The results of this test are presented in Tables 11 and 12. The Cordova, Egg Island, Haenke Island, Copper Sands (S), and Strawberry Reef populations are coastal groups most like _glaucescens_. However, the mean wing hybrid index becomes progressively darker (HI 1.59 - 2.20) along a northwest to southeast axis. These populations are included in a homogeneous subset in this test, with no significant differences at either $p < .05$ or $p < .01$ level of significance (Tables 11, 12). The wing hybrid indices constructed for Dry Bay, North Marble, and Lake Louise are significantly different from each other and from the remaining colonies at the $p < .05$ level. However, at the $p < .01$ level, the colonies of Dry Bay and North Marble form a hybrid subset, while North Marble and Lake Louise are grouped in an _argentatus-like_ subset. A genetic bridge can therefore be postulated, connecting coastal _glaucescens_ with interior _argentatus_ through hybrid colonies at the heads of fjords and bays (e<g., North Marble and Dry Bay) in southern Alaska.

In summary, the primary feather pigmentation of 174 gulls in southern Alaska was analyzed using a wing hybrid index, Individual gulls within the study area are highly variable, and the variation includes primaries lighter than the mantle with no observable pattern of melanin deposition, to a distinctly delimited and extensive

Table 11. Ranked Means for the Wing Hybrid Index for *Larus* Colonies in Southern Alaska

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

Homogeneous 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). Underlined numbers indicate there is no significant difference between the means.

Subset 1 (subterminal primaries slightly darker than mantle)

Group	Cordova	Egg Island	Haenke Island	Copper Sands (S)	Strawberry Reef
Mean	1.5870	1.9107	1.9500	2.0313	2.2000

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

Group	Dry Bay
Mean	3.1053

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

Group	North Marble
Mean	4.1250

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

Group	Lake Louise
Mean	6.000

Table 12. Ranked Means for Wing Hybrid Indices for *Larus* Colonies in Southern Alaska

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

Homogeneous 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). Underlined numbers indicate there is no significant difference between the means.

Subset 1 (subterminal primaries slightly darker than mantle)

Group	Cordova	Egg Island	Haenke Island	Copper Sands (S)	Strawberry Reef
Mean	1.5870	1.9107	1.9500	2.0313	2.2000

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

Group	Dry Bay	North Marble
Mean	3.1053	4.1250

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

Group	North Marble	Lake Louise
Mean	4.1250	6.000

black pattern including much of the outermost primaries. The complete range of variation in primary feather pigmentation between *glaucescens* and *argentatus* types is found in the colony at Dry Bay. Some gulls in the Cordova area show primaries lighter than the mantle. Mean wing hybrid indices gradually increase from coastal populations most like *glaucescens* (HI 1.59), through intermediate populations (HI 3.1 - 4.1) in fjords and bays, to an interior population of *argentatus* (I-II 6) on a freshwater lake.

The next most obvious character which differed between individual gulls and by populations in southern Alaska was eye color. Since iris pigmentation may serve as an isolating mechanism between gull populations in other areas, the following analysis of iris pigmentation seeks to demonstrate whether eye color could serve as an isolating mechanism in southern Alaska.

III. Iris Pigmentation

Iris color has been suggested as an important morphological character which exerts its effect during pair formation and copulation in gulls (Smith, 1966b). Differences in contrast afforded by eye color against the white head may function as an isolating mechanism in mate selection, e.g., in species recognition. I sought to determine, with this background in mind, whether the variation and distribution of iris color would function as a factor in species recognition between the light-eyed *argentatus* and the dark-eyed *glaucescens* in the southern Alaskan study area.

Iris color was analyzed by four main methods. First, the distribution of colors was determined by computation of a hybrid index based upon broad categories equivalent to the mid-values of Munsell hues. Second, an analysis of variance was conducted on the iris color data to test for the significance of the observed distribution. Since the resulting F-ratio was very highly significant, the data were further analyzed using Duncan's Multiple Range Test. Third, iris color was examined by qualitative comparison of the percentages of the individual Munsell categories of hue, value, and chroma. Fourth, the Munsell parameters of iris hue, value, and chroma were combined and the resulting detailed frequencies of the complete notation were analyzed qualitatively. Finally, the possible linkage of iris color with primary feather pigmentation was tested by an analysis of variance, crosstabulation, and Chi-square value.

A. Index of the Broad Categories of Iris Color

The results of the index constructed for the broad categories of iris color are presented in Table 13. The range of iris coloration within the southern Alaskan study area includes very dark brown (HI 4), dark brown (HI 5), brown (HI 6), light brown (HI 7), light yellow (HI 8), and bright yellow (HI 9). The Haenke Island population had the darkest index (6.30), the least range (6 - 7), and the smallest standard deviation (other than the monomorphic Lake Louise population), reflecting a relatively uniform population of coastal *glaucescens*-like types. Egg Island had the greatest range, extending from very dark brown (HI 4) to light yellow (HI 8). North Marble had the greatest standard deviation, reflecting a mixture of iris colors in the population. All gulls observed at Lake Louise had yellow irides (HI 9). Light brown (H1 ?) was the most frequent mean eye color, and occurred in coastal populations.

Table 13. Hybrid Index of Broad Categories of Iris Color for *Larus* Colonies in Southern Alaska

Colony	Mean	Color	Range	Standard Deviation
Haenke Island	6.30	brown	6 - 7	0.48
Egg Island	6.86	light brown	4 - 8	0.98
Strawberry Reef	7.08	light brown	6 - 8	0.95
Copper Sands (S)	7.12	light brown	6 - 8	0.96
North Marble	7.25	light brown	6 - 9	1.50
Cordova	7.26	light brown	6 - 9	0.81
Dry Bay	7.79	light yellow	6 - 9	0.81
Lake Louise	9.00	yellow	9 - 9	0.00

Analysis of Variance

Source	Degrees of Freedom	sum of Squares	Mean Squares	F-ratio
Between Groups	7	34.7799	4.9698	6.062 *
Within Groups	166	136,0477	0.8196	
Total	173	170.8276	0.8196	

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

B. Ranked Means of Eye Color Categories

Since the F-ratio for the observed distribution of iris color was very highly significant ($F = 6.062$, 173 d.f., $p < .001$), the data were further analyzed using Duncan's Multiple Range Test for subsets of ranked means. Results of this test are presented in Table 14. Inspection of this Table reveals an uninterrupted continuum of the categories of iris color from populations most like *glaucescens* to populations clearly identifiable as *argentatus*. The mean of the coastal Haenke Island colony (brown irides) is connected to the mean of the interior Lake Louise colony (clear yellow irides) by a "bridge" of intermediate colonies at North Marble (light brown) and Dry Bay (light yellow) (see Subset 3, Table 14). The Cordova population falls into this same subset, suggesting a mixture of dark and light-eyed genes is present in this population. Interestingly, the mean *wing* hybrid index for Cordova was the lightest of any population examined. This finding has implications of a genetic contact between *glaucescens* and *hyperboreus* (see Discussion).

C. Munsell Parameters of Iris Color

(1) *Hue* - the notation of a color indicating its relation to a visually equally-spaced scale. The hue notation in this study is based upon three color names: Red (R), Yellow-Red (YR), and Yellow (Y).

Qualitative analysis of the frequencies of iris hue demonstrates that Haenke Island, a geographically rather isolated colony, is most different from other populations, with the highest frequency of 7.5 YR (a brown hue) (Table 14; Fig. 16). Strawberry Reef, Copper Sands (S), and Egg Island, neighboring colonies on the Copper River Delta, have

Table 14. Ranked Means for the Broad Categories of Eye Color for *Larus* Colonies in Southern Alaska

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

Homogeneous 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). Underlined numbers indicate there is no significant difference between the means.

Subset 1 (brown - light brown)

Group	Haenke Island	Egg Island	Strawberry Reef	Copper Sands (S)	North Marble
Mean	6.30	6.86	7.08	7.12	7.25

Subset 2 (light brown)

Group	Egg Island	Strawberry Reef	Copper Sands (S)	North Marble	Cordova
Mean	6.86	7.08	7.12	7.25	7.26

Subset 3 (light brown - light yellow)

Group	North Marble	Cordova	Dry Bay
Mean	7.25	7.26	7.79

Subset 4 (light yellow - briget yellow)

Group	Dry Bay	Lake Louise
Mean	7.79	9.00

strikingly similar frequencies, with distributions of 7.5 YR (brown), 10 YR (light brown), and 2.5 Y (light yellow). The means of iris colors for these three colonies are also closely grouped around 7 (light brown) on the index (Table 14). The distribution of iris hues in the Cordova population, with high percentages of 10 YR and 2.5 Y, is quite different from that of the Capper River Delta populations, although the means of the color indices are statistically similar (Fig. 16; Table 14). The North Marble and Dry Bay populations both exhibit strong yellow hues (5 Y), which are absent in other groups except Lake Louise (Fig. 16). North Marble, compared to Dry Bay, has a higher percentage of 7.5 YR, although the means of the broad categories of eye color are statistically similar. Dry Bay, compared to all other colonies, has the highest percentage of 2.5 Y, and the lowest percentage of 7.5 YR. Lake Louise has the highest percentage of 5 Y (Fig. 16). The means of the iris color indices for Dry Bay and Lake Louise were not statistically different (Table 14).

(2) Value - the notation of a color indicating the degree of lightness or darkness in relation to a neutral grey scale.

Comparison of the percentages of iris values again demonstrates that the Haenke Island population possesses particular characteristics, here with a high concentration (80%) of the moderately dark value 4. The value 8 on the Munsell System (quite light, indicating decreased melanin pigments) is present in the irides of the North Marble and Dry Bay populations in the southern portion or the study area, and in the Egg Island and Cordova populations in the north. The value 8 is not found in the populations of Haenke Island, Strawberry Reef, and Copper Sands (S) in the central part of the study area.

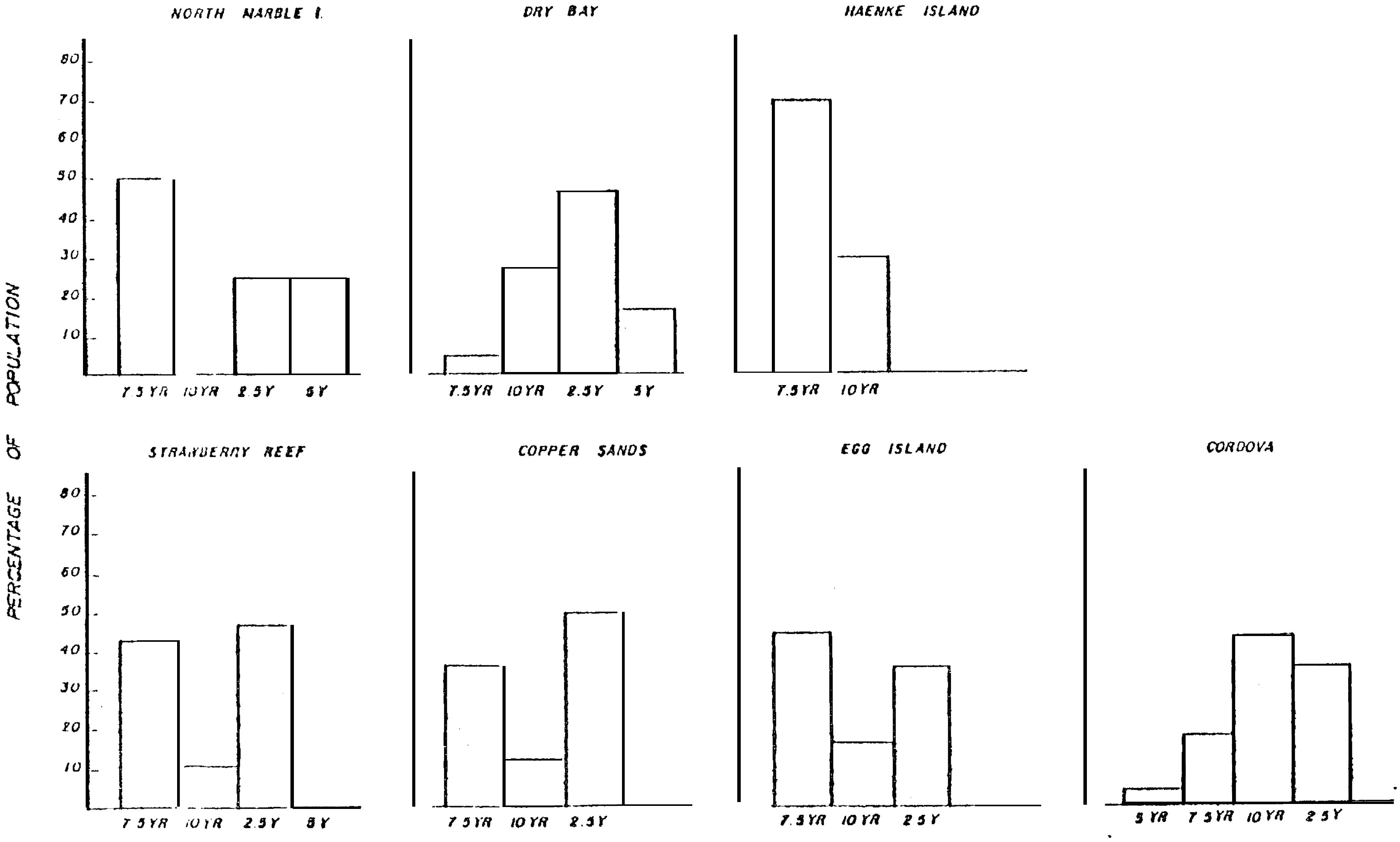


Fig. 6. IRIS HUE

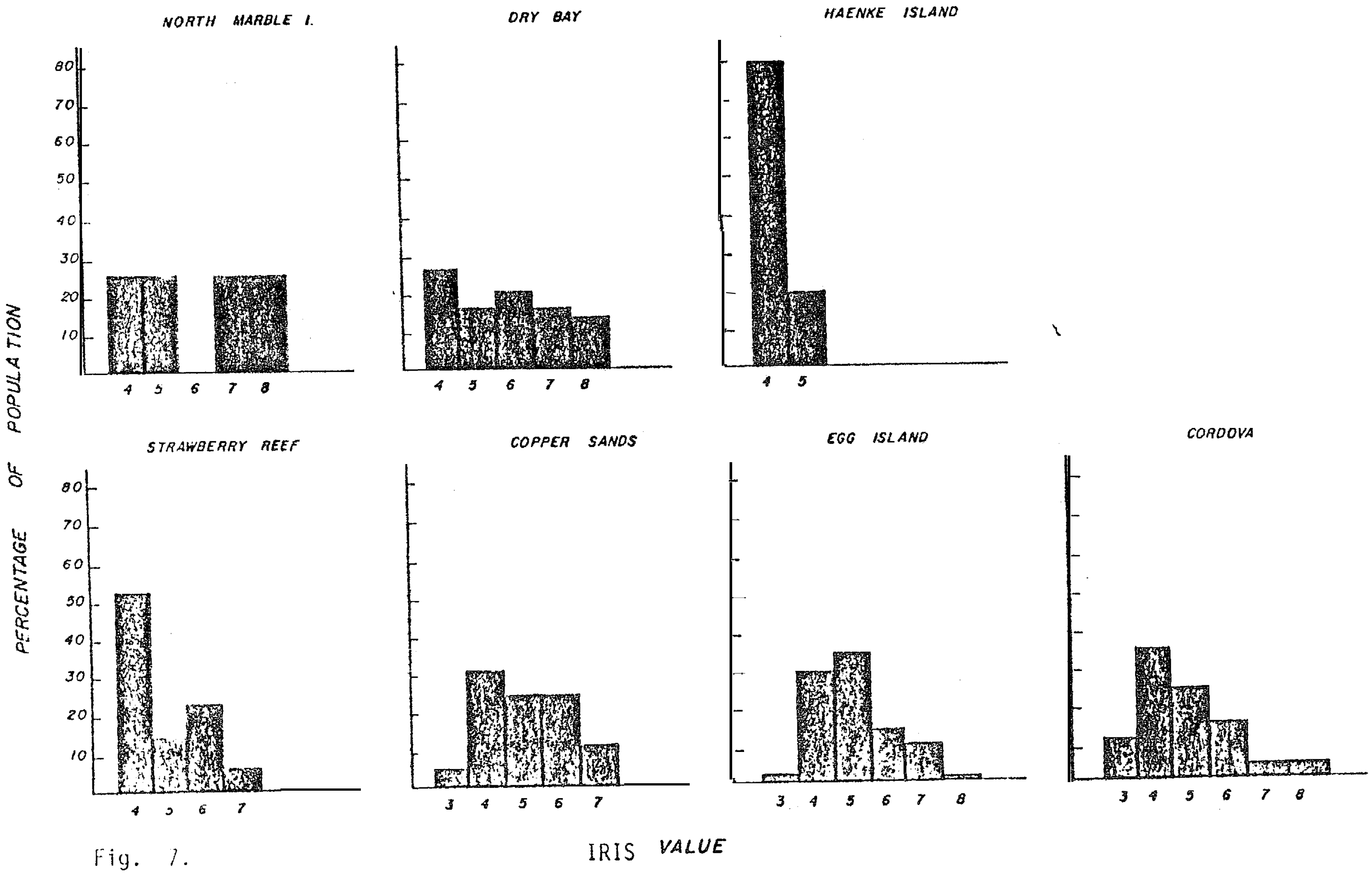

NORTH MARBLE I.
DRY BAY
HAENKE ISLAND
STRAWBERRY REEF
COPPER SANDS
EGG ISLAND
CORDOVA
PERCENTAGE OF POPULATION
80
70
60
50
40
30
20
10
4 5 6 7 8
4 5 6 7 8
4 5
4 5 6 7
3 4 5 6 7
3 4 5 6 7 8
3 4 5 6 7 8
IRIS VALUE

Fig. 7.

North Marble resembles Dry Bay in the distribution of iris values, as in many other parameters, except for a lack of the value 6, perhaps due to smaller sample size (Fig. 17). The frequency of iris values in the Strawberry Reef population, which has slightly darker primaries and longer wings than other Copper River Delta colonies, resembles that of Dry Bay, with two differences. There is a greater percentage of the dark value 4, and a complete lack of the light value 8 at Strawberry Reef.

The iris value 3 (quite dark, indicating abundant melanin pigments) is present in the Copper Sands (S), Egg Island, and Cordova populations. Interestingly, quite light values of 8 are also present at Egg Island and Cordova (see above). This somewhat paradoxical result can be explained by postulating a mixture of both light-eyed and dark-eyed genes in these populations.

(3) Chroma - 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.

All populations except Cordova show a concentration of the chroma 4 (Fig. 18). The Cordova population is quite different, with chroma rather evenly distributed among the classifications of 2, 3, and 4, with a smaller amount of chroma 6. Haenke Island shows relationship to other colonies with a high frequency of chroma 4 (but not through frequencies of hues and values). The distribution of iris chroma at North Marble is bimodal, with strong concentrations at the classifications of 4 and 8. The Dry Bay distribution is qualitatively different from that of North Marble, in comparison to the rather similar distributions of iris hues and values. (These two colonies are also related in the broad index of

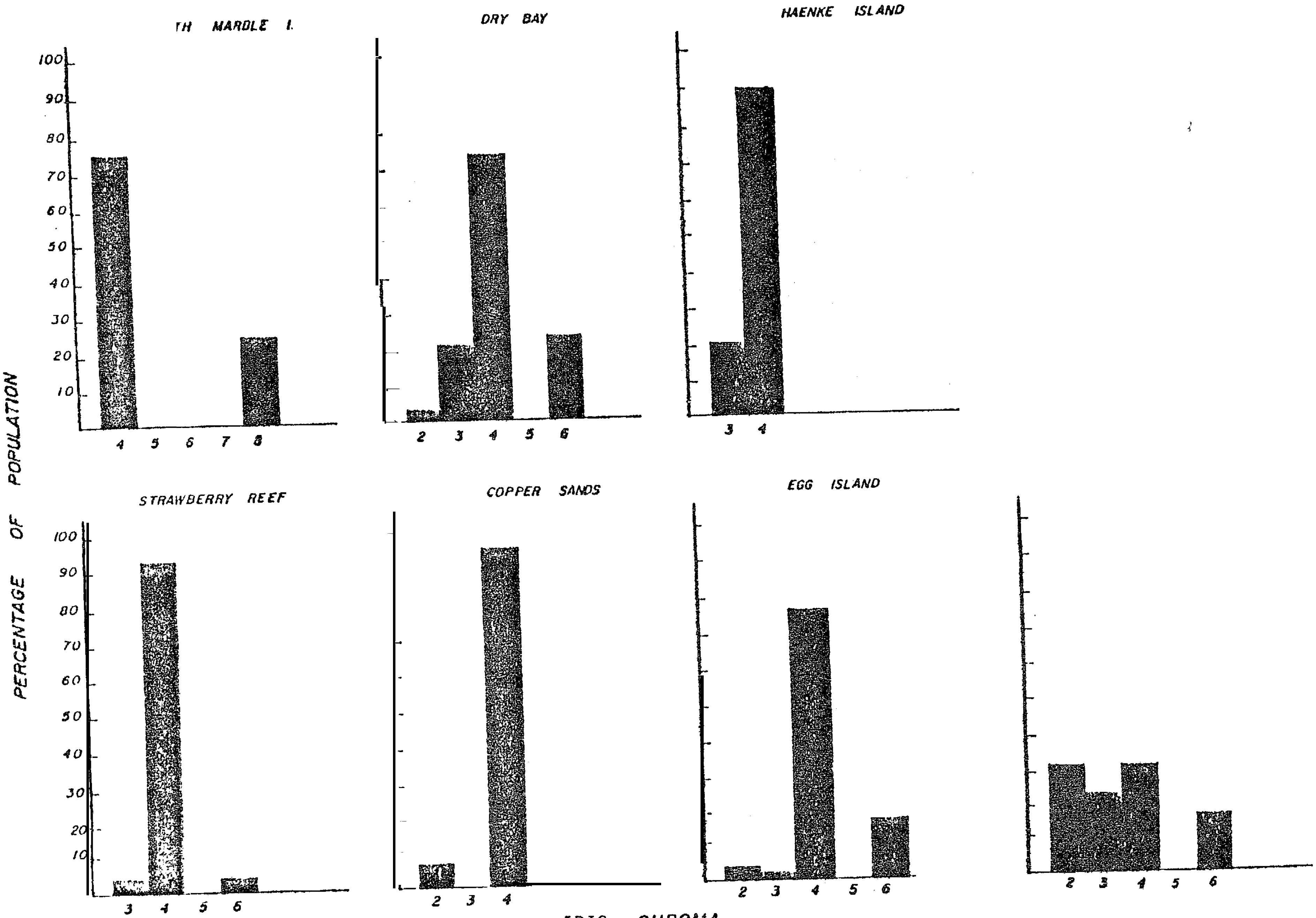

TH MARBLE I.
DRY BAY
HAENKE ISLAND
STRAWBERRY REEF
COPPER SANDS
EGG ISLAND
PERCENTAGE OF POPULATION
100
90
80
70
60
50
40
30
20
10
4
5
6
7
8
2
3
4
5
6
3
4
3
4
5
6
2
3
4
2
3
4
5
6
2
3
4
5
6
IRIS CHROMA

Fig. 18.

eye color, and the wing hybrid index.) Less intensely saturated chroma (2, 3) are present in the Dry Bay population, as well as an intermediate chroma of 6.

IV. Iris Hue, Value, and Chroma Combined

Hue, value, and chroma are the parameters which make up a complete color in the Munsell system. The iris colors of similar base hues are graphed in proximity to each other in Figs. 19, 20, 21, 22.

The combination of iris parameters extends well into the realm of individual variation. For instance, each of four gulls collected at North Marble had different colored eyes. The distribution of the combined iris parameters for North Marble is thus related to sample size. Dry Bay has the widest distribution of the combined iris parameters; there are more kinds of eye color in this colony at the mouth of the Alsek River than in any other group examined. The breeding population at Dry Bay is highly mixed in other characters such as primary feather pigmentation and orbital ring coloration. The Cordova and Egg Island populations also show a wide distribution of combined iris parameters.

Copper Sands (S) and Strawberry Reef, neighboring colonies on the Copper River Delta, have the most similar distribution of combined iris parameters. These colonies also share similar indices of primary feather pigmentation, similar distributions of the individual Munsell parameters of hue and chroma, and significant enlargement of bill depth.

In summary, qualitative comparisons of the iris frequencies of the individual Munsell categories of hue, value, and chroma, and the combinations thereof, reveal subtle aspects of relationships not apparent

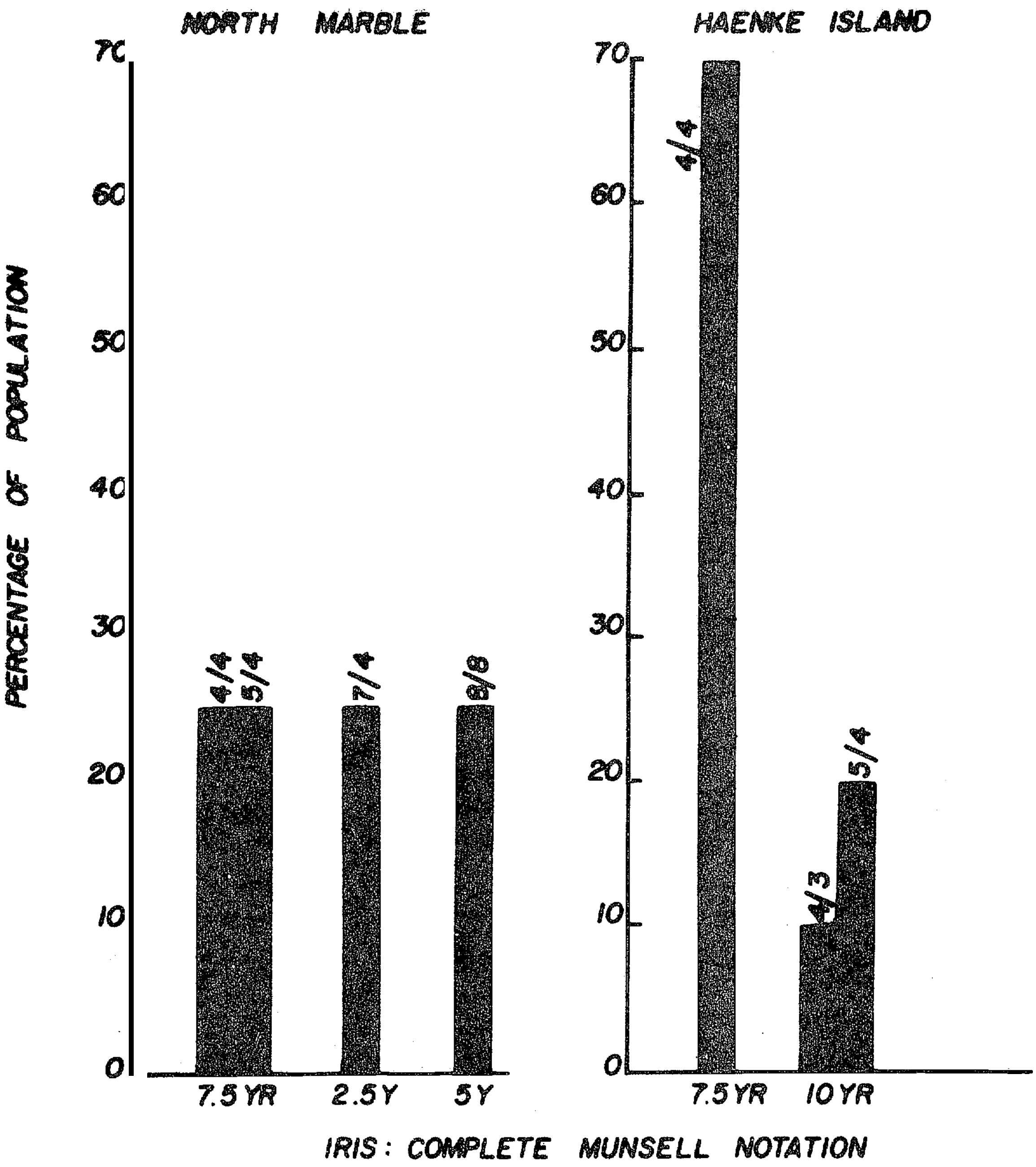
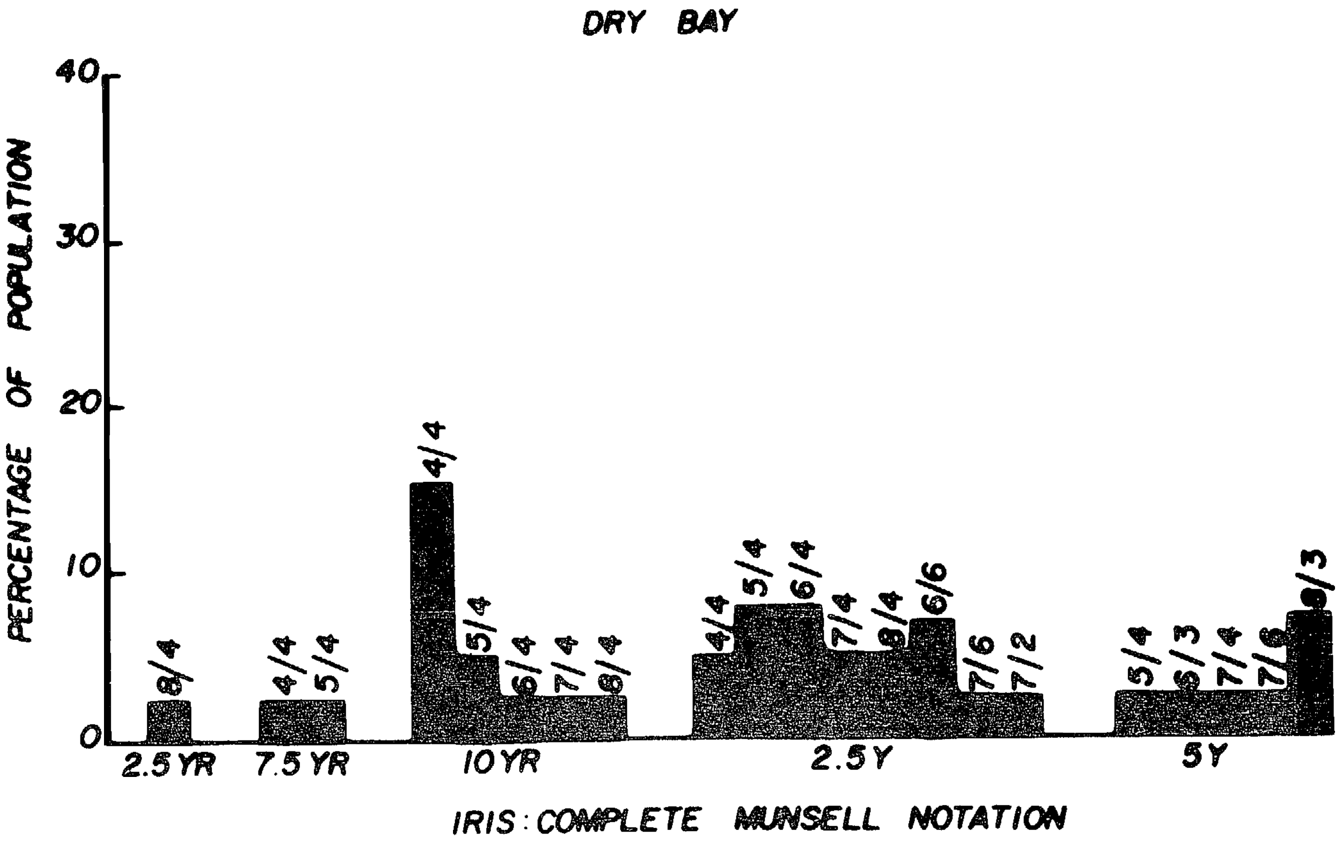

NORTH MARBLE
HAENKE ISLAND
PERCENTAGE OF POPULATION
0
10
20
30
40
50
60
70
4/4
5/4
7/4
8/8
7.5 YR
2.5 Y
5 Y
4/4
4/3
5/4
7.5 YR
10 YR
IRIS: COMPLETE MUNSELL NOTATION

Fig. 19.

Fig. 20.


DRY BAY
PERCENTAGE OF POPULATION
40
30
20
10
0
8/4
4/4
5/4
4/4
5/4
6/4
7/4
8/4
4/4
5/4
6/4
7/4
8/4
6/6
7/6
7/2
5/4
6/3
7/4
7/6
8/3
2.5YR
7.5YR
10YR
2.5Y
5Y
IRIS: COMPLETE MUNSELL NOTATION

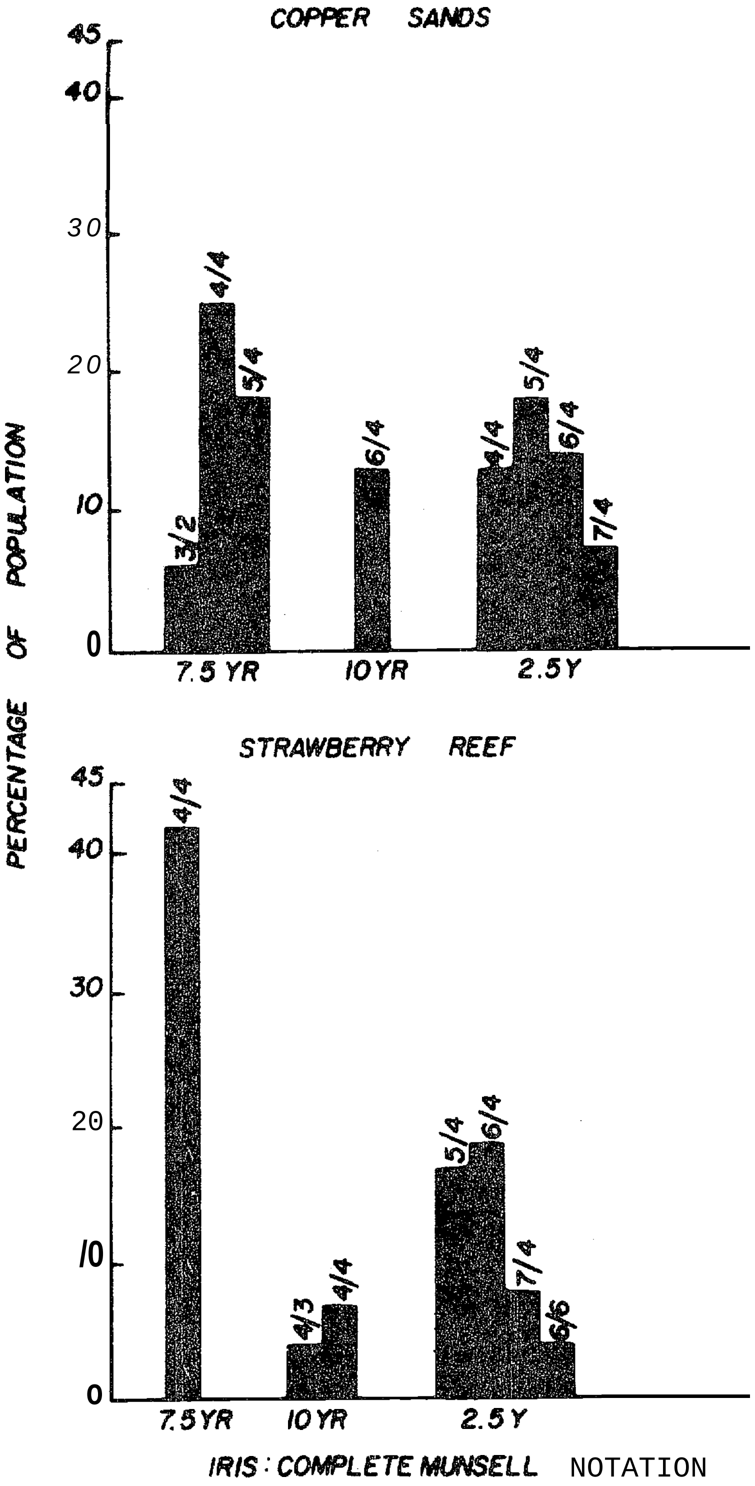

COPPER SANDS
45
40
30
20
10
0
3/2
4/4
5/4
6/4
4/4
5/4
6/4
7/4
7.5 YR
10 YR
2.5 Y
PERCENTAGE OF POPULATION
STRAWBERRY REEF
45
40
30
20
10
0
4/4
4/3
4/4
5/4
6/4
7/4
6/6
7.5 YR
10 YR
2.5 Y
IRIS : COMPLETE MUNSELL NOTATION

Fig. 21.

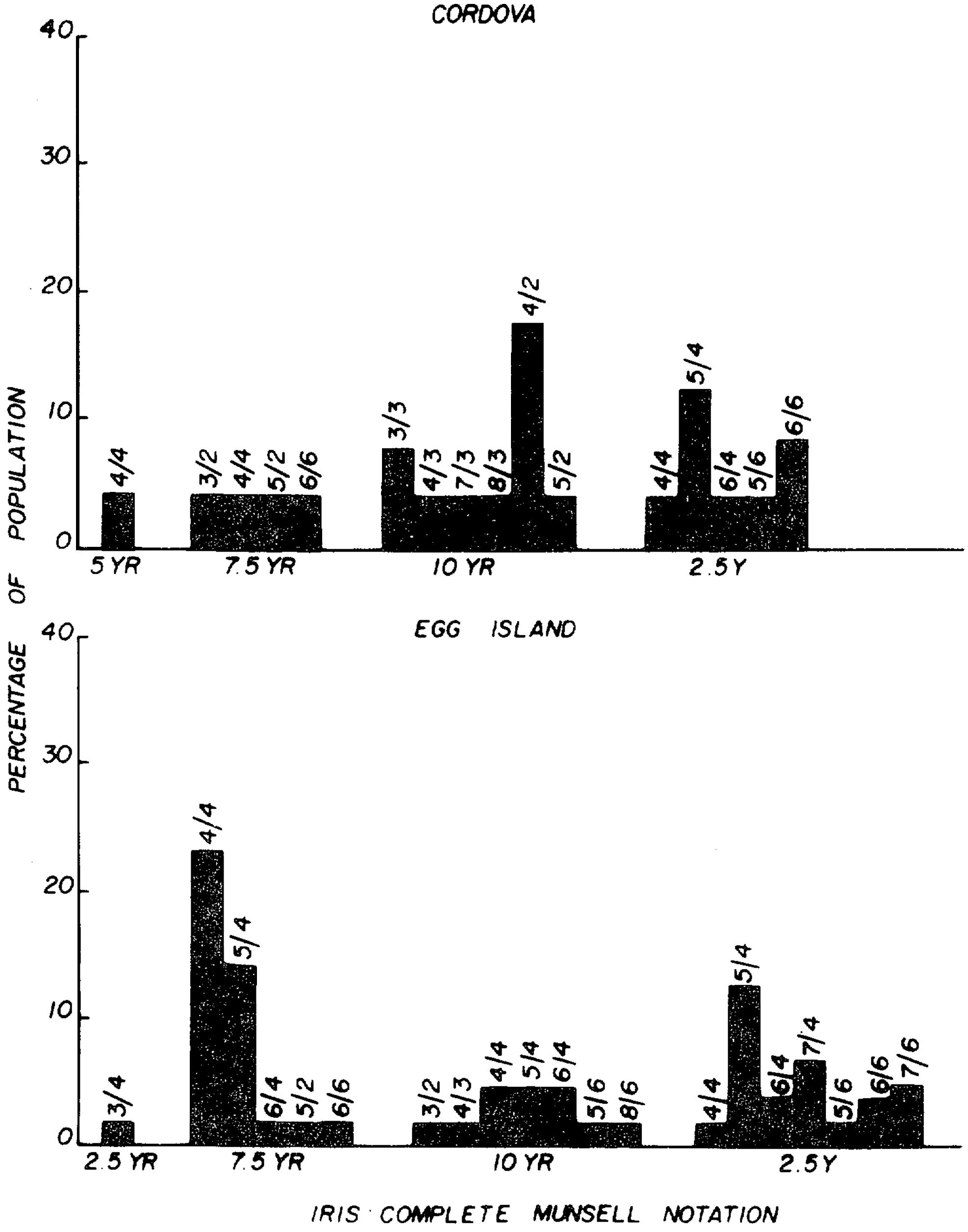

CORDOVA
40
30
20
10
0
4/4
3/2
4/4
5/2
6/6
3/3
4/3
7/3
8/3
4/2
5/2
4/4
5/4
6/4
5/6
6/6
5 YR
7.5 YR
10 YR
2.5 Y
PERCENTAGE OF POPULATION
EGG ISLAND
40
30
20
10
0
3/4
4/4
5/4
6/4
5/2
6/6
3/2
4/3
4/4
5/4
6/4
5/6
8/6
4/4
5/4
6/4
7/4
5/6
6/6
7/6
2.5 YR
7.5 YR
10 YR
2.5 Y
IRIS COMPLETE MUNSELL NOTATION

Fig. 22.

in the comparison of means of the broad categories of eye color. Neighboring colonies on the Copper River Delta have strikingly" similar distributions cf iris hues. The Cordova gull population is qualitatively different in distribution of iris hues from the Copper River Delta populations. North Marble and Dry Bay share similar, although not identical distributions of iris hues and values. Haenke Island has a particular pattern of both hues and values, but shares a concentration of chroma with other populations. Strawberry Reef resembles Dry Bay in the distribution of iris values. (Strawberry Reef gulls also have slightly, although not statistically, longer and darker wings than other Copper River Delta populations.)

All populations except Cordova show a concentration of the chroma 4. (Cordova gulls also have the lightest mean wing index, and slightly, although not statistically larger body measurements.) Cordova, Egg Island, and Dry Bay populations have a wide distribution of the combined iris parameters, indicating that gulls of different eye colors are present in these populations. Copper Sands (S) and Strawberry Reef are related in many morphological parameters, including iris color, although Strawberry Reef shows an additional affinity to a population like that inhabiting Dry Bay to the southeast.

V. Linkage of Iris Color to Primary Feather Pigmentation

To test whether iris color could be linked to primary feather pigmentation, i formulated a null hypothesis that there was no linkage between these characters. I then conducted an analysis of variance on the observed distribution of wing hybrid indices (0.0 - 6.0) as compared to the distribution of six categories of iris hue, using

Table 15. Analysis of Variance of Wing Hybrid Index by Iris Hue

Source of Variation	Sum of Squares	d.f.	Mean Square	F-ratio
Main Effects	38.605	4	9.651	7.819 *
Iris Hue	38.605	4	9.651	7.819 *
Explained	38.605	4	9.651	7.819 *
Residual	208.597	169	1,234	
Total	247.201	173	1.429	

(n = 174) * very highly significant (p <.001)

Crosstabulation of Iris hue by Wing Hybrid Index: Chi-square = 81.4322 with 36 degrees of freedom: very highly significant association of Wing Hybrid Index by Iris Hue.

data from 174 gulls. The results of this test are presented in Table 15. Inspection of this table reveals a very highly significant F-ratio. A further crosstabulation of iris hue by wing hybrid index produced a value of Chi-square (81.4322, 36 d.f., $p < .001$), indicating a very highly significant association of wing hybrid index with iris hue. I therefore rejected the null hypothesis.

Iris color is highly linked with primary feather pigmentation in gull populations between Lake Louise and Glacier Bay in southern Alaska. Light-eyed gulls tend to have dark primaries, dark-eyed gulls tend to have light primaries, and gulls with intermediate amounts of melanin deposition in the primaries have irides in various intermediate shades. There are some exceptions to this rule, notably around Cordova, where gulls may have both light eyes and primaries distinctly lighter than those found elsewhere (see Discussion).

The variation arid distribution of iris color, although apparently linked with primary feather pigmentation, seems unlikely to function in species recognition between the light-eyed _argentatus_ and the dark-eyed _glaucescens_ in southern Alaska, since the two forms are linked by a complete range of intermediates.

VI. 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 between certain species.

Larus argentatus "pure types" in southern Alaska have yellow orbital rings of the hues 2.5 Y - 5 Y. In contrast, other argentatus populations may have orange eye-rings (Smith, 1966b). Larus glaucescens "pure types" have dark pink or vinaceous orbital rings of hue 5 R. This section of the study examines the variation, distribution, and possible function of orbital ring pigmentation in southern Alaskan gulls.

Orbital ring pigmentation was analyzed by similar methods to those used in the analysis of eye color. A hybrid index was computed, based on the orbital ring hues of 174 gulls. The orbital rings in some cases were made up of two to three hues. In such cases, the indices for the individual hues were summed, giving a composite index for the orbital ring. An analysis of variance was conducted for the significance of the observed variation. An analysis was then conducted for subsets of ranked means, using Duncan's Multiple Range Test. The qualitative frequencies of the orbital ring hues were compared by colony. Finally, a crosstabulation of orbital ring hues by colony identification number resulted in a Chi-square value of the significance of the distribution.

A. Hybrid Index of Orbital Ring Pigmentation

(1) Broad Index

The results of the hybrid index of orbital ring pigmentation for gull colonies in southern Alaska are presented in Table 16. Note that the extreme pigments are dark pink and bright yellow, but six intermediate hues exist, and more than one hue may occur in an

Table 16.

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

Colony	Mean	Munsel 1 Hue	Color
Haenke Island	1.30	5 R	dark pink
Cordova	1.83	7.5 R	pink
North Marble	2.75	10 R	light pink
Egg Island	3,66	2.5 YR	yellowish pink
Copper Sands	4.00	2.5 YR	yellowish pink
Dry Bay	4:36	2.5 YR	yellowish pink
Strawberry Reef	4.60	5 YR	pinkish yellow
Lake Louise	8.50	2.5 Y	light yellow
		5 Y	bright yellow

Analysis of Variance

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-ratio
Between Groups	7	226.1396	32,3057	4.875 *
Within Groups	166	1100.0500	6.6268	
Total	173	1326.1897		

* very highly significant (p < .001). Crosstabulation of the Index of Orbital Ring Pigmentation by colony: Chi-square = 151.021 with 77 degrees of freedom; very highly significant association of index of Orbital Ring Pigmentation by colony.

individual eye-ring. Each colony examined had a different mean composite orbital ring, but the extremes are connected through increasing amounts of yellow pigment.

Haenke Island again represents a coastal population most like parental glaucescens, with orbital rings of 5 R, dark pink (Table 16). North Marble scored relatively light on the index, with a mean of 10 R, light pink, in contrast to other characters showing hybrid influence. The Cordova population mean was 1.83, closest to moderate pink values. Egg Island. Copper Sands (S), and Dry Bay were grouped around 4.00 on the index, with intermediate yellowish pink orbital rings. The Strawberry Reef population had slightly more yellow present in the orbital rings than other Copper River Delta populations, with an index of 4.60. The index jumped sharply between Strawberry Reef and Lake Louise (4.60 - 8.50). Lake Louise represents the population most like parental argentatus, with orbital rings of hues 2.5 Y - 5 Y.

Inspection of Table 16 shows that a very highly significant F-value is produced by the Analysis of Variance of the hybrid indices of orbital ring pigmentation. An additional crosstabulation of these indices by colony results in a Chi-square value of 151.021, 77 d.f., $p < .001$; a very highly significant association. Each population, therefore, had orbital rings unlike those of other populations. Since the F-ratio for the distribution of orbital ring pigmentation was very highly significant, the means were ranked using Duncan's Multiple Range Test. Three subsets of ranked means were produced at the $p < .05$ level (Table 17). Most populations (five) fall into the intermediate subset 2, with orbital rings ranging from light pink to yellowish pink. Populations from Copper Sands, Dry Bay, and Strawberry Reef are most

Table 17.

Ranked Means for Orbital Ring Indices for *Larus* Colonies in Southern Alaska

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

Homogeneous 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). Underlined numbers indicate there is no significant difference between the means,

Subset 1 (dark pink - light pink)

Group	Haenke Island	Cordova	North Marble
Mean	1.30	1.83	2.75

Subset 2 (light pink - yellowish pink)

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

Subset 3 (light yellow - bright yellow)

Group	Lake Louise
Mean	8.50

---

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

nearly intermediate between the extremes of dark pink and bright yellow orbital rings. At the $p < .01$ level, Dry Bay joins Subset '2, thereby forming a statistical continuum of orbital ring pigmentation.

(2) Solo Hues

Some orbital rings were uniformly pigmented, with the color evenly distributed on all portions of the eyelid. These will be referred to as "solo hues." Orbital rings with solo hues occurred in the North Marble, Dry Bay, Haenke Island, and Cordova populations (Figs. 23, 24, 25). Orbital rings with solo hues only were found in North Marble and Haenke Island populations.

Dark pink (5 R) was the dominant solo hue in the North Marble, Haenke Island, Dry Bay, Egg Island, and Cordova populations (Fig. 23). Yellowish pink (2.5 YR) was the second most important solo hue (after 5 R) occurring in the Dry Bay, Haenke Island, and Egg Island populations. The hue 5 R (without 2.5 YR as the second most important hue) was found at North Marble and Cordova. The North Marble population showed the maximum number of solo hues, ranging from 5 R (dark pink) to 2.5 Y (light yellow). The Dry Bay population contained every possible orbital ring hue between these two extremes (Fig. 23). Gulls with black primaries at Dry Bay had orbital ring hues including 2.5 YR (yellowish pink), 5 YR (pinkish yellow), and 10 YR (light pinkish yellow). Gulls with similar indices of primary feather pigmentation (HI 6) at Lake Louise had orbital ring hues of 2.5 Y (light yellow) to 5 Y (bright yellow).

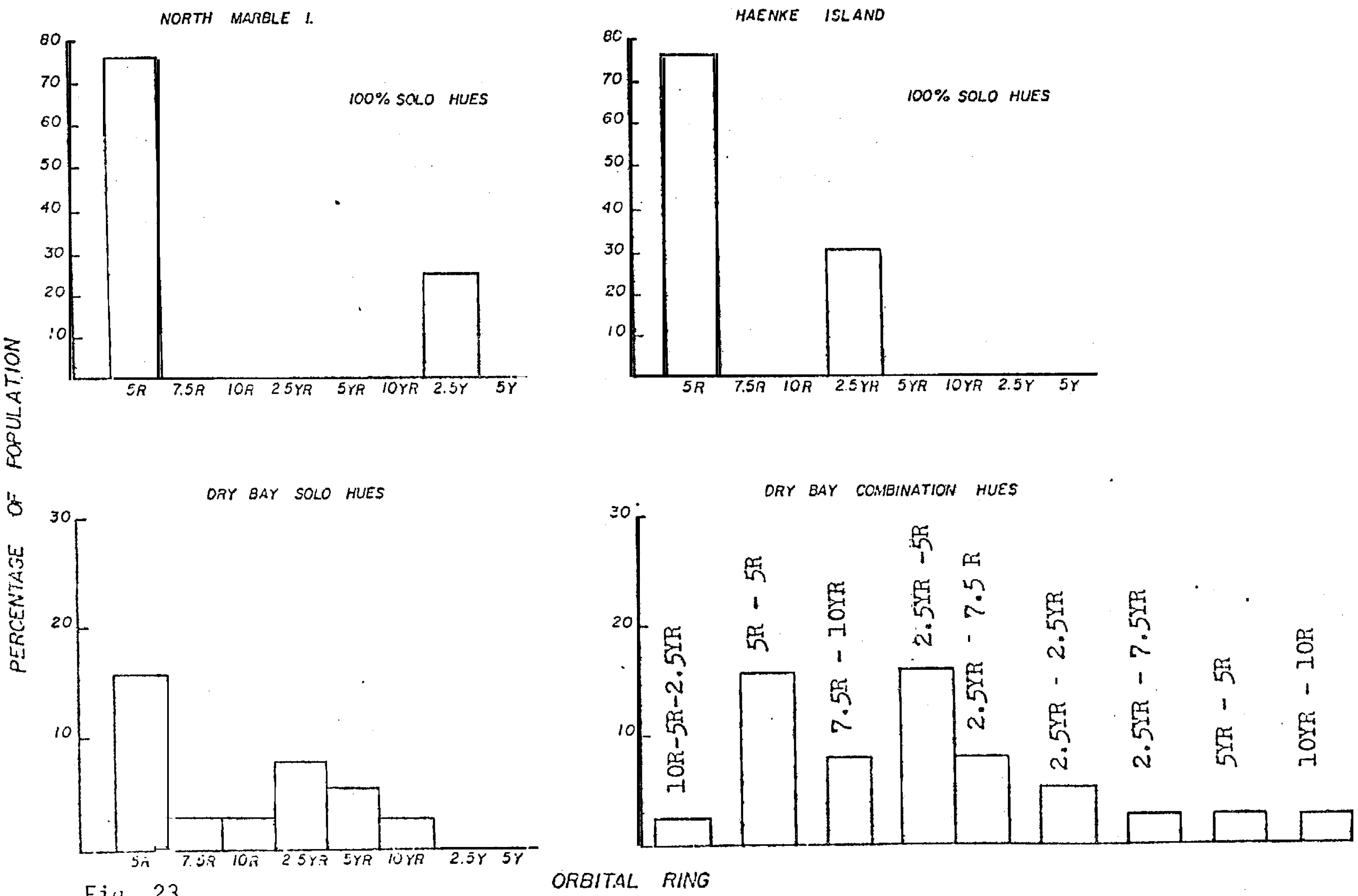

NORTH MARBLE I.
100% SOLO HUES
80
70
60
50
40
30
20
10
5R
7.5R
10R
2.5YR
5YR
10YR
2.5Y
5Y
HAENKE ISLAND
100% SOLO HUES
80
70
60
50
40
30
20
10
5R
7.5R
10R
2.5YR
5YR
10YR
2.5Y
5Y
PERCENTAGE OF POPULATION
DRY BAY SOLO HUES
30
20
10
5R
7.5R
10R
2.5YR
5YR
10YR
2.5Y
5Y
DRY BAY COMBINATION HUES
30
20
10
10R-5R-2.5YR
5R - 5R
7.5R - 10YR
2.5YR -5R
2.5YR - 7.5 R
2.5YR - 2.5YR
2.5YR - 7.5YR
5YR - 5R
10YR - 10R
ORBITAL RING

Fig. 23.

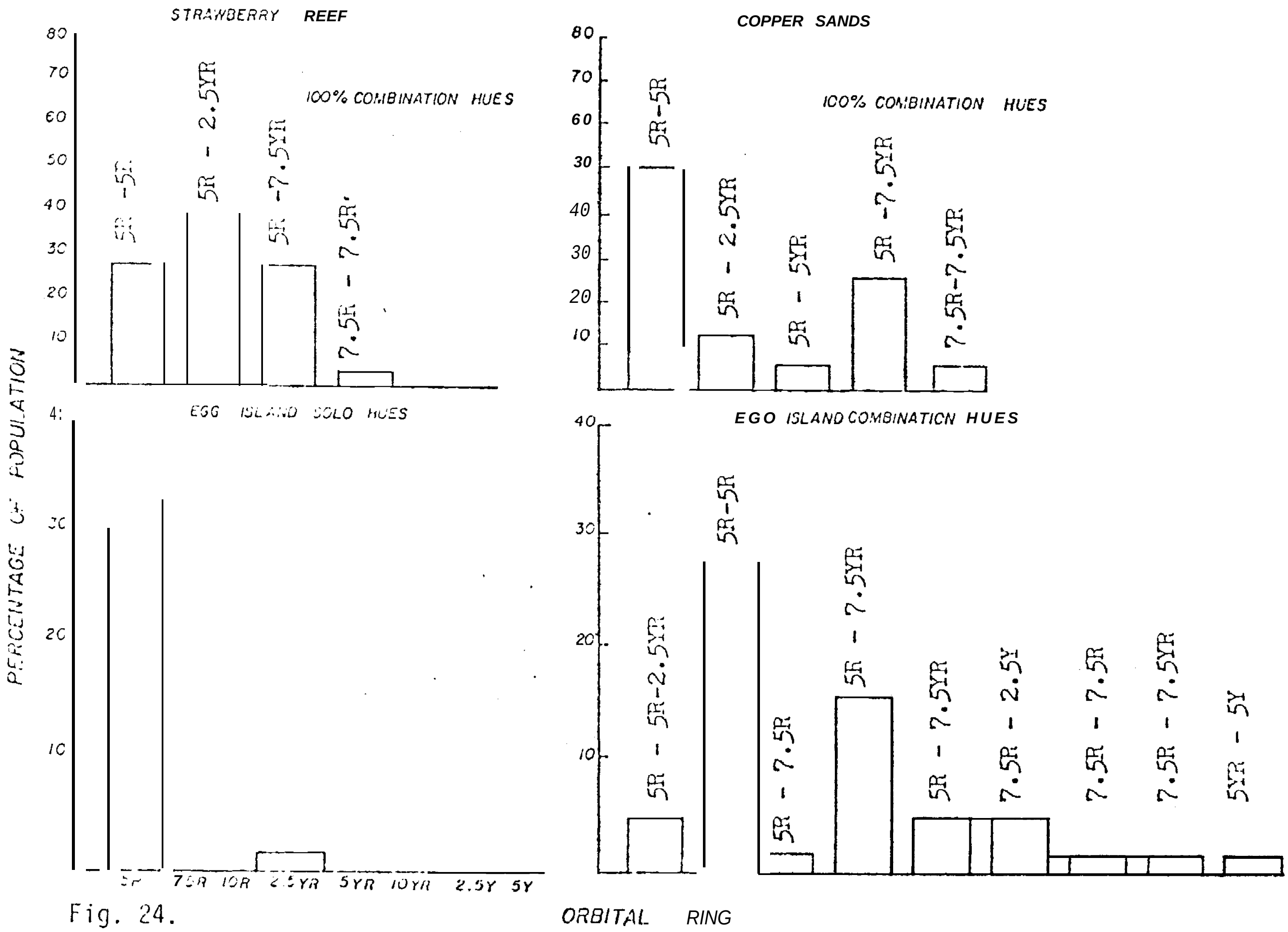

STRAWBERRY REEF
100% COMBINATION HUES
5R -5R
5R - 2.5YR
5R -7.5YR
7.5R - 7.5R
COPPER SANDS
100% COMBINATION HUES
5R-5R
5R - 2.5YR
5R - 5YR
5R -7.5YR
7.5R-7.5YR
EGG ISLAND SOLO HUES
5R
7.5R
10R
2.5YR
5YR
10YR
2.5Y
5Y
EGG ISLAND COMBINATION HUES
5R - 5R-2.5YR
5R-5R
5R - 7.5R
5R - 7.5YR
5R - 7.5YR
7.5R - 2.5Y
7.5R - 7.5R
7.5R - 7.5YR
5YR - 5Y
PERCENTAGE OF POPULATION
ORBITAL RING
80
70
60
50
40
30
20
10

Fig. 24.

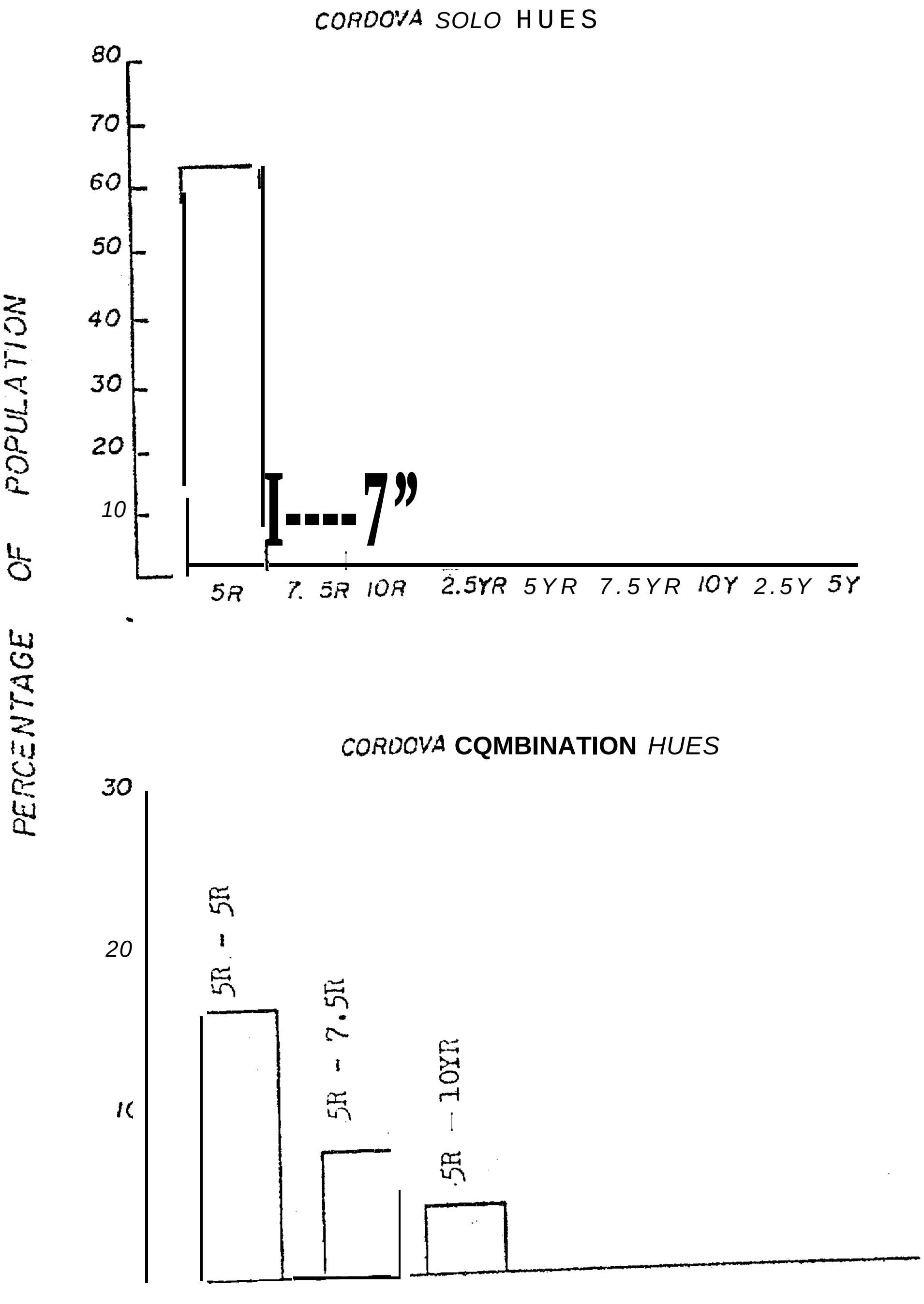

CORDOVA SOLO HUES
80
70
60
50
40
30
20
10
5R
7. 5R
10R
2.5YR
5YR
7.5YR
10Y
2.5Y
5Y
PERCENTAGE OF POPULATION
CORDOVA COMBINATION HUES
30
20
10
5R - 5R
5R - 7.5R
5R - 10YR
ORBITAL RING

Fig. 25.

(3) Combination Hues

Orbital rings with a composite index were made up of two to three hues, or “combination hues.” Orbital rings with combination hues may have similar base hues (5 Y - 5 Y), each having different value and chroma. For example, a pink eye-ring with areas of more intense reddish pigmentation occurs with a relatively high frequency in the Dry Bay, Egg Island, and Cordova gull populations (Figs. 23, 24, 25).

Only combinations of two hues occurred in the orbital rings of the Copper Sands (S) and Strawberry Reef populations, further demonstrating the close similarity of these populations (Fig. 24). An orbital ring with a pinkish hue on the upper rear portion of the eyelid, and a yellowish hue on the lower front portion, is a typical pattern in these populations. Other populations have 5 R - 2.5 YR combinations (pink with yellowish pink); or5 R - 7.5 YR combinations (pink with light pinkish yellow).

The gull populations at Egg Island and Dry Bay had individuals with a combination of three hues within a single orbital ring. An example from Dry Bay is an orbital ring of the pigmentation 10 R - 5 R - 2.5 YR (light pink, dark pink, yellowish pink). An example from Egg Island is 5 R - 5 R - 2.5 YR; this eye-ring was pink with darker pink areas on the upper rear, and yellowish pink on the lower front portion.

Egg Island had the greatest distribution of combination hues, ranging from 5 R - 5 R (pink with darker pink areas); to 5 YR - 5 Y (pinkish yellow with yellow). The 5 YR - 5 Y combination did not appear in the gull population at Dry Bay. The distribution of combination hues at Dry Bay ranged from 5 YR - 5 R (pinkish yellow to pink); to 5 R - 7.5 YR (pink to light pinkish yellow). Dry Bay had the greatest distribution of solo hues in addition to the most even distribution of combination hues.

B. Summary of Orbital Ring Pigmentation

Gulls in southern Alaska have orbital rings ranging from dark pink to bright yellow, with six intermediate hues connecting the extremes with increasing amounts of yellow pigment. Each population examined had a different composite mean orbital ring unlike those of other populations. Some orbital rings in individual gulls were uniformly pigmented, while others were composed of as many as three hues. The colony 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 in southern Alaska is unlikely, due to the spectrum of variation. However, the variability may function as a character for individual *or* population recognition.

vII. Composite Hybrid Index

Primary feather pigmentation, iris and orbital ring coloration, have been analyzed individually to discern relationships between gull populations in southern Alaska. These colorimetric characters will now be unified in a composite hybrid index in order to offer the most complete exploration of relationships between gull populations in southern Alaska.

Since the F-ratios for these individual analyses of variance were all very highly significant, it is logical that the -ratio for the composite hybrid index by colony is also very highly significant ($F = 20.614$, 172 d. f., $p < .001$). The composite hybrid index data were therefore further analyzed using Duncan's Multiple Range Test. The results of this test at the $p < .05$ level of significance are contained in Table 18.

The population with the lowest composite index, and therefore most like *glaucescens*, is from Haenke Island. The population with the highest **index**, and therefore most like *argentatus*, is from Lake Louise. Between the two extremes are four homogeneous subsets. Subset 1 contains coastal populations most like *glaucescens*. Subset 2 contains as a unit the colonies of the Copper River Delta. Subset 3 contains the hybrid colonies in bays and fjords, with individual phenotypic *argentatus* present in the populations as well as intermediates and *glaucescens*. Subset 4 contains the interior Lake Louise *argentatus* population.

The subsets of ranked means are reduced to three if the Duncan's Multiple Range Test is conducted at the $p < .01$ level of significance (Table 19). The Copper River Delta populations become unified with other populations most like *glaucescens* in Subset 1. Note that in Subset 2, the Strawberry Reef population at the east end of the Copper River Delta is included with the hybrid colonies of Dry Bay and North Marble. Subset 3 contains only the interior *argentatus* at Lake Louise, Individual gulls scoring high on the composite hybrid index, e.g., identifiable as phenotypic *argentatus*, were found at Dry Bay and

Table 18. Ranked Means for the Composite Hybrid Index for *Larus* Colonies in Southern Alaska
(Primary Feather Pigmentation + Iris + Orbital Ring)
(Duncan's New Multiple Range Test: $p < .05$ level)

Homogeneous 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). Underlined numbers indicate there is no significant difference between the means.

Subset 1 (most like *glaucescens*)

Group	Haenke Island	Cordova	Egg Island	Copper Sands
Mean	9.55	10.02	10.39	10.41

Subset 2 (Copper River Delta colonies)

Group	Egg Island	Copper Sands (S)	Strawberry Reef
Mean	10.39	10.41	11.40

Subset 3 (hybrid colonies with individual *argentatus*-types present)

Group	Dry Bay	North Marble
Mean	13.54	14.12

Subset 4 (interior *argentatus*)

Group	Lake Louise
Mean	23.5

Table 19. Ranked Means for the Composite Hybrid Index for *Larus* Colonies in Southern Alaska
(Primary Feather + Iris + Orbital Ring Pigmentation)

(Duncan's New Multiple Range Test: p <,01 level)

Homogeneous 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). Underlined numbers indicate there is no significant difference between the means.

Subset 1 (most like *glaucescens*)

Group	Haenke Island	Cordova	Egg Island	Copper Sands (S)	Strawberry Reef
Mean	9.55	10.02	10.39	10.41	11.40

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

Group	Strawberry Reef	Dry Bay	North Marble
Mean	11.40	13.54	14.12

Subset 3 (interior *argentatus*)

Group	Lake Louise
Mean	23.5

North Marble, but none were found at Strawberry Reef. However, in population parameters of primary feather pigmentation, iris and orbital ring coloration, Strawberry Reef shows argentatus influence, and is assigned at the $p < .01$ level to the category of a hybrid colony.

A geographical tendency or cline is evident with the exception of the extreme indices of Haenke Island and Lake Louise. Gull populations show increasing argentatus influence along an axis extending from the northwest to the" southeast within the study areas. Primary feathers become darker and yellow pigments increase in the irides and orbital rings of gull populations between Cordova and North Marble. North Marble is quite recently deglaciated (within the last 120 years) and was colonized thereafter. This suggests that the major source of argentatus-like genes along the North Gulf Coast of Alaska is the hybrid colony at Dry Bay, which serves as a bridge between coastal and interior Larus populations.

VIII. Analysis of Mating Patterns

L. argentatus, L. glaucescens, and adult gulls of highly variable primary feather pigmentation were observed nesting together in different habitats in Glacier Bay in 1971 (Patten and Weisbrod, 1974). These observations led to a subsequent study of mating patterns in the mixed colonies of North Marble and Dry Bay. The null hypothesis was that mating was random.

At North Marble, 162 gull pairs nesting on sloping grassy meadows were examined in 1972. The study of the pairs revealed the following: 157 apparently phenotypic glaucescens pairs, 1 "typical" argentatus paired with a "typical" glaucescens, and 3 "intermediates" paired with *glaucescens*. An intermediate is defined here as a gull not identifiable in the field as either *glaucescens* or *argentatus*, but having characteristics of both, i.e., in primary feather pigmentation and iris color. Permission was granted by Park Service officials to collect only four adult gulls at the close of the 1972 nesting season. The birds collected were the same three intermediates and the *argentatus* analyzed above.

Gull pairs at 290 nest sites were examined on North Marble in 1973. The following pairs were recorded: 276 apparent *glaucescens* pairs; 1 pair of *argentatus*; 3 *argentatus* paired with *glaucescens*; and 10 pairs of “intermediate” gulls paired with *glaucescens*. The differences between the two years were not significant ($p < .05$). The presence of species-specific pairs within the study area led to a tentative conclusion that a form of mate selection was occurring.

Mating patterns within the gull colony on flat gravel bars at Dry Bay were studied in detailduring May, 1977. The plumage and soft part colors of both parents at 112 nests were examined using a 25 x telescope and comparing them to a Munsell color chart, or in the case of primaries, a Munsell neutral value scale. The orbital ring colors, however, were beyond effective resolution of the telescope. The analysis was hence restricted to primary feather pigmentation and iris color indices (Tables 20, 21, 22).

Three statistical tests were conducted on the mating patterns of the gulls at Dry My, using the SPSS-10 CROSSTABS subroutine on the Johns Hopkins University DEC-system 10 computer. First, the index of primary feather pigmentation for each male was compared against

Table 20. 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 * 77.3 70.8 45.5	 lL- 38.9 6.3	5 ′ 7.6 35.7 4.5	3 4.5 37.5 2.7	66 58.9
1 Shade Darker Than Mantle	11 45.8 15.3 9.8	8 33.3 44.4 7.1	4 16.7 28.6 3.6	1 4.2 12.5 0.9	24 21.4
2 Shades Darker Than Mantle	5 45.5 6.9 4.5	1 9.7 5.6 0.9	4 36,4 28.6 3.6	1 9.1 12.5 0.9	11 9.8
Black Primaries	5 45.5 6.9 4.5	2 18.2 11.1 1.8	1 9.1 7.1 0.9	3 27.3 37.5 2.7	11 9.8
Column Total	72 64.3	18 16.1	14 12.5	8 7.1	112 100.0

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

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

Table 2. 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	0 YR	2.5 Y	5 Y	Row Total
7.5 YR	100 95.2 96.2 89.3	[illegible] 1.9 100.0 1.8	1 1.0 100.0 0.9	2 1.9 40.0 1.8	05 93.8
0 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.)

Table 22. 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" *Glaucescens* Primaries As Mantle Iris 7.5 YR		51 * 79.7 71.8 45.5	6 9.4 33.3 5.4	3 4.7 27.3 2.7	2 3.1 66.7 1.8	2 3.1 "40.0 1.8	0 0.0 0.0 0.0	0 0.0 0.0 0.0"	64 57.1
Male Intermediates	8	10 41.7 14.1 8.9	7′ 29.2 38.9 6.3	4 16.7 36.4 3.6	1 4.2 33.3 0.9	1 4.2 20.0 0.9	1 4.2 100.0 0.9	0 0.0 0.0 0.0	24 21.4
	9	5 50.0 7.0 4.5	1 10.0 5.6 0.9	3 30.0 27.3 2.7	0 0.0 0.0 0.0	1 10.0 20.0 0.9	0 0.0 0.0 0.0	0 " 0.0 0.0 0.0	10 8.9
	10	0 0.0 0.0 0.0	2 66.7 11.1 1.8	0 0.0 0.0 0.0	0 0.0 0.0 0.0	0 0.0 0.0 0.0	0 0.0 0.0 0.0	1 33.3 33.3 0.9	3 2.7

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

Table 22, cont'd.

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

* Each section contains: Count (Raw Chi Square = 102.63608, 36 d.f., significance = p< 0.0000 .
Row %
Column %
Total %

each of the females in 112 pairs (Table 20). The crosstabulation produced a Chi-square of 24.204′, 9 d.f., p <.004. The iris colors of the males were then crosstabulated against the iris colors of the females in each pair, resulting in a Chi-square of 34.823, 9 d.f., p <.0001 (Table 21). The indices of primary feather pigmentation and iris color were then combined for each individual gull, and the sums of the males in the 112 pairs were crosstabulated against the sums of the females. This produced a Chi-square value of 102.636, 36 d.f., p <.00001 (Table 22).

The mating patterns of the gulls were therefore very highly significantly assortative; the null hypothesis was rejected. Gulls tend to choose mates similar to themselves, but in some cases select mates of widely different phenotypes, forming mixed pairs and apparent backcrosses. Although primary feather pigmentation and iris color are both significant in mate selection, iris color is considerably more significant than primary feather pigmentation, and the combination of the two characters is much more significant than either as a single factor in mate selection.

IX. Nest Site Selection: Slope, Substrate, and Cover

Southern Alaskan argentatus and glaucescens nest on a variety of substrates ranging from bare cliff ledges in Glacier Bay, to sloping grassy meadows at Egg Island, North Marble, and Lake Louise, and to flat gravel bars at Dry Bay. Glacier Bay is recently deglaciated; while not in the arctic, it approximates high latitude conditions in some areas. In Glacier Bay *argentatus* is most often found in fjords close to glacier fronts; *glaucescens* concentrates in more marine regions, but not exclusively. *L. argentatus* and *glaucescens* were first observed nesting together with gulls of variable primary feather pigmentation in July, 1971, on sea cliffs at William Field Cairn #3. This colony is located 4 km from the active front of the Johns Hopkins Glacier, on the north side of Johns Hopkins Inlet. The cliff was deglaciated within the last 20 years; therefore, the colony could not have been occupied for long. In subsequent field seasons *argentatus*, *glaucescens*, and mixed pairs were found nesting together on low rocky islets, flat gravelly islands, and sloping grassy hillsides in Glacier Bay (Table 23).

Dry Bay, at the mouth of the Alsek River, northwest of Glacier Bay, supports 500 pairs of mixed *argentatus* and *glaucescens* nesting on flat gravel bars. The low alluvial islands, washed by high waters in late summer and during winter storms, are of unstabilized substrate. Vegetation is sparse and indicates a combined maritime and fresh-water influence. Vegetative cover is important in nest site selection, since nests are clumped near drift logs, willow bushes, and grass patches.

Thousands of *glaucescens* at Egg Island, off the Copper River Delta, nest on dunes covered with *Elymus* meadows. The nest sites are usually in proximity to old drift logs or *Sambucus* bushes. Slope of the dunes is shallow, with a mean less than 3 %. The highest dunes on Egg Island are only 10 m above sea level .

North Marble, as Egg Island, has highest nesting densities on grassy meadows; the dominant vegetation is *Hordeum*. Some sites

Table 23.

Nest Site Substrates in *Larus* Colonies in Southern Alaska, British Columbia, and Yukon Territory

colony	Species Composition	Substrate
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
Strawberry Reef	*glaucescens*	*Elymus*-covered dunes
Copper Sands	*glaucescens*	*Elymus*-covered dunes
Egg Island	*glaucescens*	*Elymus*-covered dunes
Lake Louise	*argentatus*	sloping grassy islet
Dezadeash Lake Y.T.	*argentatus*	boreal lake, forested islet shores
Atlin Lake, B.C.	*argentatus*	low rocky islet

Table 24. Nest Site Slope in *Larus* Colonies in Southern Alaska

Colony	Species Composition	Mean	Range	S.D.	n
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

at North Marble, however, are precipitous, approaching 50 % slope. Sympatric and interbreeding *glaucescens* and *argentatus* are found on the grassy slopes of North Marble. Allopatric *argentatus* at Lake Louise nest on a grassy (*Calamagrostris*) islet, with slope and substrate similar to North Marble (Tables 23, 24). Study of other colonies at Dezadeash Lake, Yukon Territory, and Atlin Lake, British Colombia, revealed that *argentatus* also nest on low rocky islets and on the edges of forested islands in boreal lakes (Table 23).

In summary, both allopatric and sympatric *argentatus* and *glaucescens* are flexible in nesting habitat selection in coastal southern Alaska and the adjoining interior lakes. Nest site substrate ranges from gravel bars to cliff faces and includes from 0 % to over 50 % slope. Favored sites for both forms are grassy slopes.

X. Clutch Size

Clutch size, hatching success, and fledging success of *Larus* gulls in southern Alaska were examined for evidence of post-zygotic isolating mechanisms. Populations of *argentatus* were compared against *glaucescens* and mixed populations, and "pure" pairs were compared against mixed pairs. Analysis of variance, and if F-ratios were significant, Duncan's Multiple Range Test, were used.

There is spatial and temporal variation in clutch size in gull populations in southern Alaska. The range of clutch size in *argentatus*, *glaucescens*, and mixed populations between 1972 to 1977 includes means of 2.05 to 3.0 eggs per nest. Notably, the extremes both occur in *glaucescens* populations (Table 25). The 1975 Egg Island population was at the low end of the range. Clutch size increased significantly

Table 25. Clutch Size, and Number of Fledglings Per Nest in *Larus* Colonies in Southern Alaska

Colony	Year	Species	Number of Nest Examined	Mean Clutch Size	Mean Number of Fledglings
North Marble	1972	mixed			
East			94	2.8	1.8
Nest			36	2.9	2.2
North			20	2.8	1.5
lop			12	2.1	0.4
Total			162	2.8 *	1.75 *
North Marble	1973	mixed			
East			104	3.0	1.6
West			60	2.9	2.2
North			15	3.0	1.7
Top			12	2.9	1.6
Total			191	2.96 *	1.80 *
Dry Bay	1977	"pure"	76	2.93	1.40
		mixed	36	2.89	1.47
Total			112	2.92 *	1.44 *
Egg Island	1975	*glaucescens*	153	2.05	1.03
Egg Island	1976	*glaucescens*	186	2.56	1.12
Lake Louise	1977	*argentatus*	77	2.74	0.95

* weighted means

between 1975 and 1976 (Table 27). Analysis of population parameters at Egg Island suggests an expanding population with a high proportion of young females, which tend to lay smaller clutches than older adults (Patten and 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 for "pure" *glaucescens* pairs at Dry Bay in 1977 (2.93).

The weighted means for the mixed North Marble Island population were quite high {2.8(I in 1972; 2.96 in 1973; combined 2.90). Only the North Marble “Top Colony,” composed of 12 *glaucescens* pairs, had a significantly smaller clutch size compared to other sites in 1972 (2.1; F = 6.066; p <.01). Differences were not significant in 1973.

Phenotypes of both parents were determined for 112 nests in two study plots at Dry Bay in 1977. The categories containing pairs with at least one hybrid parent were combined for analysis. Only one *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, “pure” pairs of *argentatus* at Lake Louise have been compared against coastal *glaucescens* and mixed pairs.

The analysis of variance for clutch size in southern Alaskan *Larus* colonies produced a highly significant F-ratio of 35.574 (7 d.f., p <.001) (Table 26). The data were therefore further analyzed using Duncan’s Multiple Range Test. The differences between 1972 and 1973 for the colonies on North Marble were not significant, with the exception of the Top Colony. The Top Colony, however, due to its small size, did not significantly depress the population mean. The North Marble data were thus included as a single mean.

Table 26. Analysis of Variance of Clutch Size

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F-ratio
Between Groups	8	88.7920	12.6846	35.574 *
Within Groups	796	283.8299	0.3566	
Total	173	372.6219		

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

Table 27 contains the results of Duncan's Multiple Range Test at the $p < .05$ level of significance. Note that the Dry Bay colony is broken down into two groups: "pure" glaucescens, and mixed pairs; but that North Marble data are combined as one mean.

In the Duncan's Multiple Range Test (at the $p < .05$ level), there are four homogeneous subsets of clutch sizes for argentatus, glaucescens, and mixed populations, between the two extreme clutch sizes (both glaucescens) (Table 27). Subset 1 contains the 1975 Egg Island population. Subset 2 contains populations of glaucescens, argentatus, and mixed pairs, not significantly different in clutch size. In Subset 3, clutch size of argentatus is not significantly different from two mixed populations. In Subset 4, the mixed pairs at Dry Bay are not signifificantly different from the "pure" pairs, or from the mixed colony at North Marble.

At the $p < .01$ level of significance, homogeneous subsets of ranked means for clutch size are reduced to three. The 1976 clutch size for glaucescens at Egg Island is not significantly different from that of argentatus at Lake Louise, nor from that of mixed pairs at Dry Bay. In Subset 3, argentatus clutch size is not significantly different from that of glaucescens, mixed pairs, or the mean of the combined colonies at North Marble (Table 28).

In summary, while there are significant temporal and spatial differences in clutch size between Larus colonies in southern Alaska, populations of argentatus are not significantly different from mixed or glaucescens populations. Within the colony at Dry Bay, "pure" pairs of glaucescens are not significantly different from mixed pairs in mean clutch size.

Table 27. Ranked Means for Clutch Size for *Larus* Colonies in Southern Alaska

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

Homogeneous 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). Underlined numbers indicate there is no significant difference between the means.

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

* hybrid = pairs containing at least one intergrade gull

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

Table 28.

Ranked Means for Clutch Size for *Larus* Colonies in Southern Alaska (Duncan's New Multiple Range Test: p <.01 level)

Homogeneous 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). Underlined numbers indicate there is no significant difference between the means.

Subset 1	*glaucescens*			
Group	Egg Island - ?975			
Mean	2.05			
Subset 2	*glaucescens*	*argentatus*	hybrid *	
Group	Egg Island - 1976	Lake Louise	Dry Bay	
Mean	2.56	2.74	2.89	
Subset 3	*argentatus*	hybrid	combined **	*glaucescens*
Group	Lake Louise	Dry Bay	North Marble	Dry Bay
Mean	2.74	2.89	2.90	2.93

* hybrid = pairs containing at least one intergrade

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

XI. Hatching and Fledging Success

Factors influencing hatching and fledging success in southern Alaskan Larus colonies have been analyzed in detail in a previous series of publications (Patten, 1974; Patten and Patten, 1975, 1976, 1977, 1978). The purpose of this concluding section on results is to present highly condensed data on reproductive success of glaucescens, argentatus, and mixed populations, and to compare fledging success of “pure” glaucescens versus “hybrid” pairs within the colony at Dry Bay. "Hybrid" pairs are here considered to be those containing at least one intergrade, and thus include F_1 and F_2 backcrosses.

Hatching success in southern Alaskan Larus colonies is influenced by three principal factors: eggs disappearing from the nest, due to predation, which are considered “lost”; eggs which are inviable, i.e., those which remain in the nest but fail to hatch; and eggs which pip but the embryo fails to emerge and dies (Table 29). The most important factor influencing hatching success is egg loss to predation, ranging from 4 % to nearly 30 % of eggs laid. In most cases, egg predation is due to Larus gulls. The glaucescens colony at Egg Island (1975-76) and the mixed colony at North Marble (1972-73) do not differ significantly from each other in egg loss due to predation, but both have significantly ($p <.05$) higher rates from the mixed colony at Dry Bay (Table 29). Data on egg loss to predation and hatching success is not available for the argentatus colony at Lake Louise. Inviable eggs range from 1.9 % in the Egg Island glaucescens population, to 6.2 % in the argentatus population at Lake Louise. Inviable eggs in the mixed colonies of North Marble

Table 29. "Lost," Inviable, and Pipped Eggs Failing to Hatch in *Larus* Colonies in Southern Alaska (1972 - 1977)

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%)		(< %)
Egg Island	19 6	*glaucescens*	4 6	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%)

and Dry Bay have similar low frequencies ranging from 0 % to 4.8 %. Differences between the populations in frequencies of inviable eggs are not significant ($p <.05$). The last cause of failure to hatch is eggs which pip, without emergence of the embryo. In all cases, this is well below 1 % at any colony.

Hatching success in southern Alaskan _Larus_ colonies ranged from 67 % to 93 % (Table 30). The 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; hatching success was thus inversely related to predation. The Egg Island _glaucescens_ population was not significantly different in hatching success or observed chick mortality from the mixed colony at North Marble, but chick disappearance was significantly higher ($p <.05$) at Egg Island than North Marble (Table 30). This was most likely related to the much greater meadow area on Egg Island. Dry Bay, due to intense eagle predation, had the highest rate of chick disappearance. An active eagle nest was located within 1 km of the colony. Gull chicks found dead within the colony usually showed peck wounds to the head, presumably from territorial defense by other adult gulls. North Marble had the highest percentage of chicks fledged of those hatching, and Dry Bay the lowest percentage. However, the final fledging success as measured in chicks produced per nest depends additionally upon the clutch size and the hatching success.

The summary comparison of the mean clutch size and the mean number of fledglings produced per nest provides the clearest picture of reproductive success in _Larus_ colonies in southern Alaska. The

Table 30. Hatching Success, Chick Mortality, and Fledging Success in *Larus* Colonies in Southern Alaska (1972 - 1977)

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

* Most chick disappearance was due to sustained eagle predation.

Table 31. Comparison of Mean Clutch Size and Fledging Success in *Larus* Colonies in Southern Alaska

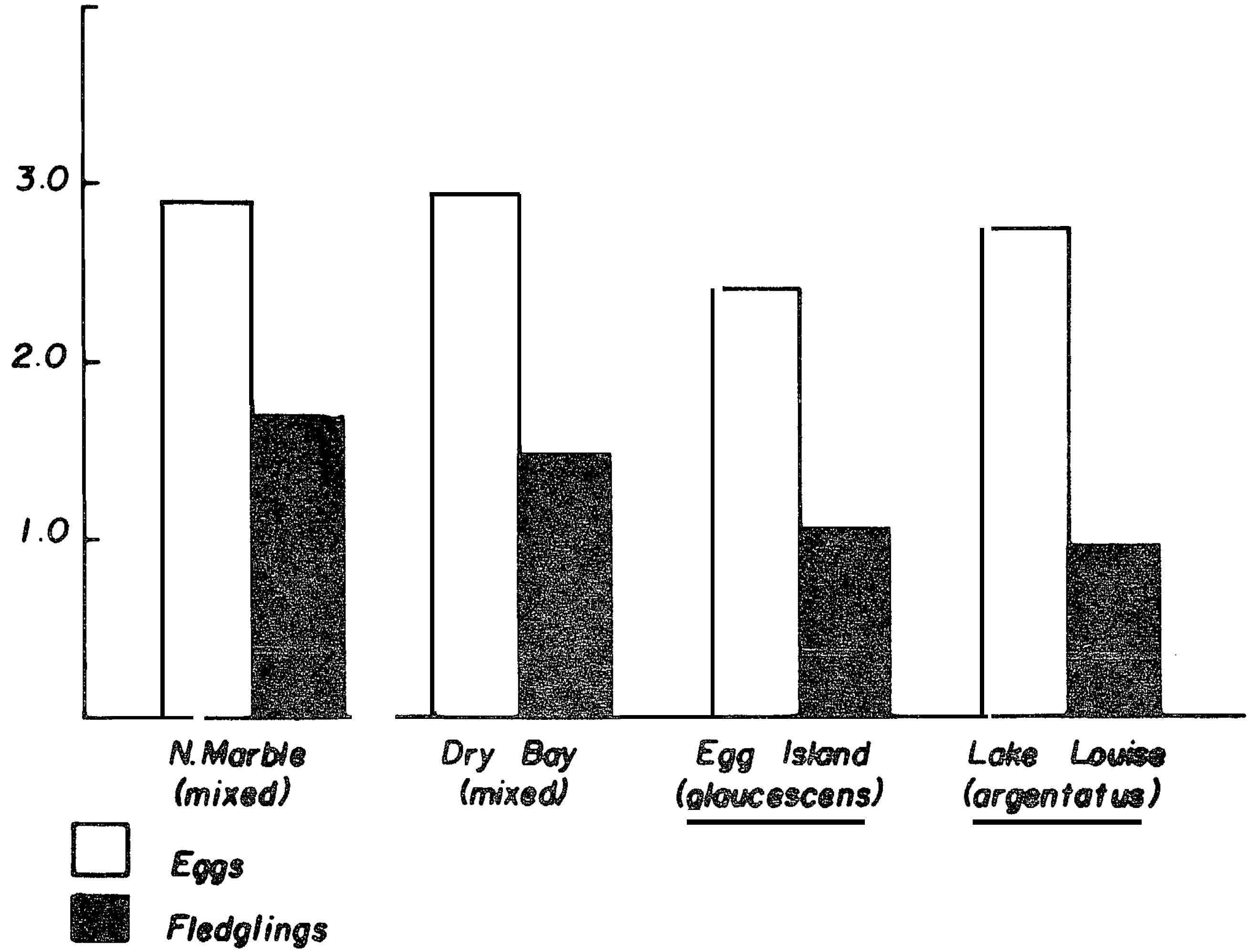
Colony/ Species Composition	Mean Clutch Size	Mean Number of Fledgings Per Nest	Mean Territory Size (m2)*	Number of Nests Examined
North Marble (1972-1973) (mixed)	2.90	1.77	18 m^2	162-191
Dry Bay (1977) (mixed)	2.92	1.44	32.2 m^2	112
Egg Island (1975-1976) (*glaucescens*)	2.40	1.08	29.6 m^2	153-186
Lake Louise (1977) (*argentatus*)	2.74	.95	13.5 m^2	77

* Substrates: North Marble: Willoughby limestone with *Hordeum* meadows.
Dry Bay: alluvial sand and gravel with sparse vegetation.
Egg Island: sand dunes with *Elymus* meadows.
Lake Louise: rocky islet with *Calamagrostris* meadows.

colonies where interbreeding is occurring, e.g., North Marble and Dry Bay, have higher mean clutch sizes and net productivity than colonies of either *glaucescens* or *argentatus* "pure" parental types (Table 31). Within the mixed colony at Dry Bay, however, the "hybrid" pairs had a reproductive success of 1.47 chicks fledged per nest, while in comparison, the phenotypically "pure" *glaucescens* produced 1.40 chicks per nest. The differences between the two groups in fledging success were not significant, nor were the differences in mean clutch size (2.89 vs. 2.93).

In summary, although clutch size and fledging success of "hybrid" versus "pure" pairs within the individual colony at Dry Bay are not significantly different, the hybrid pairs are reproducing *slightly* better than the *glaucescens* phenotypes, and southern Alaskan colonies with mixed populations are producing considerably more offspring per pair than colonies of either *argentatus* or *glaucescens* parental types (Fig. 26).

Fig 26. MEAN CLUTCH SIZE AND FLEDGING SUCCESS



CHAPTER 6: DISCUSSION

I. Ancestral Populations

The ancestral Larus populations most likely emerged from eastern Siberia during the early Pleistocene, spreading in both easterly and westerly directions across the Eurasian land mass, and crossing the Bering Strait Land Bridge into the North American continent (Hopkins, 1962; Haag, 1962). Expanding ice masses subsequently separated the ancestral gull populations, forcing them into refugia in Europe, Asia, and North America during successive glaciation. With an increasingly severe climate, and with small populations, the opportunities for differentiation would have been considerable.

North American gull populations resembling argentatus stock were pushed back by continental glaciation to an interior refugium along the Yukon-Kuskokwim - Bering Strait Land Bridge. Other populations were forced to retreat southward along the Pacific Coastline to the Puget Sound region, where they evolved in proximity to glacier fronts. The relatively uniform mantle and primary feather pigmentation of glaucescens resembles that of high latitude arctic species such as glaucoides, which. breeds on exposed cliffs in similar glacier environments (Hoffman et al., 1978).

As the ice sheets retreated, Larus populations which had continued to evolve in separate pathways rejoined, and in some cases interbred, and on other cases did not. While these gulls shared a common gene pool at one time, enough evolution occurred to account for certain calorimetric differences between argentatus and glaucescens, for instance in the amount and pattern of melanin deposition in the primary feathers, and in orbital ring and iris coloration, and to account for certain habitat preferences.

L. argentatus is a wide-ranging species currently found along the Eastern Seaboard, the Great Lakes, and on boreal lakes of North America, exhibiting tolerance for both freshwater and marine conditions. L. glaucescens is a coastal Pacific Northwest species, generally confined to marine environments. The more flexible argentatus, breeding on boreal lakes, and wintering offshore in the Pacific, appears to possess the capacity to colonize the southern Alaskan coastline, while glaucescens is not found in the interior. The area where these two gull forms come into contact is the region of the Pacific Northwest coastline between southeastern Alaska and the Alaska Peninsula.

II. Larus Populations in Southern Alaska

Williamson and Peyton (1963) collected a series of specimens which were intermediate between argentatus and glaucescens from the Cook Inlet region, near Anchorage, Alaska. The authors suggested that sympatry between breeding argentatus and glaucescens occurs in southeastern Alaska. The preceding chapter has demonstrated that additional sympatry and interbreeding of glaucescens and argentatus occurs in southcentral and southeastern Alaska. Mixed populations exhibit a higher reproductive rate than colonies of parental phenotypes.

These Larus gulls inhabit geologically dynamic nesting habitats along the southern Alaskan coastline, ranging from recently deglaciated fjords to earthquake-influenced sandbar barrier islands and delta gravel bars. Nesting habitat selection is flexible, and ranges from flat gravel bars to sloping grassy hillsides and nearly vertical cliff faces. Onset of breeding is flexible within an individual colony, and is related to weather conditions and snow cover. The mixed colony at. Dry Bay at the mouth of the Alsek River exhibits the most flexibility in timing of breeding of seven colonies examined, although over fifty percent of the eggs are laid in just over a one-week time span.

Clutch size of "pure" versus mixed pairs within the colony at Dry Bay is not significantly different. Hatching success in the entire colony was quite high, due to low rates of egg inviability and egg predation. Hybrid, F_2 and apparent backcross zygotes, with a slightly enhanced fledging success, are clearly not reduced in viability to fledging stage. Analysis of morphology and pairing indicates that individuals of mixed genetic background survive to adulthood and may interbreed with parently types, usually glaucescens. The complete range of variability is expressed by the offspring of the backcrosses. Mating patterns, however, are strongly assortative, with individuals of intermediate phenotypes tending to select mates of similar phenotypes, although exceptions occur regularly.

This outline of the two forms and the environment in which they meet presents fundamentals of the argentatus - glaucescens interaction in southern Alaska: the two calorimetrically different but interfertile forms. largely kept apart by dissimilar natural environments, are interbreeding in a zone of contact in ecologically dynamic coastal Alaska. In addition to the rapid geological and successional changes in coastal southern Alaska, certain aspects of the environment are becoming progressively more altered by human influence, notably with the development of intensive fisheries, with increasing amounts of fish offal and similar garbage.

Four theoretical alternative hypotheses for the existance of a narrow hybrid zone between argentatus and glaucescens in south coastal Alaska will be explored in search of the best explanation for the data collected. These four hypotheses are not mutually exclusive, and the "best fit" for the southern Alaska Larus situation may involve combinations of segments of several hypotheses.

The ephermal-zone hypothesis, e.g., that hybridization will end in either speciation or fusion of the hybridizing taxa by means of introgression (Dobzhansky, 1940, 1951; Sibley, 1957, 1959, 1961; Wilson, 1965; Remington, 1969; Moore, 1977) is inappropriate to the southern Alaskan argentatus - glaucescens contact zone for several reasons. Speciation requires selective pressure against those individuals which enter into mixed pairs, and is to be expected if the populations have diverged to the extent that the hybrids would serve as a bridge for introgressive hybridization. While historical data on the duration and extent of the contact are not available, other than from Williamson and Peyton (1963), natural selection is apparently not acting against hybrid zygotes in the coastal environment, at least until fledging stage. Further, analysis of adult morphology indicates intermediate adults are common and reproduce as well as "pure" types within the contact zone. The viable and fertile hybrids could serve as a bridge for introgressive hybridization, yet evidence suggests that glaucescens genes are not penetrating interior argentatus to the degree that the converse is occurring. Therefore, rapid speciation or fusion of these two forms is not occurring, although the glaucescens population is increasing in variability.

The dynamic equilibrium hypothes s, as postulated by Bigelow (1965) and discussed by Moore (1977), requires influxes of genes from both parental populations. This hypothesis has aspects which apply to the southern Alaskan Larus contact zone. The migration pattern of argentatus from offshore wintering areas, which extend from the Gulf of Alaska to southern California (Barrington, 1973; Sanger, 1975) towards breeding localities in interior Alaska and the Yukon, includes major river valleys such as the Alsek and the Susitna. These rivers pass through major mountain formations, such as the Alaska and St. Elias ranges. Local glaucescens populations at colonies near mouths of rivers 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 immigration of parental types is assisting in maintenance of the apparently stabile glaucescens - occidentals contact zone in western Washington state. Bigelow (1965) proposed that stabile 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. The evolution of an antihybridization mechanism in the restricted zone of contact might be disrupted by migrants moving into the restricted zone from more extensive areas of allopatry. However, hybrids are apparently not selected against in the southern Alaskan contact zone, and theoretically, mating should be random in a stabile hybrid zone. There is strong evidence that assortative mating is occurring, possibly counter to evolution of an equilibrium.

There is also the additional evidence that more *argentatus* genes are entering coastal populations than the reverse, e.g., not an equilibrium state.

The hybrid superiority hypothesis suggests 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 indicates that this possibility certainly exists. There is evidence of hybrid fertility, backcrossing, morphological intermediacy, and hybrid viability. At first, the assortative mating pattern seems to counter the hybrid superiority hypothesis, but intermediates which select like types as mates within the contact zone should increase their reproductive fitness by the production of offspring adapted to the intermediate environment.

Zones of contact (cf., Mayr, 1963) usually involve only small portions 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 *occidentals* (Hoffman et al., 1978), to the north and south. 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 occur, in this case the radical division of interior from coastal Alaska by very high mountain ranges. The abrupt division 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 ethnological pre-mating isolating mechanisms (Jackson, 1973).

The concept that ecological factors are most important in determining the fitness of these hybrids is central to the development of the hybrid superiority hypotheses (Moore, 1977). The extent of a contact zone is determined by the geographical range of ecological conditions to which the intermediates are adapted, or to which the parental phenotypes are less well adapted. Most hybrid zones are narrow and occur at the juxtaposition of the ranges of the parental populations (Moore, 1977). The *argentatus* x *glaucescens* contact zone is clearly narrow and at the interface between the two parental populations (Short, 1969; Fig. 1).

The fourth explanation to be considered to account for the *argentatus* x *glaucescens* contact zone is based upon the following logic: most stabile hybrid zones appear to occur in ecological conditions that are ecotones, disclimax, marginal habitats, or perpetually disturbed habitats (Moore, 1977). This explanation, along with aspects of the hybrid-superiority hypothesis discussed immediately above, provides the best possible explanation for what has been observed in *Larus* populations in southern Alaska. The mixed populations of gulls are found when *argentatus* of the boreal lakes meets the marine *glaucescens* at the mouths of rivers and in recently deglaciated fjords. The occurrence of the zone of overlap and hybridization 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. These ecotones probably provide marginal habitats for the forms which represent ecological communities on either side of the ecotone.

L. argentatus and *L. glaucescens* are forms which have diverged in response to particular external conditions exerted by the respective communities in which they evolved. The *argentatus* x *glaucescens* hybrid may be physiologically homeostatic and no less adapted to the transitional habitat than are the parental phenotypes. The selection gradients exerted by the distinctly integrated West Coast Marine and Boreal Interior communities on either side of the ecotone prevent expansion of the hybrid zone. However, complete reproductive isolation is not evolving because, when the opportunity to hybridize occurs, there is no selection against the mixed forms. The hybrids are able to survive in the dynamic southern Alaskan contact zone because they do not have to compete in stabile communities with species that are well adapted to those communities. Since the hybridization is occurring in zones of marginal habitat for both parental phenotypes, the hybrids would not have to overcome rigorous competition from either *argentatus* or *glaucescens* phenotypes and therefore persist in the dynamic ecotones.

River valleys are among the most variable of environments (Anderson, 1949). Extant. conditions may be drastically altered within a short period of time by river action. The connection between disturbed environments and the results of hybridization is typical of many cases of hybridization (Anderson, 1949; Grant, 1971; Moore, 1977). The greater the number of gene differences between the parental types, the greater will be the number of special new habitats 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 that present all possible recombination of the contrasting differences of the parental environments (Anderson, 1949). 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 mouths of the Alsek and Susitna Rivers in southern Alaska. These sites are apparently the center of gull interbreeding along this section of Pacific Coastline, since *argentatus* gene frequencies (as analyzed by calorimetric hybrid indices) diminish with distance away from these areas.

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 open for colonization. Tinbergen (1960) 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 nonspecific mates. Thus, even though their pre-mating isolating mechanisms could be as completely developed as those in the center of the range, such as in the eastern Canadian arctic (Smith, 19660), the threshold of the pioneering *argentatus* will eventually diminish to a low enough level that they will hybridize with *glaucescens* rather than not reproduce at all (Mayr, cited by Sibley, in Blair, 1961). *L. argentatus* is distinctly less common than glaucescens within the fjordlands of Glacier Bay. Individual argentatus may not find nonspecific mates, and the instinctive mating drive eventually overcomes the inhibitory drive of potentially incorrect species-specific recognition signals and a mixed argentatus x glaucescens pair is formed. The viable offspring, with mixed genomes, may have a selective advantage in the rapidly changing environment.

Man, in addition to catastrophic natural forces, creates new, artificial niches in which hybrid segregants might survive and reproduce (Anderson, 1949). 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 stabile 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 niches for Larus gulls are garbage piles, sewage outfalls, and concentrations of fish offal around canneries and processing plants. The rapid development of coastal and marine fisheries in Alaska, with production of huge amounts of offal in addition to the refuse associated with increased gas and oil development on the continental shelf, is providing large amounts of "loose" energy. L. argentatus is an excellent example of a vertebrate "weedy" species, adapted to man-disturbed environments and to utilize artificial food (Drury, pers. comm.). When humans occupy new areas, barriers between other species are broken down and new ecological niches are created in which hybrid segregants can survive (cf., Sibley, 1950, 1954; Sibley and West, 1958; Sibley and Sibley, 1954}. The effect of human disturbance is to give weedy species, such as L. argentatus, much greater opportunities to hybridize with similar forms than would otherwise be encountered. 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. Hybridization is expected to continue between Larus populations in Alaska in coming years, and intermediate gulls will become more common. The gene flow between large white-headed gull populations will be increased in future years as a secondary consequence of human activities, and may lead to a new adaptive peak in these commensal forms.

111. Relation to the Circumpolar Formenkreis through Eastern Siberia

Dr. Kistchinski of the Soviet Academy of Sciences (pers. comm.) reports a similar Larus situation to that in Alaska on the eastern side of the Bering Strait. Species composition differs slightly. L. glaucescens breeds on the Aleutian Chain and extends into Soviet territory only on the Commander Islands. Ms. Ludmila V. Firsova of the Ornithology Department, Zoological Institute, Leningrad, has been studying the breeding biology of glaucescens in this area. L. schistisagus, the Slaty-backed Gull, occupies the coastal niche of glaucescens on the eastern shores of the Sea of Okhotsk and the Kamchatka Peninsula. L. argentatus vegae occupies interior eastern Siberia, as L. a. smithsonianus occupies interior Alaska. A zone of overlap and hybridization exists between schistisagus and vegae where rivers descend from the southern Koryak Highlands and enter the Bering

Sea (Fig. 27). *L. schistisagus* typically nests on cliffs facing the Bering Sea, and *vegae* usually nests in scattered pairs on boreal lakes. However, Portenko (1963) and Kistchinski (pers. comm.) found *vegae* and *schistisagus* breeding sympatrically from Barykov Cape to the Khatyrka River mouth and somewhat to the south on the Siberian coast. Hybrid colonies are found on Koryak river deltas and on sea cliffs in the northern Koryak Highlands. The colonies on river deltas 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.

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

L. hyperboreus breeds northward from the Koryak Highlands on the coastal lowlands, where it is not in sympatry with *vegae* on the boreal lakes. *L. hyperboreus pallidissimus* nests on arctic shores westward across northern Siberia, and on the periphery of Wrangel

Island. Mixed colonies of vegae and hyperboreus are found in the interior of Wrangel Island, with no interbreeding. A representative composition in these colonies is 70 % vegae, 30 % hyperboreus. Small numbers of L. a. vegae enter U.S. territory on St. Lawrence Island, where they breed on cliffs (Fay and Cade, 1959; Searing, 1976; Drury, pers. comm.). St. Lawrence Island is a fragment of the former Bering Strait land bridge, connecting Eurasia with North America, across which the ancestral populations of argentatus moved from Eastern Siberia into North America during the early Pleistocene.

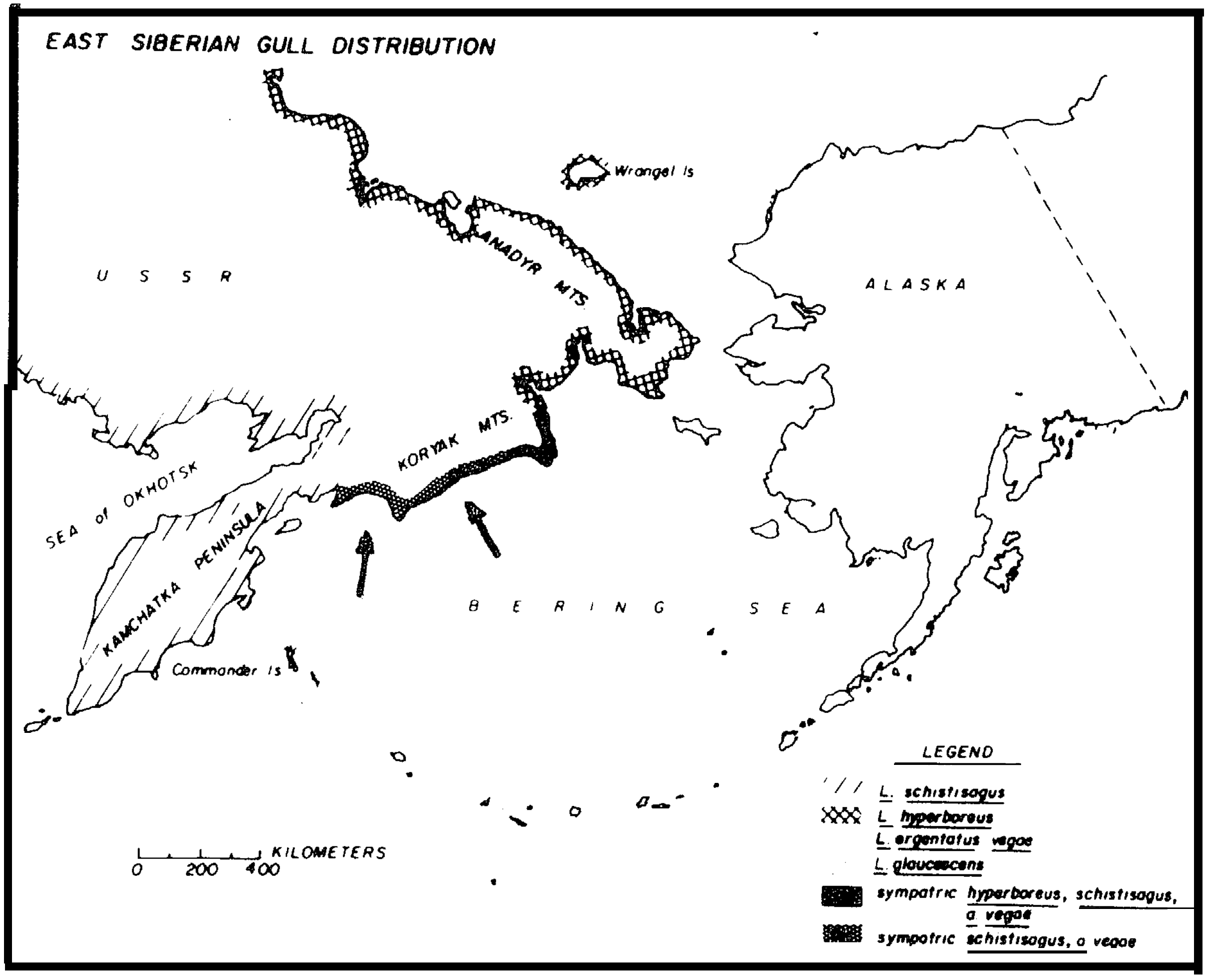

EAST SIBERIAN GULL DISTRIBUTION
Wrangel Is
U S S R
ANADYR MTS
ALASKA
KORYAK MTS
SEA of OKHOTSK
KAMCHATKA PENINSULA
BERING SEA
Commander Is
0 200 400 KILOMETERS
LEGEND
L. schistisagus
L. hyperboreus
L. argentatus vegae
L. glaucescens
sympatric hyperboreus, schistisagus, a. vegae
sympatric schistisagus, a vegae

Fig. 27.

IV. 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 conjunction along a narrow belt. The relations ps 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 that of species and of subspecies. Ripley (1945) called semispecies "emergent interspecies."

Mayr, Linsley, and Usinger (1953) first defined semispecies as the species of which a superspecies is composed; semispecies are a special kind of species, not a category different from the species. However, Mayr (1963) later agreed with Lorkovic (1958) that the term should be broadened to include the additional meaning of populations that have acquired some, but not yet all, attributed of species' rank; borderline cases between species and subspecies. Thus, gene exchange would still be possible among semispecies, but not as freely as among nonspecific populations (cf. Amadon, 1966). Hoffman, Wiens, and Scott (1978) suggested that the semispecies concept should be further expanded to include apparently stable zones of overlap and hybridization, such as the glaucescens - occidentals contact in Western Washington (Fig. 1).

Data gathered in southern Alaska during research for this investigation support the above concept developed by Hoffman et al. (1978). Similar to the glaucescens - occidentals contact, the analyses of morphology and mating patterns of glaucescens and argentatus demonstrate that Short's (1969) and Mayr's (1963) criteria for conspecifity are not met, i.e., that the zone of contact should be characterized by random mating, complete intergradation, absence of pure parental types, with introgression into the adjacent parental populations. However, evidence from western Alaska suggests that the *hyperboreus* - *glaucescens* contact zone may meet these criteria.

L. hyperboreus barrovianus, breeding in northern and western Alaska, as well as in the western Canadian arctic, is characterized by smaller size arrd darker mantle than other *hyperboreus* subspecies (Rand, 1952; Manning et al., 1956; McPherson, 1961). Swarth (1938) found gulls on Nunivak Island off western Alaska to be nearly completely intermediate between *glaucescens* and *barrovianus*. Johansen (1958) suggested that *barrovianus* showed a probable *glaucescens* influence. 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 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* is of considerable antiquity, especially as compared to the parapatric *glaucescens* - *argentatus* zone.

Short (1969) first suggested that *glaucescens* and *argentatus* are semispecies. The results of my research confirm this suggestion. Further, *argentatus, glaucescens*, and *occidentals* 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 into

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*Drury (pers. comm.) recently reported a mixed pair between *hyperboreus* and *L. argentatus vegae* on the Seward Peninsula of Alaska.

contact, including *hyperboreus*. This chain is in turn linked through *L. schistisagus* and *L. argentatus vegae* of the Siberian coastline with the circumpolar *Formenkreis*.

The appropriate taxonomic treatment for semispecies is to retain the binomial nomenclature. Thus, the Herring Gull of Alaska should remain *Larus argentatus*, and the Glaucous-winged Gull *L. glaucescens*.

SUMMARY

This study investigates mensural characters, 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 problem is approached through a comparative field study of allopatric and sympatric gull populations.

After an introduction to the evolution and systematic of the Herring Gull group (*Larus argentatus*) Chapter 1), two Alaskan members of the genus *Larus* are described. Questions are posed in search of answers to pre- and post-mating isolating mechanisms between these two forms. The intent in answering these questions is to clarify taxonomic and ecological relationships between *glaucescens* and *argentatus*, relate the Alaskan situation to the larger *Formenkreis*, and aid in further understanding the complex systematic of the Herring Gull group.

The literature on the morphology and evolution of Palearctic and Nearctic *Larus* gulls is summarized in Chapter II. There is 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 Aralo-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 *occidentals,* among others.

Post-glacially, *L. a. smithsonianus* emigrated to Europe from eastern North America, coming into contact with the westward-expanding *cachinnans-fuscus* group, to which *argentatus* is partially isolated. The classic overlap of a "ring" species (*Formenkreis*) is thus formed. The connecting links in the *Formenkreis* are the sympatric populations of *Larus* gulls in central Siberia, which hybridize on a large scale.

Evidence is presented linking the Western North American *Larus* populations with the circumpolar *Formenkreis*. A review of the evolutionary status of large gulls of the West Coast suggests none of these *Larus* populations are completely reproductively isolated by pre-mating mechanisms, since they interbreed in narrow zones of sympatry. Breeding biology of large white-headed gulls is reviewed to assist in understanding dynamics of the interbreeding forms.

The study areas are discussed in Chapter 3. After an introduction to the general environmental conditions on the south coast of Alaska, eight individual study sites are described. These sites consist of six coastal colonies, and one major feeding area, located between Juneau and Prince William Sound. A gull colony on fresh-water lake in interior Alaska, north of Valdez, is included in the study. The geology of the coastal sites is dynamic, due to recent deglaciation, major earthquakes, and floods. Slope and substrate of the study colonies vary from horizontal gravel bars to nearly vertical cliff faces. Two coastal colonies support interbreeding *argentatus* and *glaucescens*. The interior colony at Lake Louise is composed of allopatric *argentatus*. Principal periods of study for these colonies are given.

Materials and Methods are presented in Chapter 4. Techniques of marking nests, chicks, and adults are described in addition to the methods of obtaining morphological measurements of adult gulls. The Hybrid Index is discussed as a method for analyzing hybridization. Numerical scores are assigned to the variation exhibited by the parental types and intermediate forms. Colors analyzed in the study are identified and recorded by the Munsell System of Color Notation.

Chapter 5 contains the Results of the research. Statistical tests reveal that a minor sex-linked difference in bill depth at posterior nares exists between two Copper River Delta _glaucescens_ colonies, and all other populations. There is, however, broad overlap between populations in other mensural characters.

The study therefore includes such calorimetric characters as primary feather pigmentation, iris and orbital ring colors. The primary feather pigmentation of 174 gulls is analyzed. Individual gulls within the study area are highly variable, and the variation includes primaries lighter than 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 is found within the individual colony at Dry Bay, at the mouth of the Alsek River, southeast of Yakutat, Alaska. As a-general trend, mean wing hybrid indices gradually increase from coastal populations resembling _glaucescens_ forms through intermediate populations in fjords and at river mouths to an interior population of _argentatus_ on a freshwater lake.

The range of iris coloration in gulls within the study area includes very dark brown, dark brown, brown, light 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, reveal that neighboring colonies on the Copper River Delta have strikingly similar distributions of iris hues; however, the Cordova gull population is qualitatively different in distribution of iris hues from the Copper River Delta populations. The mixed populations at North Marble and Dry Bay share similar, although not identical, distributions of iris hues and values. The distribution of iris values in irides of the Strawberry Reef population resembles that of the population inhabiting Dry Bay. The Copper Sands (S) and Strawberry Reef *glaucescens* populations are closely related, although Strawberry Reef additionally resembles the hybrid population inhabiting Dry Bay.

A Chi-square test demonstrates that iris color is linked with primary feather pigmentation in *Larus* populations in the southern Alaskan study area. Light-eyed gulls tend to have dark primaries, dark-eyed gulls tend to have light primaries, and gulls with intermediate amounts of melanin in the primaries have irides of various intermediate shades.

The variation and distribution of iris color, although linked with primary feather pigmentation, is unlikely to function in species recognition between the light-eyed *argentatus* and the dark-eyed *glaucescens* in southern Alaska, since the two forms are linked “by a complete range of intermediates.

The extreme pigments in orbital rings of *glaucescens* and *argentatus* in southern Alaska are dark pink and bright yellow, but six intermediate hues exist, and more than one hue may occur in an individual eye-ring. Each colony examined had a different mean composite orbital ring, but an analysis of variance confirms that the orbital ring colors of the populations at both ends of the distribution are connected by increasing amounts of yellow pigment. Orbital rings of some individual gulls in the study area are uniformly pigmented. Other gulls possess orbital rings with two to three hues. The population at Dry Bay has 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 in southern Alaska is unlikely, due to the spectrum of variation. However, the variability may function as a character for individual or population recognition.

The composite hybrid index demonstrates a cline of increasing _argentatus_ influence along a 480 km axis extending from the northwest to the southeast between Prince William Sound and Glacier Bay. Primary feathers become darker and yellow pigments increase in the irides and orbital rings in gull populations along this axis. The major source of _argentatus_-like genes along the North Gulf Coast of Alaska is the hybrid colony at Dry Bay, which serves as a bridge between coastal and interior _Larus_ populations.

Three statistical tests are conducted on the mating patterns of gulls in 112 pairs at Dry Bay. These tests indicate that mating patterns are significantly assortative; _i.e._, gulls tend to choose mates similar to themselves, but in some cases select mates of widely different phenotypes, forming mixed pairs and apparent backcrosses. Statistically, the combination of both iris color and primary feather pigmentation is considerably more important than either as a single factor in mate selection.

Both allopatric and sympatric *argentatus* and *glaucescens* are flexible in nesting habitat selection in southern Alaska. Nest site substrate ranges from gravel bars to cliff faces including from 0% to over 50% slope. Favored sites for both forms are grassy island slopes.

Clutch size, hatching success and fledging success of *Larus* gulls in southern Alaska are examined for evidence of post-zygotic isolating mechanisms. While there are statistically significant temporal and spatial differences in clutch size between *Larus* colonies in southern Alaska, populations of *argentatus* are not significantly different from mixed or *glaucescens* populations. Within the colony at Dry Bay, "pure" pairs of *glaucescens* are not significantly different from mixed pairs in mean clutch size.

The colony with the highest hatching success is the mixed population at Dry Bay in 1977. Rates of egg inviability in all colonies are low, and differences between populations in frequencies of inviable eggs are not significant.

The colonies where interbreeding is occurring, e.g., North Marble and Dry Bay, have higher mean clutch sizes and net productivity than colonies of either *glaucescens* or *argentatus* "pure" types. Although clutch size and fledging success of mixed versus "pure" pairs are not significantly different within the individual colony, the mixed pairs are reproducing slightly better than the *glaucescens* phenotypes, and southern Alaskan colonies with mixed populations are reproducing considerably more offshore per pair than colonies of either *argentatus* or *argentatus* parental types.

Chapter 6 contains a discussion of the research results, beginning with a section on the evolution of ancestral *Larus* populations. Current conditions for *Larus* populations in southern Alaska are discussed in the following section. Four theoretical alternative hypotheses for the existence of a narrow hybrid zone between *argentatus* and *glaucescens* are explored in search of the most reasonable explanation for the data collected during. this research. Aspects of the hybrid superiority hypothesis, combined with evidence that hybridization is occurring in geologically disturbed habitats, ecotones, and disclimax areas, provide an explanation for the *Larus* contact zone in southern Alaska. The *argentatus* x *glaucescens* contact zone is clearly narrow and at the interface between the two parental populations. The mixed populations of gulls are found as *argentatus* of the boreal lakes meets the marine *glaucescens* at the mouths of rivers and in recently deglaciated fjords. These conditions correlate with a change in climatic conditions from West Coast Marine to Boreal Interior, or from West Coast Marine to circumstances which mimic arctic conditions. The ecotones probably provided marginal habitats for the forms which represent ecological communities on either side of the ecotone. The gull hybrids are able to survive in the dynamic southern Alaskan contact zone because they do not have to compete in stable communities with species that are well adapted to those communities. The theoretical expected intermediate habitat providing maximum survival for F_2 and subsequent generations is a fresh-water/saltwater mosaic within a mixed West Coast Marine - Boreal Forest environment, precisely the environment near the mouths of the Alsek and Susitna Rivers in southern Alaska.

Pioneering gull populations in recently deglaciated fjordlands may hybridize because nonspecific mates are not available. The viable offspring, with mixed genonomes, may be at a selective advantage in the rapidly changing post-glacial environment.

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. Hybridization is expected to continue between Larus populations in Alaska in coming years. The gene flow between large white-headed gull populations will likely increase in future years as a secondary consequence of human activities., and may 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 is found to resemble that occurring between Larus gulls on the Siberian. coastline, and the relationship to the circumpolar Formenkreis is indicated.

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PART II

Breeding Ecology

Table of Contents

List of Tables

List of Figures

Figure

INTRODUCTION

The Larinae (gulls) have a world-wide distribution with 42 species. Gulls as a group may have evolved in the North Pacific and North Atlantic (Fisher & Lockley, 1954). Sixteen species of gulls are found in the North Pacific (Vermeer, 1970). Birds of this family have been considered chiefly inshore feeders, and most coasts support a smaller scavenging species and a larger more piratical type (Cody, 1973). Recent evidence indicates that large white-headed gulls can behave as essentially marine species, feeding far out at sea and coming to land only occasionally or to breed (Sanger, 1973; Isleib & Kessel, 1973; Harrington, 1975; Lensink, pers. comm.). Most gulls live in flocks; they forage together in characteristic patterns the year around and nest in colonies during the breeding season (Tinbergen, 1960). These gregarious birds nest in a wide variety of habitats ranging from vertical cliffs to open marshes (Smith, 1966a). Gulls lend themselves to population analysis, especially productivity, because of their colonial breeding tendency (Kadlec & Drury, 1968).

An important reason for studying gulls is their use as indicators of the health of the environment (Vermeer, 1970). Chemical pollution of the environment poses an increasing and immediate threat to all organisms, including man. A recent survey conducted by the U.S. Fish & Wildlife Service of chemical residues in marine avifauna showed gulls to be among the most contaminated birds examined, probably due to their feeding habits (Ohlendorf, pers. comm.). Since gulls nest in colonies, changes in breeding populations can be monitored and related to environmental conditions, among which are industrial development and the concurrent changes in food supply.

An additional reason for studying gulls is that the age structure, mortality rate, life expectancy and survival rates of gull populations aid in the general understanding of population mechanisms. The mere knowledge of the size of a population from year to year indicates little about population problems without such data (Paynter, 1949).

The size, age structure, growth or decline of a population are a result of fluctuations in time and space of natality and mortality, in addition to movement into or out of a population of a species. Breeding adults form the base of the population structure structure, because only by successful production of young can a population grow or maintain itself (Kadlec & Drury, 1968).

Reproductive rate has an important effect on age structure and growth of the population. The average number of young which a breeding pair can raise to fledging is a good measure of gull reproductive success. Meadow-nesting gulls are excellent subjects for a study of reproductive success because eggs and young are readily accessible. Information is available on breeding biology and dynamics of gulls near large urban centers or in recent post-glacial environments; but comparative base-line data on gulls along the southern coastline of Alaska prior to the development of oil resources is completely lacking.

This report presents results of a study of meadow-nesting gulls in widely-spaced colonies in the northeast Gulf of Alaska. These sites have been selected for research because of the incipient development of oil resources in the vicinity and the necessity to provide base-line information on marine birds along this relatively wild stretch of Alaskan coastline.

The overall objective of this study has been an investigation of the reproductive biology of the "brown rat with wings" to answer the key question of reproductive rate and the factors which influence it prior to the development of oil resources. Reproductive rate in gulls can be measured in chicks produced per nest per year. We have studied colony sites, behavior of adults and young, and feeding areas. We gathered supporting information on distribution and pathologies which will become increasingly important and compared the data to our knowledge of other Alaskan gull populations. We banded a large number of gulls, and color-marked, collected and removed blood samples from others. We carried out a concentrated investigation of the breeding biology of Larus glaucescens on Egg Island near the mouth of the Copper River, in Chugach National Forest, near Cordova, Alaska, and surveyed other gull colonies on barrier islands off the Copper River Delta. We examined a mixed colony of Larus argentatus and Larus glaucescens at Dry Bay, mouth of the Alsek River, in Tongass National Forest near Yakutat, Alaska. Included in this report is information preciously gathered on a L. glaucescens colony on Haenke Island at Disenchantment Bay (near Yakutat) and data from North Marble Island in Glacier Bay National Monument (Fig. 1).

The Glaucous-winged Gull (L. glaucescens), which breeds along the coast from Washington Stare to the Aleutians, is quite closely related to the Herring Gull (L. argentatus), a common and widely distributed species. Herring Gulls make, up a low proportion of the breeding gulls in the northeast Gulf of Alaska, but occur more commonly in winter and offshore. The Herring Gull replaces the Glaucous-winged Gull in interior Alaska, British Columbia, and the Yukon. The Glaucous-winged Gull is morphologically similar to the Herring Gull except that the black pigment on the tips of the -primaries is replaced by a light grey usually matching the rest of the mantle. Conversely, the eye of the Glaucous-winged Gull is darker than that of the Herring Gull. These two gulls are considered separate species in the A.O.U. Checklist of North American Birds (1957), but the taxonomic and ecological relationships between the two have not been clearly defined. In some areas hybrids are common (Fig. 2a,b).

We gathered information on other species of plants and animals inhabiting coastal areas of the northeast Gulf of Alaska to support the main objectives of our study. This final report presents the results and analysis of data collected in 1975-1978 in addition to material from previous years of research.

SCOPE AND SIGNIFICANCE OF THE STUDY

The nature of this study has been to examine reproductive biology in colonies of Herring and Glaucous-winged Gulls in the northeast Gulf of Alaska. This report covers information from 1978 and earlier field seasons. We have studied several aspects of gull breeding biology for comparative purposes. Such information is available in the literature for gull populations outside of Alaska and from Glacier Bay to the southeast of the current study area (see Lit. Cited section). The comparison serves as a basis from which to draw conclusions.

An important aspect of this report is the data on fledging success. As can be *seen* from the literature review, fledging success can serve as an index to the dynamics of an avian population. If fledging success is poor over a number of seasons, a population will decline through adult mortality and low recruitment of breeding adults. If fledging success is high, one can expect a stable or expanding population. We present here 1975 and 1976 fledging success from the largest gull colony in the northeast Gulf of Alaska. We offer supporting data from other colonies in the NEGOA (1972-1978).

Results from this study provide the National Oceanic and Atmospheric Administration and the Bureau of Land Management with specific information concerning, the status of a marine-oriented animal population during successive breeding seasons prior to the development of oil resources. More broadly, this report indicates additional areas to be investigated for a better understanding of an Alaskan marine bird species under environmental conditions certain to change with increasing human activity.

CURRENT STATE OF KNOWLEDGE

The breeding biology of gulls, especially the Herring Gull, has been studied in detail by Goethe (1937), Paludan (1951), Tinbergen (1960), Harris (1964) and Ludwig (1966). Their results consistently indicate that Herring Gulls raise an average of one young per pair per year to fledging. Extremes of variation are shown to be 0.5 by Paludan (1951) and 1.5 by Ludwig (1966) (in Kadlec and Drury, 1968). The population dynamics of the Herring Gull in eastern United States and. Canada have been reasonably well Investigated by Kadlec and Drury (1968). : Kadlec and Drury (loc. cit.) found the usual productivity is apparently 0.8 to 1.4 young per nest in the New England Herring Gull, averaging about 50 percent fledging success. They showed this to be a major factor in the structure of the New England Herring Gull population, which has been rapidly increasing since the turn of the century. In a later paper (Kadlec et al., 1969) they examined the critical period between hatching and fledging for mortality factors.

Their results indicate the average clutch size in the Herring Gull is nearly always three, and. variations are small (Keith, 1966; Brown, 1967b; Paynter, 1949; Kadlec and Drury, 1968). Hatching success is usually 60 to 80 percent. Keith (1966) has discussed in detail the problems of accurately measuring success, which are due to predation or cannibalism of eggs and chicks before they can be counted. Critical factors effecting hatching and fledging rate are chick and egg loss through cannibalism, chick mortality due to aggressive behavior of adults, and weather conditions during the breeding season (Paynter, 1949; Paludan, 1951; Tinbergen, 1960; Brown, 1967b).

In contrast to the intensive investigations of Herring Gulls in Europe and eastern North America, few workers have studied gulls along the Pacific Coast of North America. Breeding biology of the Western Gull (Larus occidentalis) has been studied by Coulter (1969), Schreiber (1970), Harpur (1971) and Coulter, et. al. (1971). Aspects of the breeding biology are similar to those of the closely related Herring Gull, but nesting habitat selection and nest materials differ because of the drier conditions on California islands. Recently Hunt and Hunt (1973) and Hunt and McLoon (1975) have investigated supernormal clutches, aberrant pairing, and chick mortality in Western Gulls.

Vermeer (1963) published a major work on the breeding biology of the Glaucous-winged Gull, although Schultz (1951) reported on growth in this species. In most aspects the Glaucous-winged Gull is similar to the Herring Gull, including plumage sequences (Schultz, ins).

Other important papers on gulls are those of Coulson and White (1956, 1958, 1959, 1960) on the Kittiwake (Rissa tridactyla), in which they attempt to refute Darling's (1938) contention that egg-laying synchrony in the Herring Gull and the *Lesser* Black-backed Gull was related to social facilitation, Darling's (1938) hypothesis of social stimulation suggests that stimulation received from other birds in a colony produced greater synchrony of egg-laying within the colony. This in turn resulted in earlier egg-dates and a shorter spread of egg-laying in large colonies. Coulson and White (1956), however, showed that the difference in breeding times between colonies of the Kittiwake was not significant and that the spread of egg-dates increased with the size of the colony. Coulson and h'bite (1960) observed that the greater part of the differences in time of breeding were correlated with density. They found that the spread of breeding was greatest in dense colonies of Kittiwakes, which does not support Darling's contention. Moreover, breeding occurred earlier in the more dense colonies. Hunt and Hunt (1975) have found in the Western Gull, which tends to nest on level ground, that territory size expands and agonistic interactions increase with the hatching of chicks.

Cullen (1957) reported on adaptations of the Kittiwake to cliff-nesting, which was followed by N.G. Smith's (1966a) work on adaptation to cliff-nesting in arctic gulls (Larus), and his more extensive study (1966b) on evolution in arctic gulls. Smith found four sympatric species on Baffin Island to be reproductively isolated due to such mechanisms as species recognition and nesting habitat selection. Ingolfsson (1970) noted rapid evolution in Icelandic gulls (Larus argentatus and Larus hyperboreus since 1925, probably due to a secondary contact between these species associated with the development of large-scale Atlantic fisheries and the concurrent spread of the Herring Gull to Iceland.

In summary, one finds that the Herring Gull and relatives in North America lay a clutch of three from which they normally fledge one young per nest per year. Predation and attacks by members of the same species are the primary factors responsible for egg and chick loss. Gulls have increased rapidly in Europe and eastern North America within the last seventy years. The increase in gull population is associated with environmental deterioration, due to increases in refuse, fish scraps, and similar garbage (Fig. 6).

Breeding Ecology

Nest Site Selection: Slope. Substrate. and Cover

Southern Alaskan argentatus and glaucescens nest on a variety of substrates ranging from bare cliff ledges in fjords in Glacier Bay to flat gravel bars at Dry Bay to sloping grassy meadows at Egg Island, North Marble and Lake Louise.

Glacier Bay is rather interesting in this context . It is recently deglaciated; while not in the arctic, it approximates high arctic conditions in some areas. Smith (1966b) reported that argentatus are present in small numbers at the heads of fjords around Baffin Island in the eastern Canadian arctic. We also found argentatus in Glacier Bay in fjords close to glacier fronts; glaucescens tend to concentrate in lower regions, more marine, in Glacier Bay, around the Marble Islands and the Beardslee Narrows. But argentatus and glaucescens also nest together on cliff faces near the glaciers. There are apparently insufficient isolating mechanisms in both nesting habitat selection and species recognition because they hybridize. From field notes of 24 July 1971, at William Field Cairn #3, 4 km from the front of Johns Hopkins Glacier, on the north side of Johns Hopkins Inlet, facing the glacier:

> "Sea cliffs. Cliffs several hundred meters long and several hundred meters high in near vertical slope. Sat for several hours--in fact all morning--observing birds from cairn #3. Noted Herring Gulls, Glaucous-winged Gulls, and some intergrades between them in the amount of black on the primaries. Herring Gulls have cat-yellow iris . Glaucous-winged have dark iris. All different amounts of black on wing-tips seen--some just very tips of primaries black, some with just ends and tips of primaries black, and some typical of usual Herring Gulls."

We also observed partially fledged -chicks on ledges on the cliff face. In subsequent field seasons we found glaucescens and argentatus nesting together in Glacier Bay on low rocky islets, flat gravelly islets, and sloping grassy hillsides (Part I, Table 23).

Dry Bay, at the mouth of the Alsek River, south of Yakutat and northwest of Glacier Bay, provides different conditions. About 500 pairs of gulls nest on flat gravel bars near the river mouth. The low alluvial islands are washed by high waters following summer storms and snow-melt in the mountains. Vegetation as a consequence of unstabilized substrate plus periodic flooding is sparse and indicates a combined maritime and fresh-water influence. Japanese glass floats found on the gravel bars indicate winter storm tides flood Dry Bay with salt-water. The gull population, hybrids between argentatus and glaucescens, reflects these mixed coastal and interior conditions. Vegetation cover is important for nest site selection, since nests are clumped near drift logs, willow bushes and grass patches. Gravel beds where gulls do not nest divide parts of the island colony at Dry Bay (Pt. I, Figs. 5 & 6). When melt-waters combine with heavy rainfall (as a summer storm follows days of sunshine), the river rises and fills the gravel beds. If gulls nested on these gravel beds or too close to the periphery of the island, their nests would be washed away under these conditions. Physical conditions subject to rapid changes influence nest sits selection at Dry Bay and in colonies off the Copper River Delta (see Egg Island study area, in Methods), but less so at North Marble and Lake Louise.

L. glaucescens and L. argentatus and hybrids must be flexible in nesting habitat selection due to the dynamic conditions in which they nest. L. glaucescens and L. occidentals also nest in a variety of habitats when sympatric (Scott, 1971; Hoffman, 1976; see also Vermeer, 1963; Coulter et al., 1971).

Thousands of glaucescens at Egg Island nest on stabilized meadow-covered dunes, usually in proximity to old drift logs or Sambucus bushes

Slope of the dunes is shallow, averaging less than 3%. The highest dunes are only ten meters above sea level. Egg Island, as North Marble, has highest densities of nesting gulls on completely open meadows. Some sites on North Marble are precipitous, however, approaching 50% slope (Part I Table 24). Gulls in both colonies tend to select breeding habitat where approaching predators can be easily detected. Few gulls nest in brush fringes on North Marble, but some *glaucescens* nest directly beneath bushes On Egg Island. Brush-nesting *glaucescens* are previously reported by Vermeer (1963) and Manuwal (pers. comm.) in Puget Sound. Tinbergen (1960) noted nesting *argentatus* react positively to bushes. Haycock and Threlfall (1975) observed *argentatus* in Newfoundland nesting in proximity to prominences such as boulders, trees or stumps. This form of nest site attraction may represent previous affinity for cliff-nesting. *L. argentatus* at Lake Louise nest on a grassy islet with similar slope and substrate to North Marble *glaucescens*, *argentatus*, and hybrids (part I, Table 23).

According to Smith (1966), the *Larus* gulls around Baffin Island freely intermixed only during the few days after arrival in the Arctic, when they occurred together in flocks along the edge of the land-fast ice, and when they moved onto the cliff faces. Habitat separation may reduce the potentiality for mixed matings among gulls in the eastern Canadian Arctic. Knudsen (pers. comm.) is further investigating this topic in Baffin Island and New Brunswick. *L. argentatus* in the eastern Canadian Arctic tends to select a nesting place on small islets in flat marshy areas (Smith 1966). Despite selective pressure exerted by ground predators, *argentatus* has not colonized cliff faces. The isolating effect was apparently greatest in Smith's area between *argentatus*, and the cliff-nesting *hyperboreus*, *thayeri* and *glaucoides kumlieni*. In other areas, such as New Brunswick, Niagara Falls, N.Y., and the Lake Superior shoreline in Wisconsin, argentatus nest on cliffs (Emlen, 1963; Harris and Matteson, 1975; Andrle, 1976), and are otherwise plastic in nest site selection. Drury and Nisbet (1972) find argentatus in New England highly adaptable to changing circumstances, since the seashore is subject to continuous changes in detail.

Territory Size

The definition of territory, as Hinde (1956) states, is "any defended area." This definition does not necessarily imply the defended area is sharply delimited, but in practice many workers on territory (references in Hinde, 1956) imply the existence of such borders by measuring territory size. Using the measure of territory for gulls defined by Harpur (1971), we calculated the area of each nesting territory as a circle with a radius half the distance to the nearest active nest. In reality, gulls do not defend neat circles. Actual territory size depends upon the stage of the reproductive cycle, expanding with hatching of chicks, and declining as chicks grow older (Hunt & Hunt, 1975). Nevertheless we have elected to use Harpur's measure because it is standardized and can be compared to other studies. The distance to nearest neighbor, upon which we calculate territory size, may be an important factor in determining gull chick survival (Hunt & Hunt, 1975).

Patten (1974) previously reported a mean territory size of 18 m^2 for the colony at North Marble, but territory size varied from sub-colony to sub-colony and from year to year (Table 2). At Dry Bay 'A' colony in 1975 mean territory size was 29.8 m^2, suggesting room for more breeding pairs (mean distance to nearest neighbor was 6.16 m^2). Mean -territory size at Dry Bay 'A' colony in 1977 was quite similar, 30.9 m^2, with virtually the same number of pairs inhabiting the identical survey area. Dry Bay 'B' colony in 1977, which had not been previously surveyed, was less densely utilized, with a mean territory size of 48.51 m^2 and a relatively large internest distance of 7.86 m. Both 'A' and 'B' colonies produced well over one chick per nest to fledging (Table 1).

Table 1

Gull Reproductive Parameters, Dry Bay 1977

	Colony 'A' - 300 m x 50 m	Colony 'B' - 30 m in 0
Clutch Size	2.94 (90 nests - 265 eggs)	2.86 (22 nests - 63 eggs)
Egg Loss	10 (3.8%)	7 (11.1%)
Infertile Eggs	8 (3%)	0
'Pipped' but failed to hatch	2 (.8%)	0
Hatching success	245/265 (92.4%)	59/63 (93.6%)
Chick Loss	111/245 (45.3%)	31/59 (52.5%)
Chicks Fledged	134	28
Fledging Success	1.49 chicks/nest	1.27 chicks/nest
or	50.5% chicks fledged/ eggs laid	44.4% chicks fledged/ eggs laid
or	54% chicks fledged/ chicks hatched	47.5% chicks fledged/ chicks hatched

NOTES : 1 supernormal clutch of 4 eggs in 'A' colony, which hatched. (1/90 = 1.1%)

1 replacement clutch of 3 eggs in 'A' colony. (1/90 = 1.1%)

Chick loss was due mostly to sustained, heavy eagle predation (eagle nest within 2 km of the gull colony).

Chick loss was clearly the major factor influencing fledging success at Dry Bay in 1977.

Mean territory size on Egg Island in 1975 was 28.9 m^2. (mean distance to nearest neighbor was 6.06 m) (Table 2). Territory size, as at Dry Bay, remained practically identical the next season surveyed, but there were 20% more nests in the study area (30.2 m^2; mean distance to nearest neighbor 6.2 m^2). This suggests gull pairs distribute themselves due to social attraction at this density but clearly do not use all available space (weighed mean territory size for 1975 and 1976 was 29.6 m^2).

The migratory population of argentatus, breeding at the interior Lake Louise in 1977, showed a mean territory size of 13.5 m^2 and a mean inter-nest distance of 4.3 m. 77 pairs bred in a relatively confined area of 0.36 hectare on a lake islet (Part I, Fig. 13; Part II, Table 2).

We found large differences in internest spacing and territory size for glaucescens breeding on grassy meadows on Egg Island and the mixed colony dominated by glaucescens at North Marble, also nesting on grassy meadows. Hybrid gulls nesting on gravel bars at Dry Bay and glaucescens on meadow-covered dunes on Egg Island had similar territory sizes (Table z). Notable is the large territory size at both Egg Island and Dry Bay. The study area at Egg Island showed an increased number of pairs the second field season, while the Dry Bay colony did not. The argentatus nesting on the sloping grassy meadows at Bird Island at Lake Louise had small territory sizes, in sharp contrast to large portions of the meadows on Egg Island, not even colonized due to recent ('64) earthquake activity doubling the island surface area. This suggests interior argentatus are close to using all available nesting space, but other argentatus-group populations are flexible in internest distances and are not limited by available nesting space in their northeast Gulf of Alaska breeding sites. It is not unreasonable to expect increasing gull populations in coastal districts, with an increasing food supply due to human activities. This is especially true off the Copper River Delta.

Since territory, as expressed as a multiple of the distance to nearest neighbor, may be important in determining gull reproductive success, we have explored the influence of territory size by plotting various parameters against it. We have plotted mean clutch size, egg loss, chicks hatching, and chicks fledging against mean territory size by colony and by year. The results are presented in the following Figures: clutch size against territory size (Figs. 5, 6, 7, and 8); egg loss against territory size (Figs . 16, 17, 18, 19); chicks hatching against territory size (Figs. 28 29,30,& 31) and chicks fledging against territory size (Figs. 36,37,38 and 39) .

Egg-Laying

Gulls at North Marble, Dry Bay, Egg Island, and Lake Louise began to lay eggs in mid- to late May without regard to taxonomy. A remarkable degree of synchronization was apparent when comparing percentages of eggs found in sequential dates of observation through the nesting period (Figs. 9, 10 and 11). There was a strong tendency in these colonies for the majority of eggs to be laid in just over one week.

Egg-laying on North Marble was closely synchronized in all sub-colonies, although most eggs were laid two weeks earlier in 1973 than in 1972. In 1972, 50% of eggs *were* laid in a seven day period in late May (Fig. 9). In 1973, 60% of eggs were laid between June 5th and June 7th. The evidence from North Marble indicated not only a colony-wide synchrony, but a synchronous egg-laying in four partially contingent colonies, suggesting the gulls on North Marble were acting as one large colony.

The Dry Bay colony demonstrated flexibility in timing of breeding from year to year, as at North Marble (see pp41-43) but synchrony once the process began (Fig. 11). Gulls at Dry Bay laid 50% of eggs in an eight day period between May 15th and May 23rd, a pattern quite similar to North Marble.

The colony at Egg Island had 50% of eggs laid in just over one week, between May 30th and June 7th, similar to Dry Bay and North Marble (Fig. 10).

Incubation in Alaskan glaucescens did not begin until after the clutch of three was completed, usually about a week after the first egg was laid. Mean interval between eggs was two days (Patten, 1974). The onset of incubation at North Marble, Dry Bay, and in the Egg Island study areas was quite synchronized, and began immediately after the week in which most eggs were laid.

Table 2. Clutch Size, Number of Fledgl: and Territory Size in Southern Alaskan Gull c. .onies, 1972-1977

~lGr.v/Year		Number Of Nests Examined	Mean clutch Size	Mean Number of Fledglings	Mean Territory Size (m^2)
North Marble	1972				
East		94	2.8	1.8	14.3
West		36	2.9	2.2	18.3
North		20	2*6	1.5	32.7
Top		12	2.1	0.4	52.1
Total		162	2.8*	1.75*	20.2*
North Marble	1973				
East		104	3.0	1.6	14.0
West		60	2.9	2.2	12.5
North		15	3.0	1.7	36.1
Top		12	2.9	1.6	36.9
Total		191	2.96*	1.80*	16.7*
Dry Bay					
'A' Colony	1975	100	--	--	29.8
	1977	90	2.9	1.5	30.9
'B' Colony	1977	22	2.9	1.3	48.5
Egg Island	1975	153	2.4	1.0	28.3
Egg Island	1976	186	2.4	1.1	30.2
Lake Louise	1977	77	2.7	0.9	13.5

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* weighted means

The conspicuous exception was the Top Colony on North Marble in 1972, which resembled Egg Island.

We suggest age of the female as the most important factor influencing clutch size in southern Alaskan gull colonies. Clutch size increased in the North Marble Island Top Colony as the females became older and more experienced. This influenced reproductive success as measured in chicks fledged. Territory size was inversely related to clutch size *because* of the tendency of young, inexperienced pairs to nest on the periphery of the colony, in marginal sites, or in newly colonized areas, where internest distances (upon which we calculate territory size) were larger. This has important implications for the growth of the Copper River Delta gull populations in that clutch size and fledging success of these populations may increase over time, given sufficient sources of artificial food (see below).

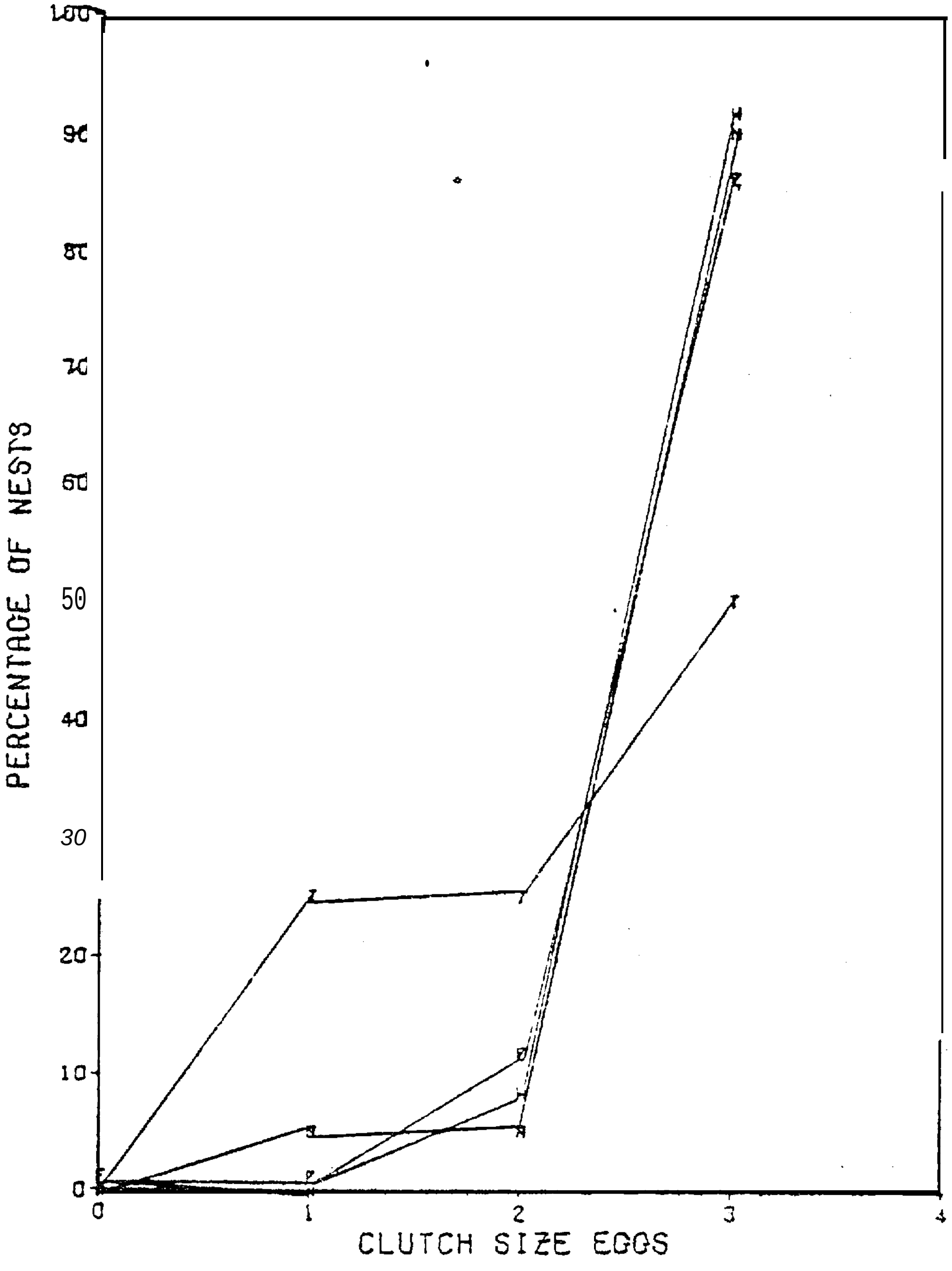


Figure 1. Clutch size plotted against percentage of nests, North Marble Island, 1972.
E = East Colony, W = West Colony, N = North Colony, T = Top Colony.
The Top Colony is different in clutch size; East, West, and North are similar.

The most likely explanation for the difference is young females laying for the first time produce smaller clutches.

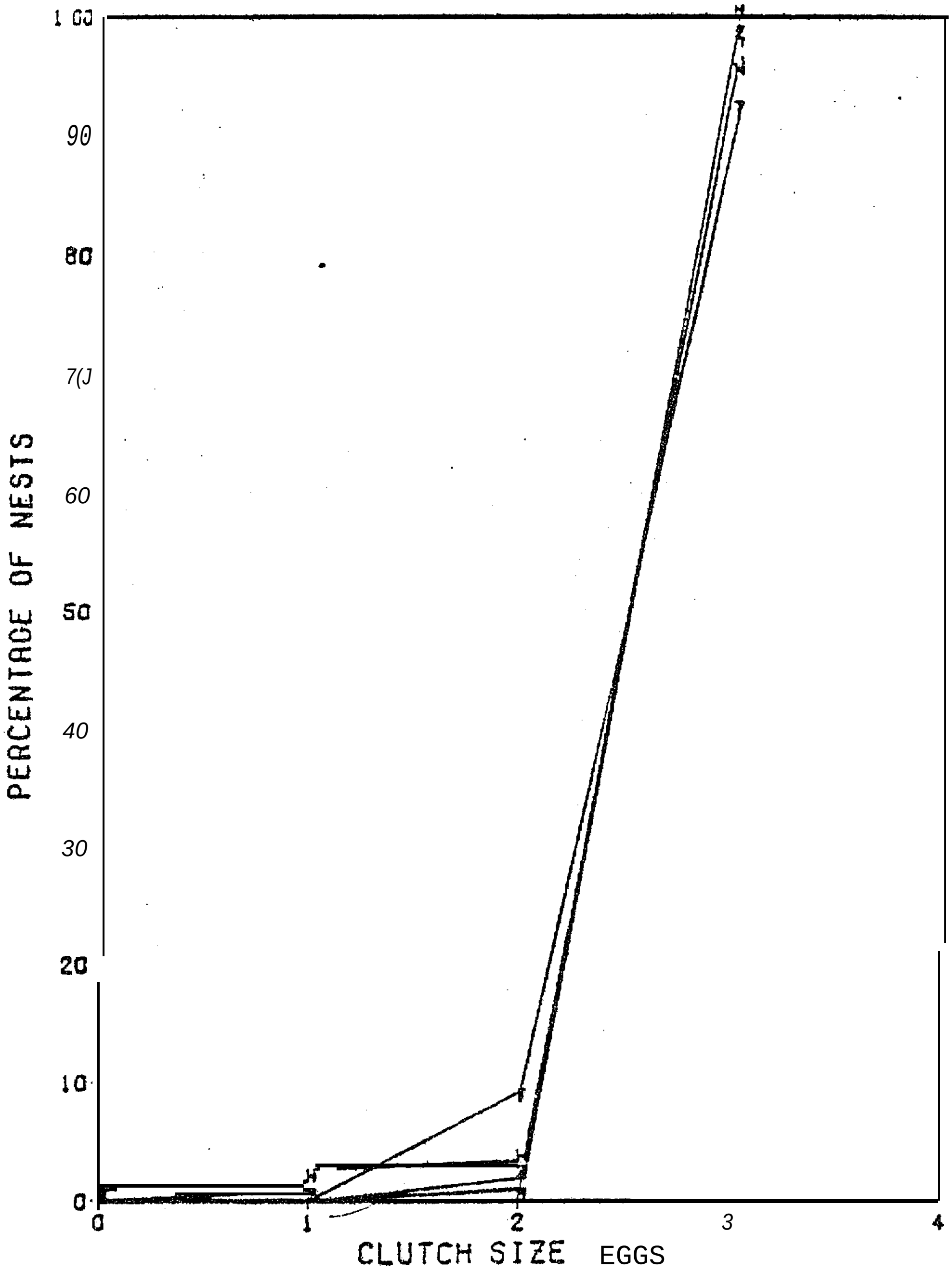


Figure 2. Clutch size plotted against percentage of nests, North Marble Island, 1973. E = East Colony, W = West Colony, N = North Colony, T = Top Colony.

All colonies show similar tendencies.

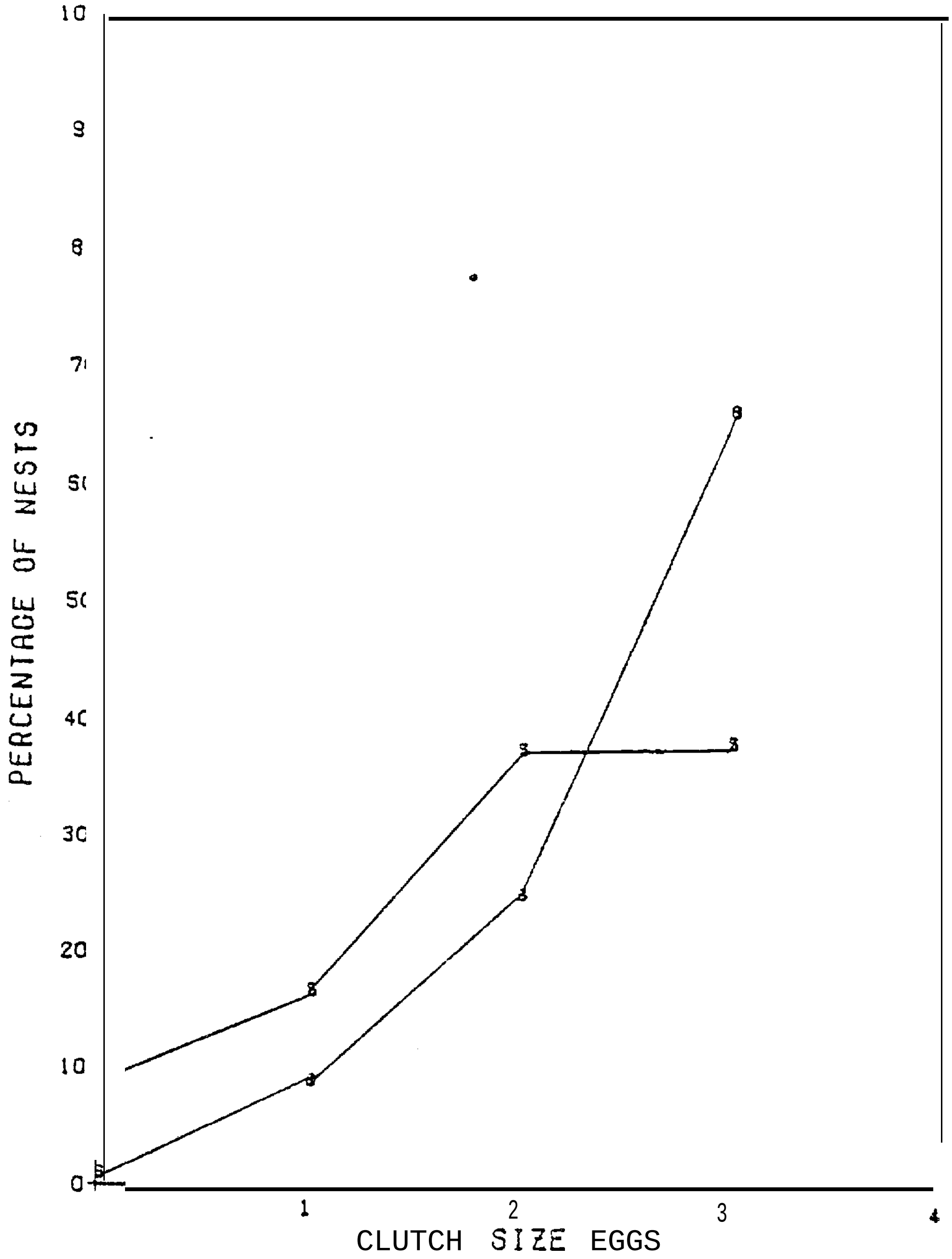


Figure 3. **Clutch size plotted against percentage of nests, Egg Island 1975 - 1976.** 5 = 1975 survey, 6 = 1976 survey.

Clutch *size* is *smaller on* Egg Island than on North Marble, probably due to the expanding population on Egg Island, with a higher percentage of young females producing smaller clutches. Egg Island most resembles the Top Colony on North Marble in 1972.

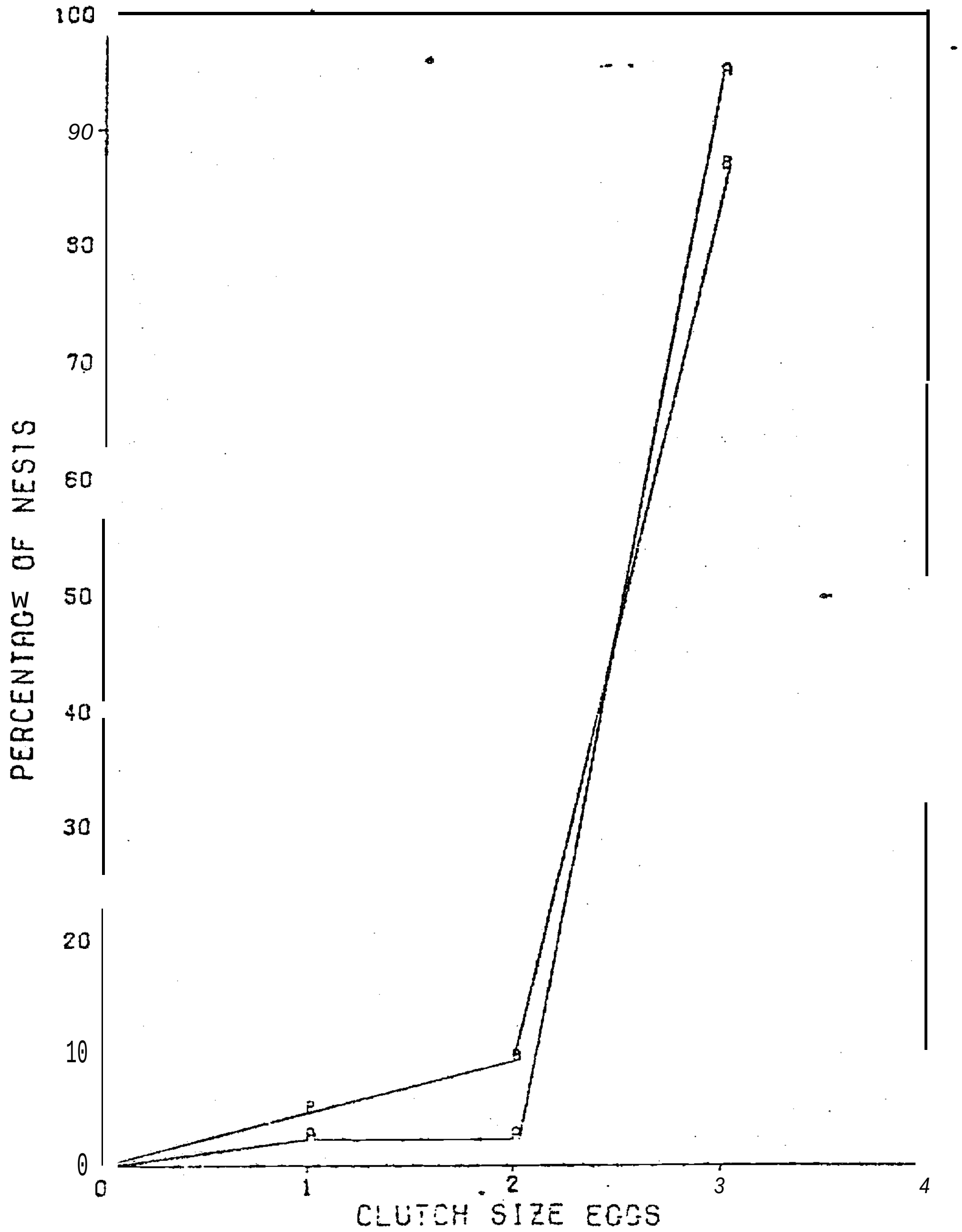


Figure 4. Clutch size plotted against percentage of nests, Dry Bay, 1977.
A = 'A' Colony, B = 'B' Colony

Both colonies are similar in clutch size and resemble clutch sizes on North Marble in 1973.

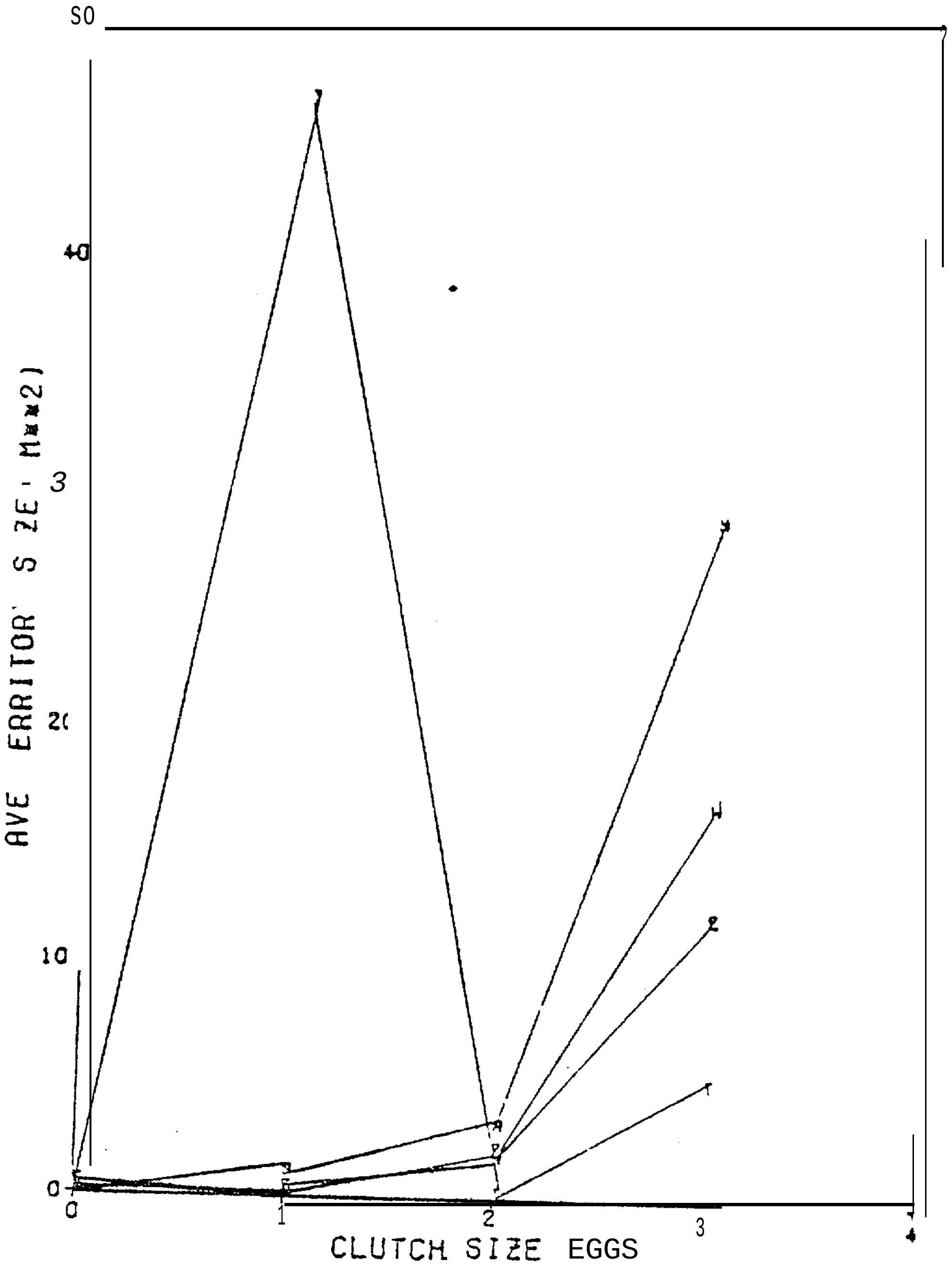


Figure 5. Clutch size plotted against average territory size, North Marble, 1972.
E = East Colony, W = West Colony, N = North Colony, T = Top Colony.

East, West, and North Colonies show rather similar tendencies. Top Colony is strikingly different, with a large mean territory size and concurrent 1-egg clutches.

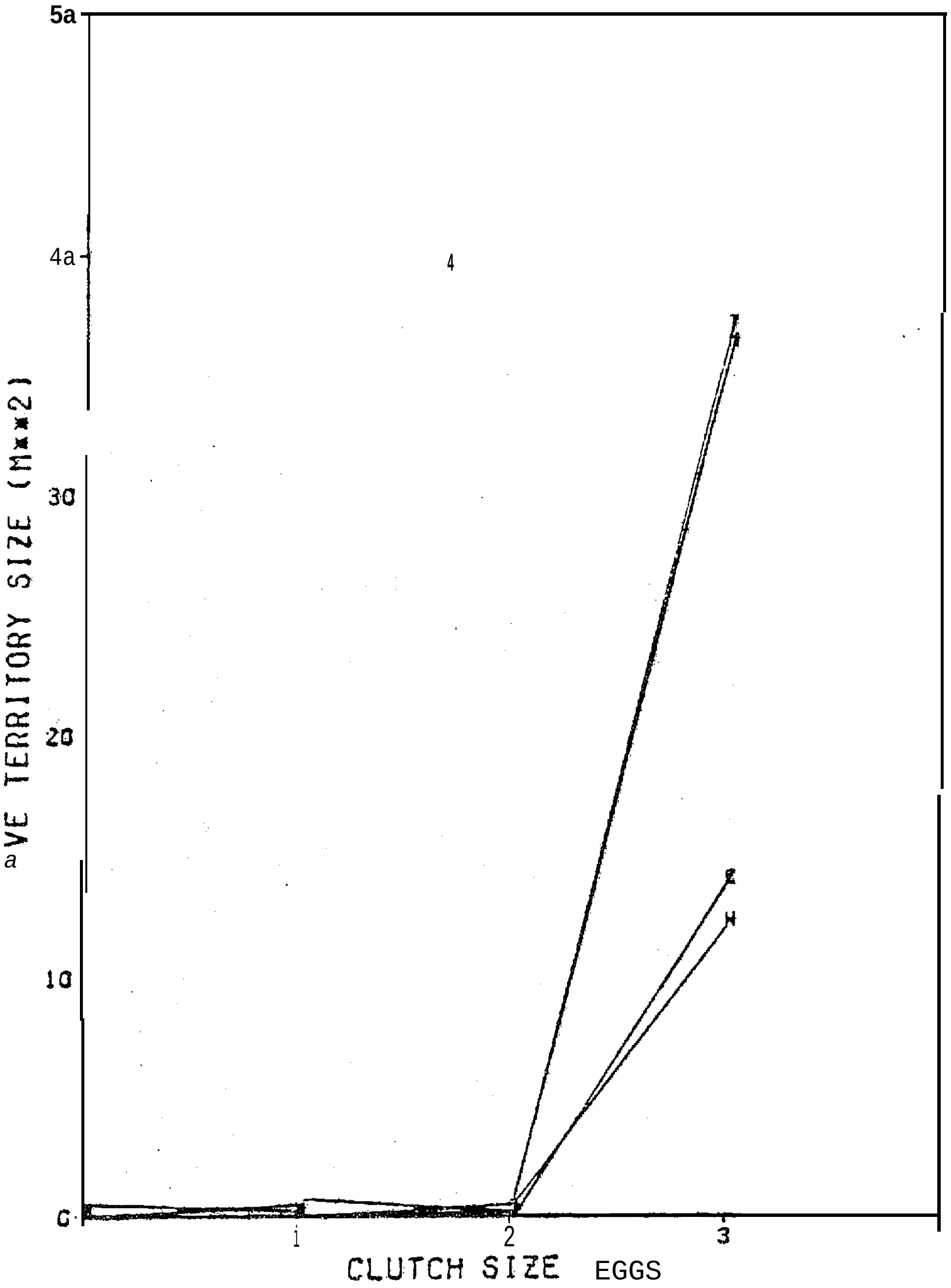


Figure 6 . Clutch size plotted against average territory size, North Marble, 1973.
E = East Colony , W = West colony , N = North Colony , T = Top Colony.

East and West Colonies are close in average territory size , as are Top and North Colonies. However all colonies exhibit a high proportion of three-egg clutches.

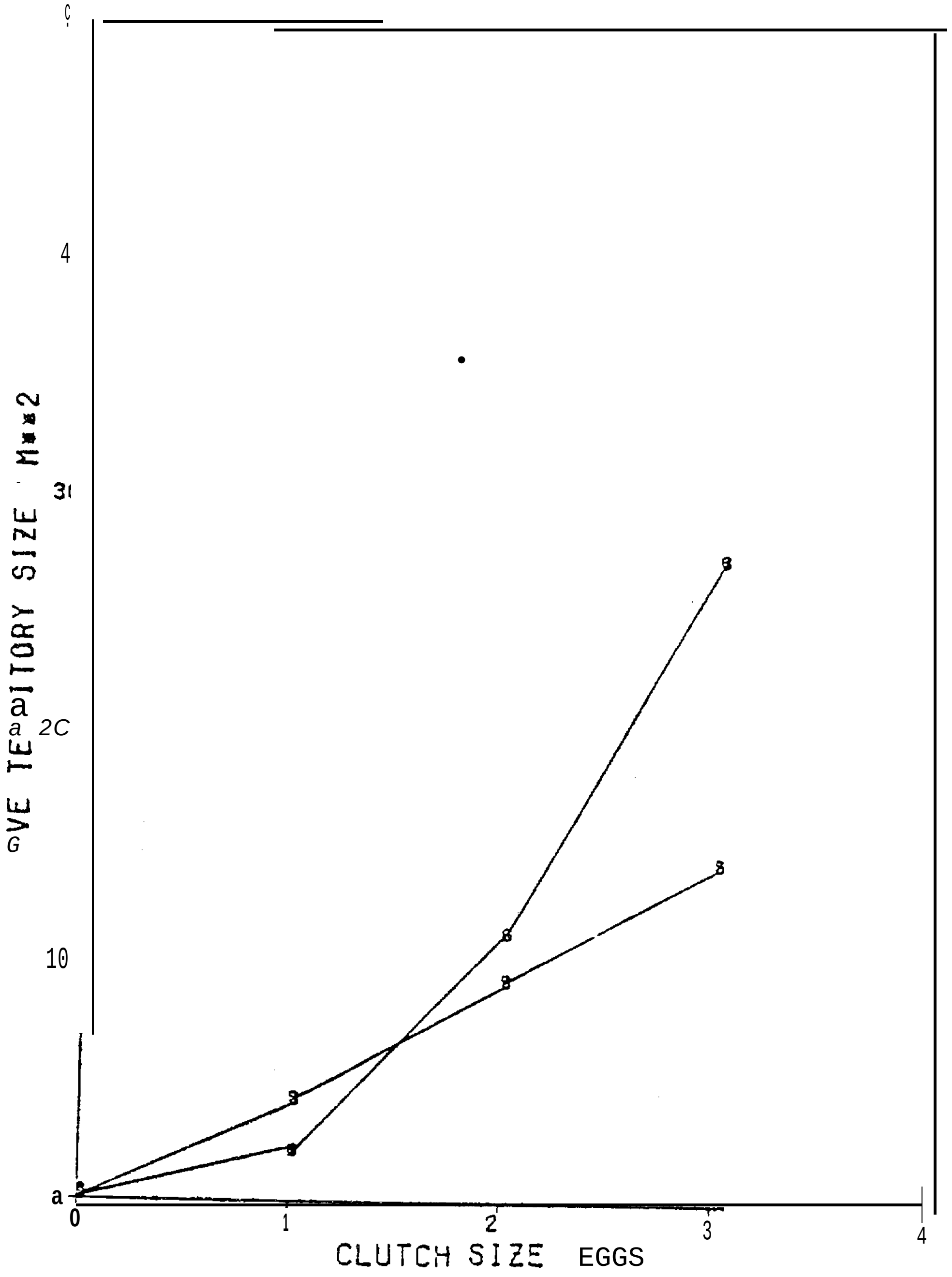


Figure 7. Clutch size plotted against average territory size, Egg Id.anti 1975 - 1976.
5 = 1975 survey, 6 = 1975 survey.

Territory size is significantly larger on Egg Island compared to North Marble, with a smaller pert--%e of three-egg clutches and a greater proportion of one-egg and two-egg clutches. The conspicuous exception is the Top Colony in 1972 (Figure 6), with large territory size and high percentage of one-egg clutches.

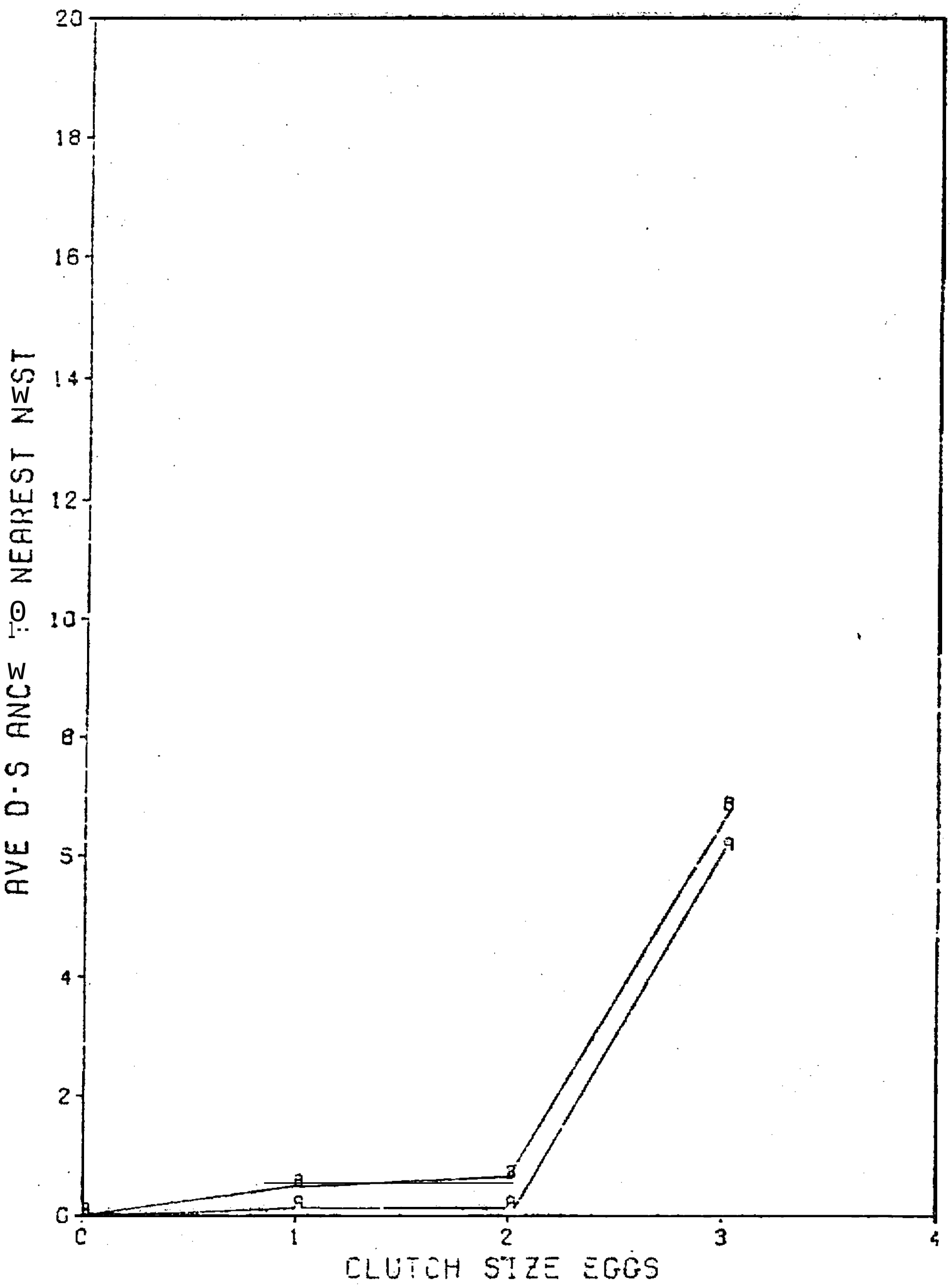


Figure 8. Clutch size plotted against mean distance to nearest nest, Dry Bay 1977.
A = 'A' Colony, B = 'B' Colony.

'A' and “'J' Colonies exhibit similar relationships in clutch sizes and distance to nearest neighbor.

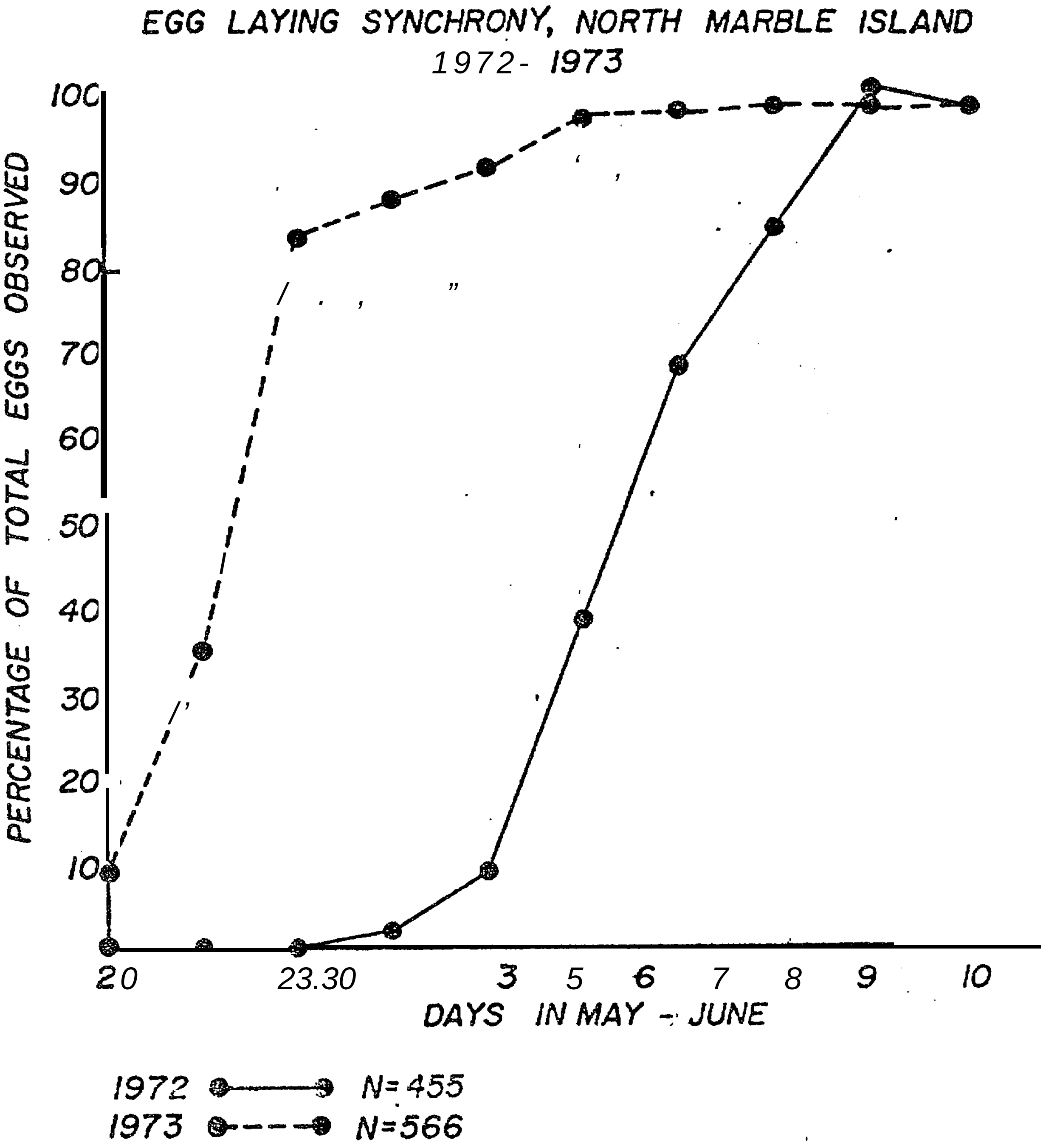

EGG LAYING SYNCHRONY, NORTH MARBLE ISLAND
1972- 1973
PERCENTAGE OF TOTAL EGGS OBSERVED
100
90
80
70
60
50
40
30
20
10
20
23.30
3
5
6
7
8
9
10
DAYS IN MAY - JUNE
1972 N=455
1973 N=566

Figure 9

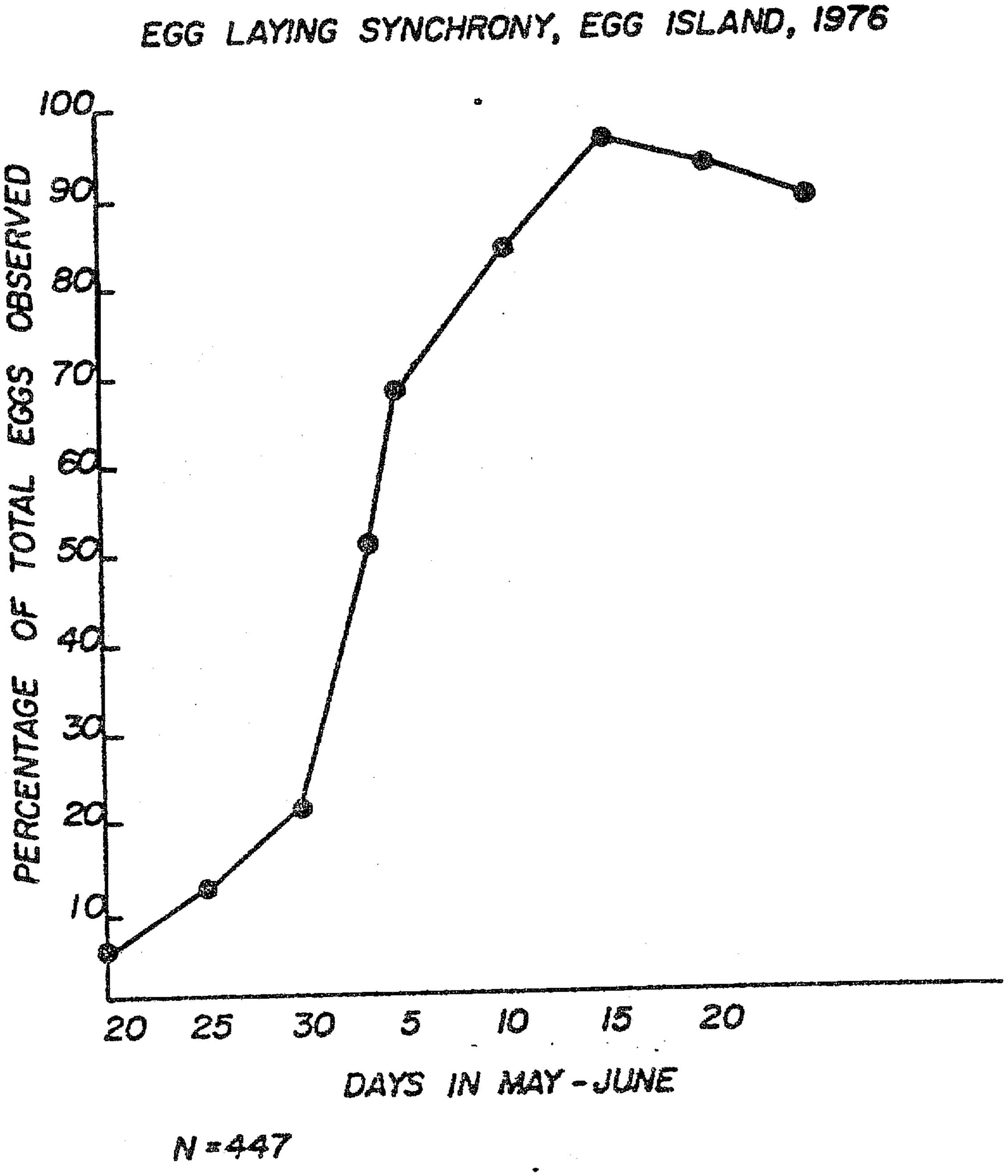

EGG LAYING SYNCHRONY, EGG ISLAND, 1976
PERCENTAGE OF TOTAL EGGS OBSERVED
100
90
80
70
60
50
40
30
20
10
20
25
30
5
10
15
20
DAYS IN MAY-JUNE
N=447

Figure 10

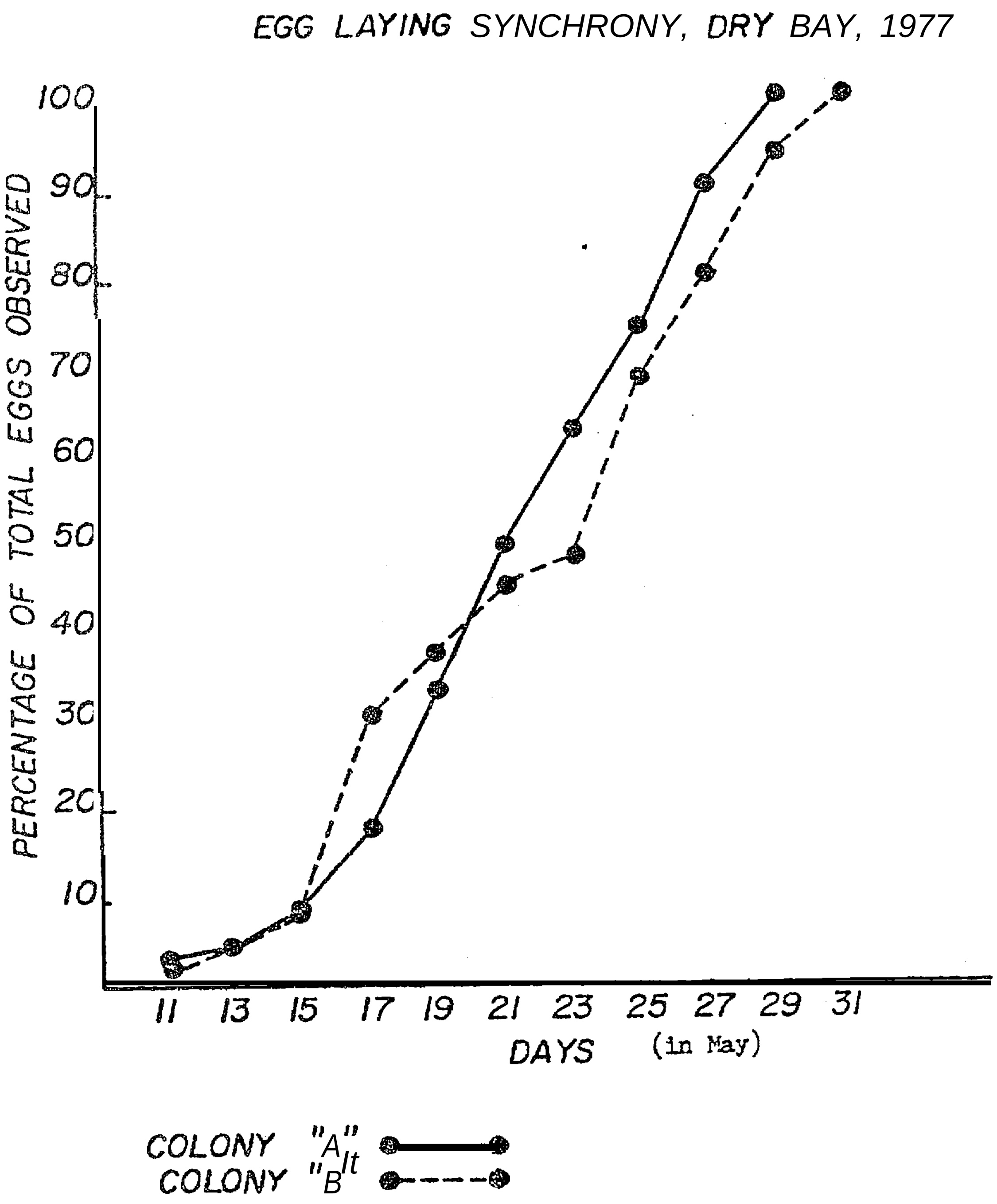

EGG LAYING SYNCHRONY, DRY BAY, 1977
PERCENTAGE OF TOTAL EGGS OBSERVED
100
90
80
70
60
50
40
30
20
10
11
13
15
17
19
21
23
25
27
29
31
DAYS (in May)
COLONY "A"
COLONY "B"

Figure 11

Hatching Failure

We attribute hatching failure in southern Alaskan gull colonies to three factors, using Paynter's (1949) formation: (1) eggs disappearing (lost) from the nest during incubation; (2) eggs remaining in nests but not hatching (dying); and (3) eggs which pip but the chick dies before emerging. We consider lost eggs to be hatching failures because almost all egg loss was due to predation in which eggs were destroyed.

Loss of eggs through predation was the principle factor influencing hatching race on North Marble (1972-73) and at Egg Island (1975-76) (Table 3). Results of the 1972-73 North Marble investigation indicated a 26-27% egg loss within a colony of 500 pairs (Table 3). Proportionate egg loss was similar from colony to colony at North Marble in 1972-73. Egg 105s plotted against average territory size (Fig. 16) . showed the following variations. The East and West colonies in 1972 were quite similar in percentage egg loss, while the Top colony had a high percentage loss of two eggs per nest. The North colony had a 20% complete clutch loss (3 eggs per nest). All colonies showed similar patterns of egg loss plotted against territory size in 1973 (Fig. 17).

The plot of egg loss against average territory size for Egg Island showed a correlation between large territory size and loss of one or two eggs in 1976; egg loss in 1975 resembled the pattern on North Marble (1972-73). Total" egg loss in the Egg Island study area (1975-76) was 26% (Table 3). These figures suggest a ±25% egg loss frequently occurs in gull colonies in the Northeast' Gulf"of Alaska. Natural predation 3.s due to other gulls, ravens, crows and jaegers. Subsistence egging by fishermen and natives causes much higher rates of egg loss in certain areas, notably on Egg Island near Cordova.

Egg loss was significantly lower (p< .05) at Dry Bay in 1977, compared to either North Marble or Egg Island. The low rate of egg loss (3% to 11%), was due to few ravens and crows on the Alsek Delta (Table 3). Minor egg loss was due to jaegers and other gulls. Colonies 'A' and 'B' at Dry Bay showed quite similar percentage egg loss suggesting little relationship to distance to nearest nest (Fig. 48 ; Table 3). Dry Bay most resembled North Marble in 1973 in egg loss to predation (Figs. 15,13).

A minor cause of non-productivity on Egg Island, North Marble, Dry Bay, and Lake Louise was eggs remaining in the nests but not hatching (dying). Study of the few decayed eggs did not reveal developed embryos or specific reasons for mortality (as in Paynter, 1949). We tentatively concluded the eggs were Infertile since the relative percentage of unhatched eggs was low (Table 3) and eggshells showed no signs of fragility or pesticide contamination.

The last cause of failure to hatch occurred when the chick pipped the shell but failed to emerge and died. There were only two cases in the Egg Island study area (1975-76); two each at Dry Bay and Lake Louise in 1977; and three cases on North Marble (1972-73). The rate at every colony was well below one percent of total eggs laid in the study areas (Table 3). These are not significant rates.

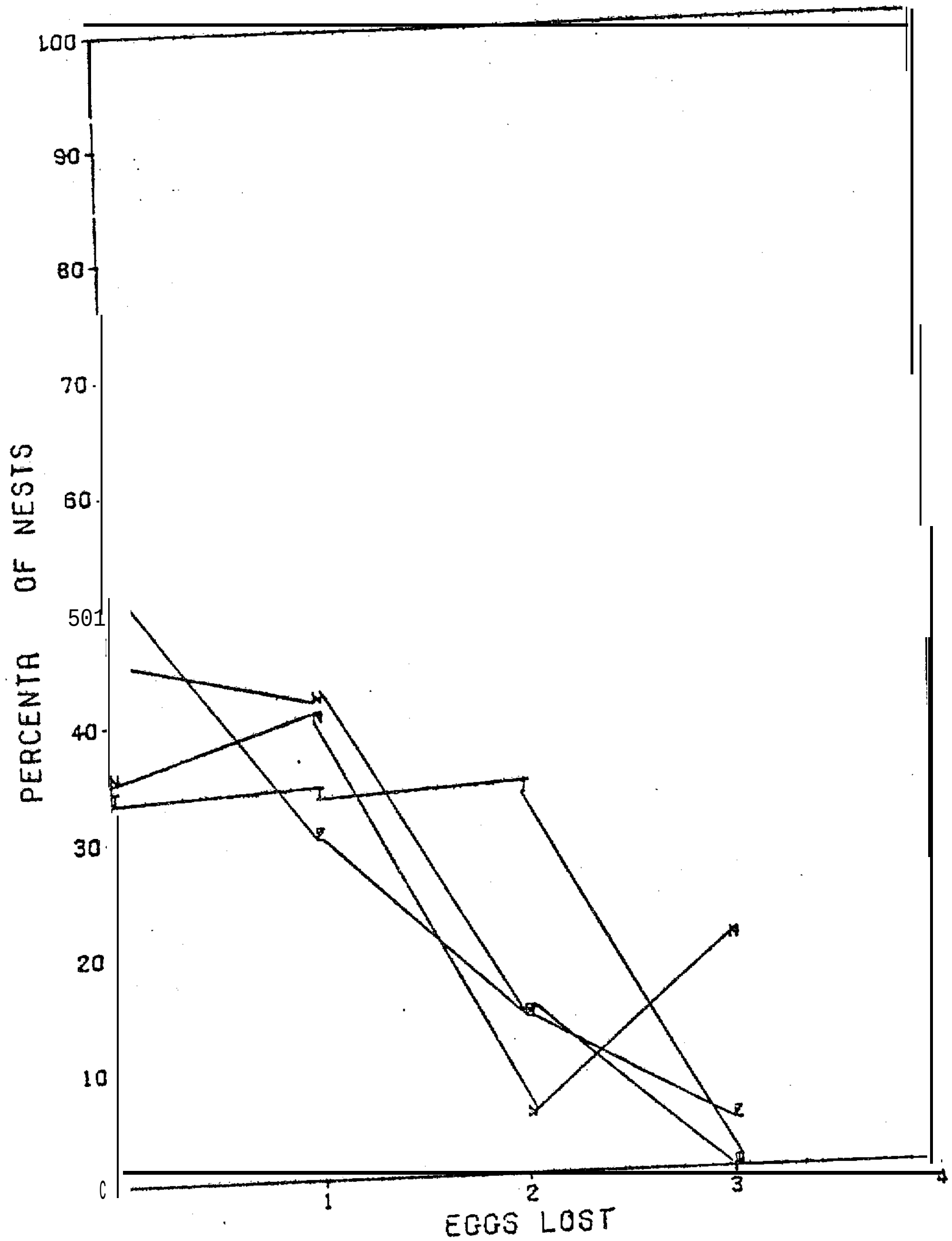


Figure 12. Eggs lost plotted against percentage of nests, North Marble, 1972. E = East Colony, W = West Colony, N = North colony, T = Top Colony.

East and West Colonies are quite similar in percentage egg loss. Top Colony had a higher percentage 2-egg loss, and North Colony had 20% complete clutch loss.

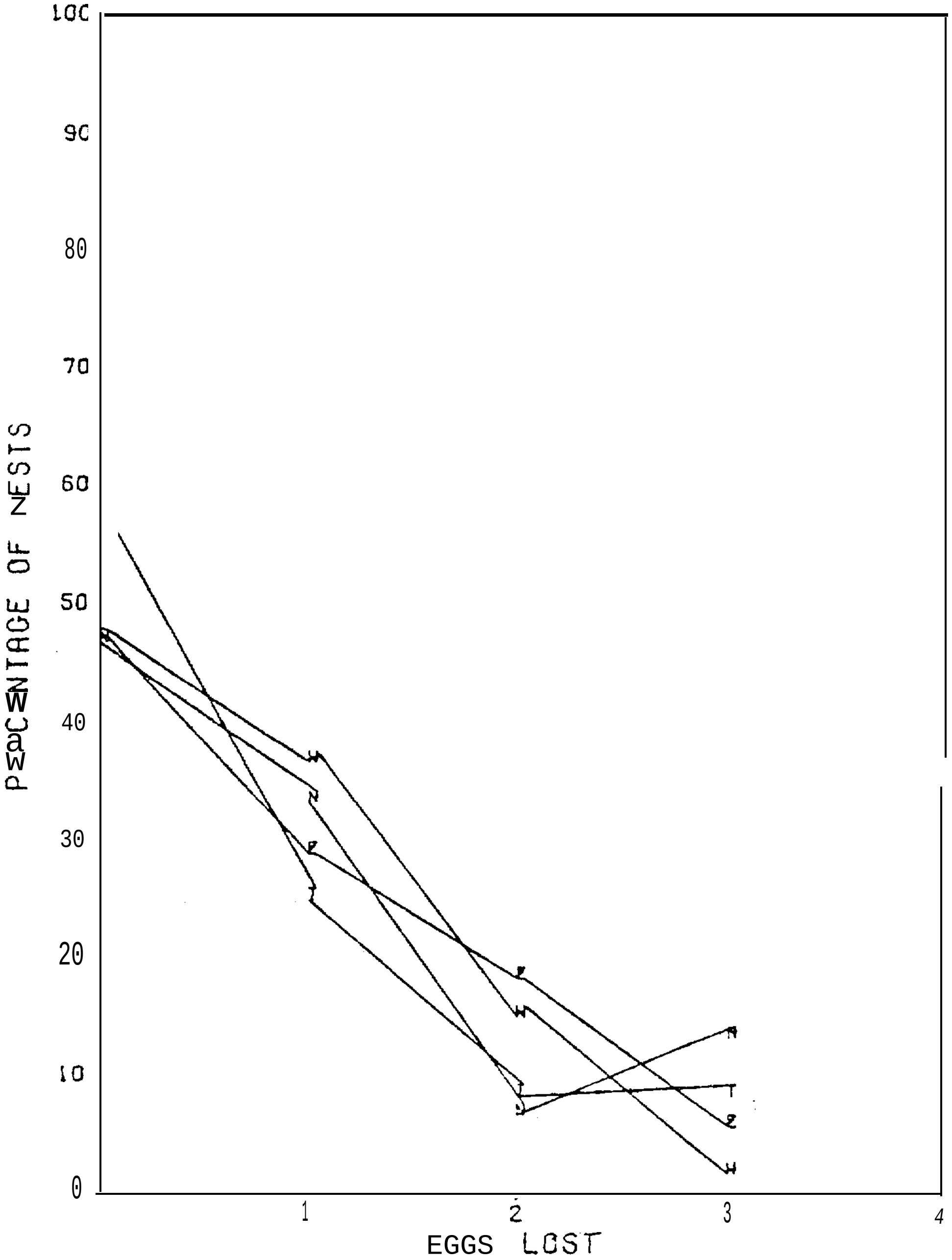


Figure 13. Eggs lost plotted against percentage of nests, North Marble, 1973.

All colonies show highly similar tendencies in eggs lost to predation. Predators are mostly conspecific adults.

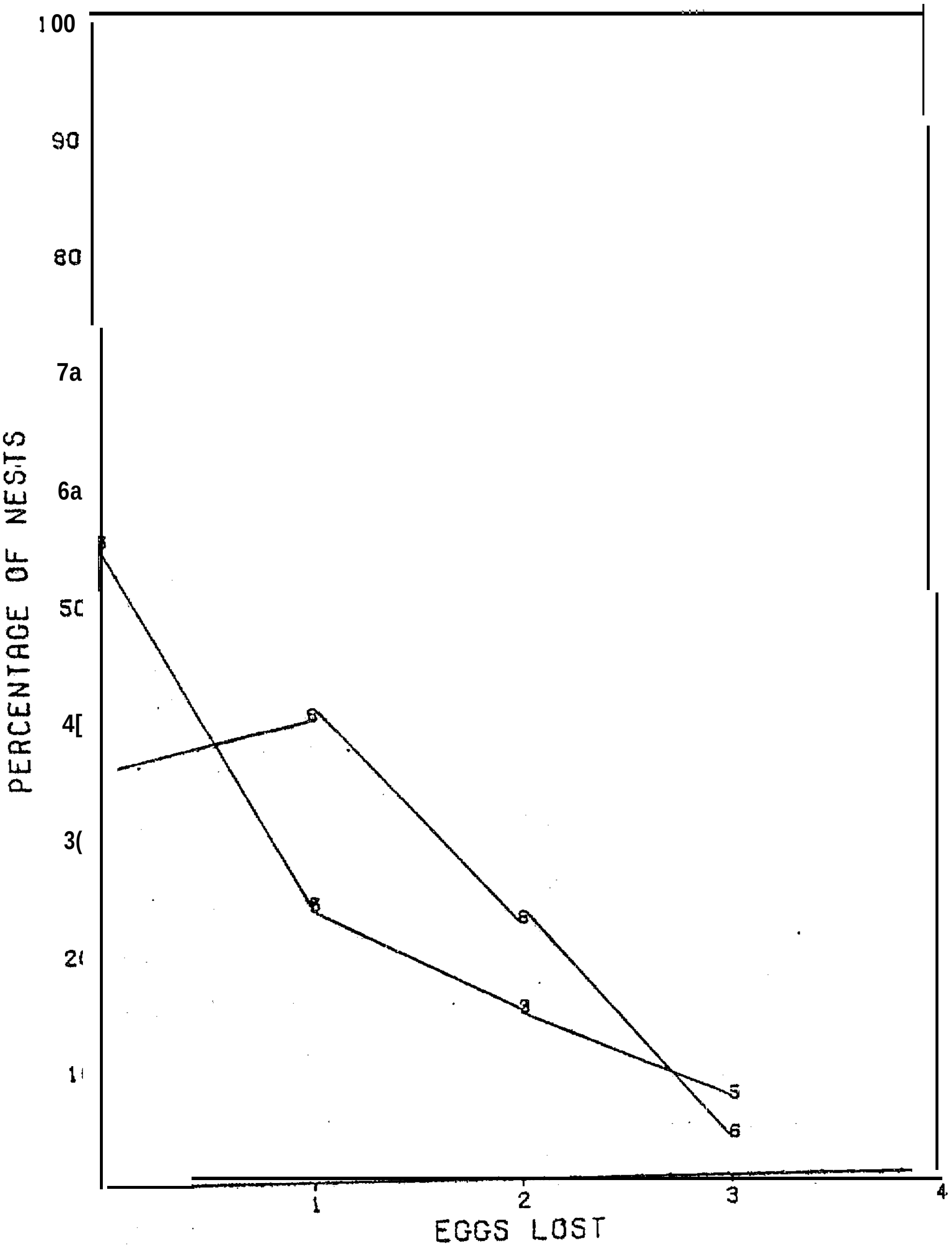


Figure 14. Eggs lost plotted against percentage of nests, Egg Island, 1975 - 1976. 5 = 1975 survey, 6 = 1976 survey.

Egg Island is similar to North Marble in egg loss to predation.

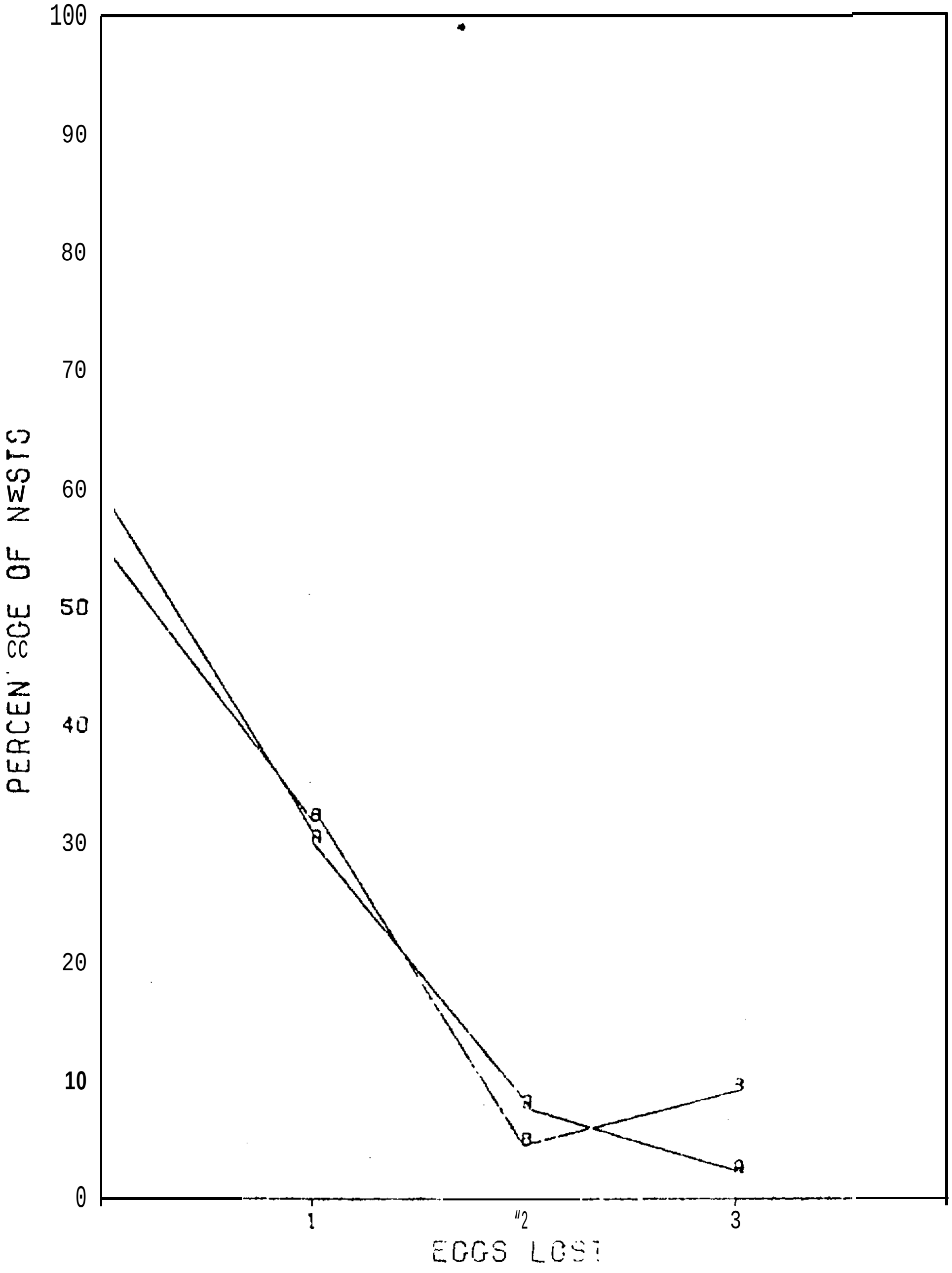


Figure 1'). Eggs lost plotted against percentage of nests, Dry Bay, 1977.
A = 'A' Colony, B = 'B' Colony.

Eggs lost to predation at Dry Bay show a rate most similar to North Marble in 1973.

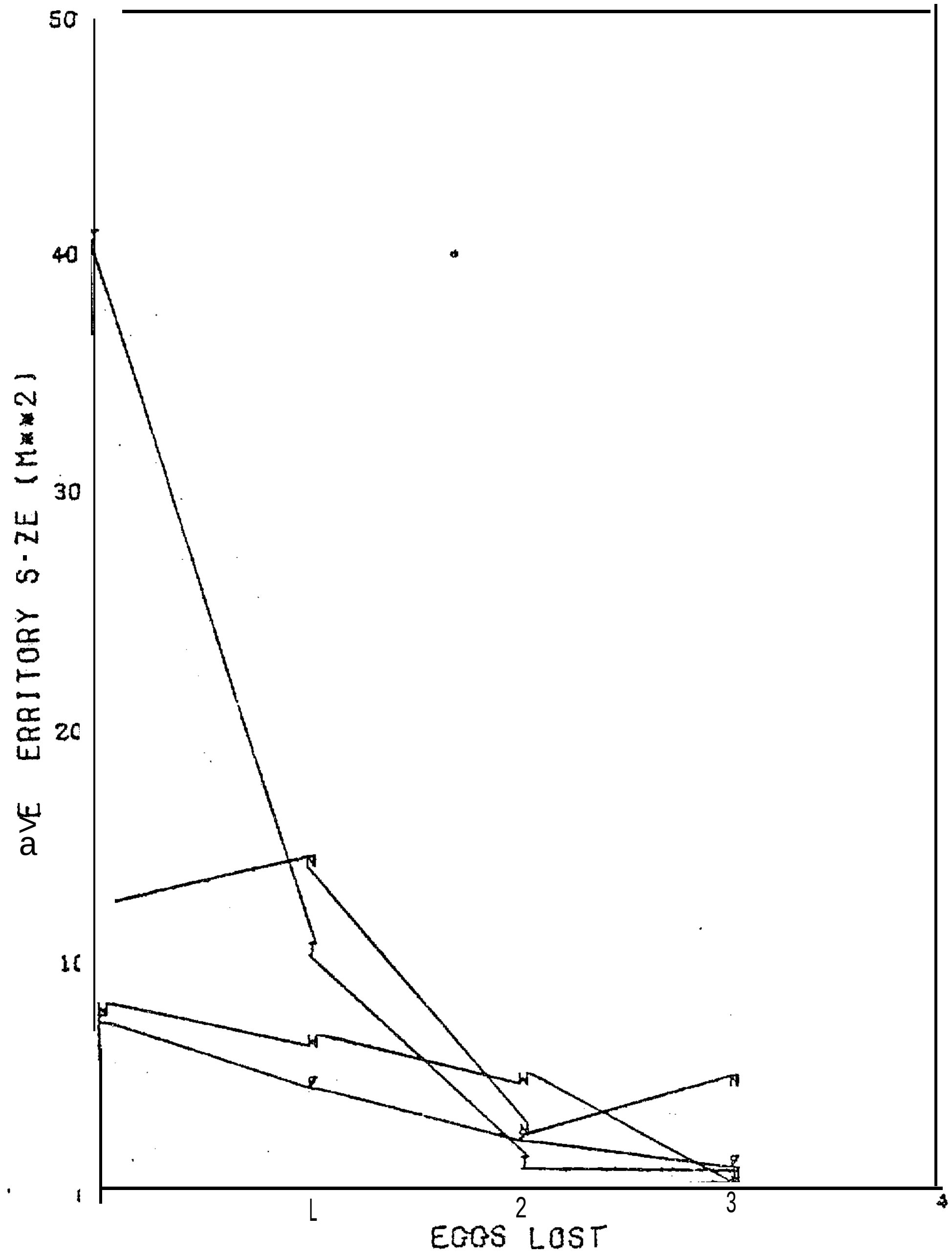


Figure 16. Eggs lost plotted against average territory size, North Marble, 1972.
E = East Colony, W = West Colony, N = North Colony, T = Top Colony.

Although Top Colony is significantly larger in average territory size, proportionate egg loss is similar to other colonies.

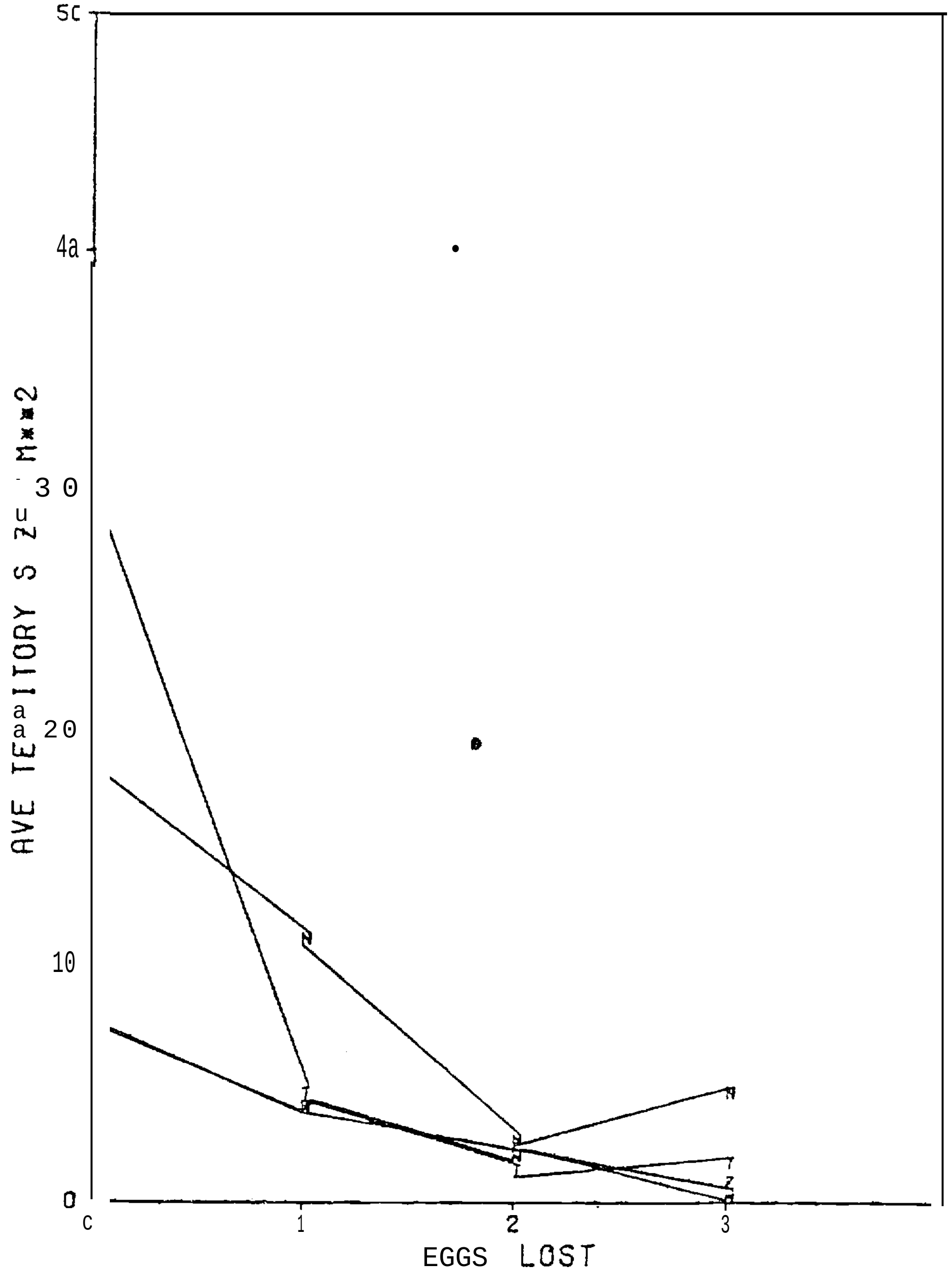


Figure 17. Eggs lost plotted against average territory size, North Marble, 1973.
E = East Colony, W = West Colony, N = North Colony, T = Top Colony.
All colonies show similar trends in eggs lost.

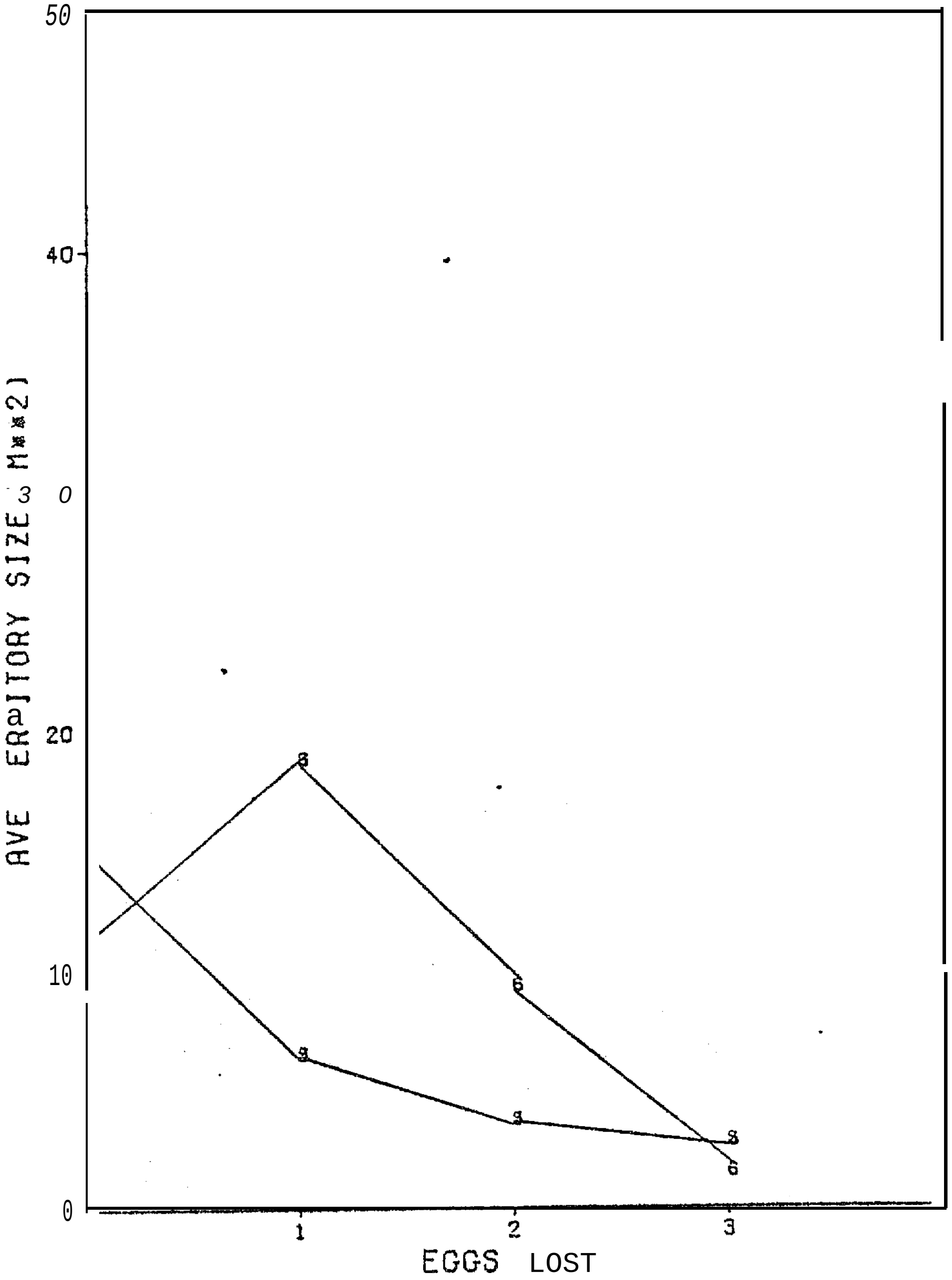


Figure 18. Eggs lost plotted against average territory size. Egg Island, 1975 - 1976.
5 = 1975 survey, 6 = 1976 survey.

Gulls with larger territory sizes tended to loose one or two eggs in 1976.
Egg loss in 1975 resembled that of 1972 and 1973 on North Marble.

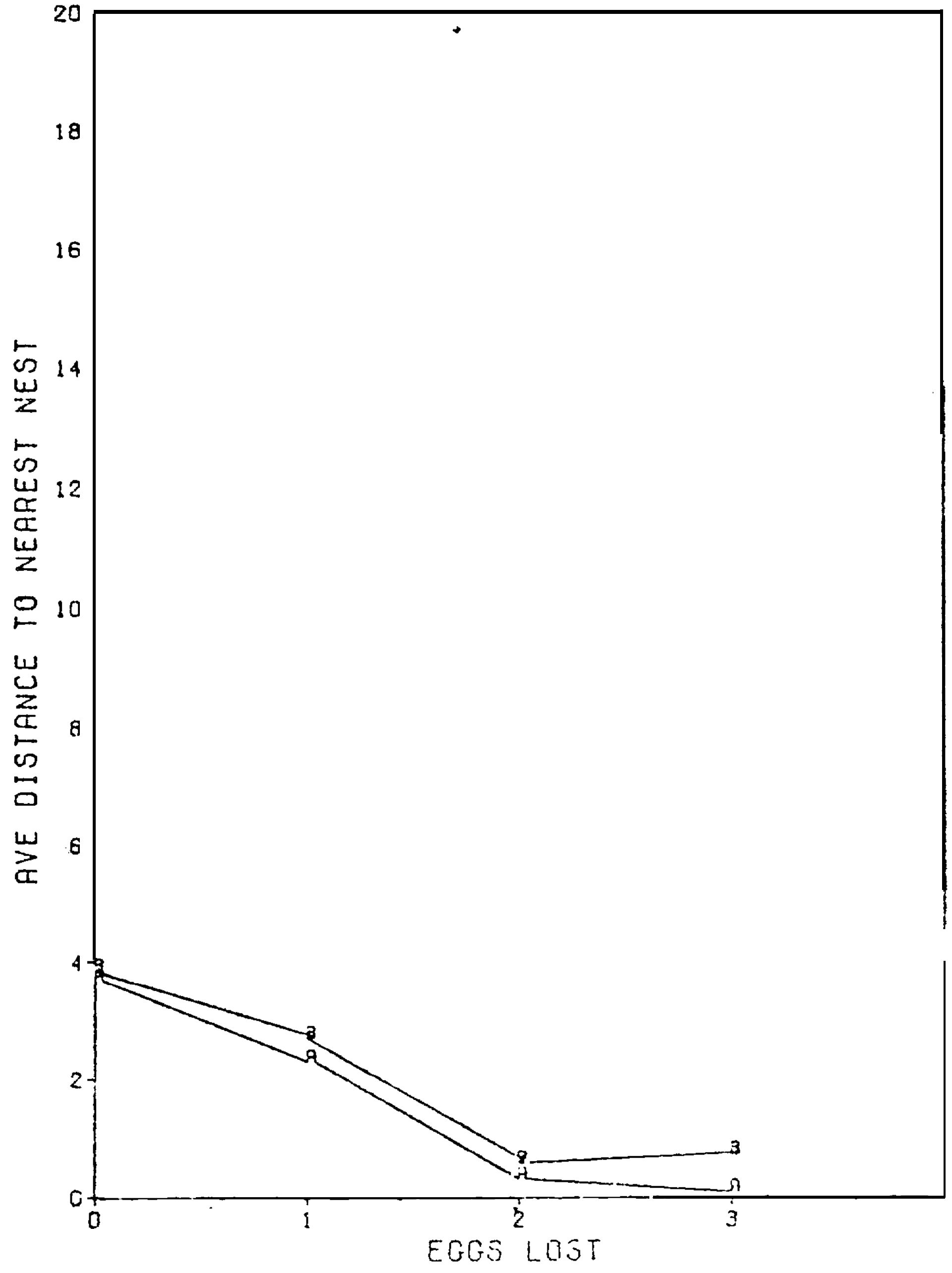


Figure 19. Eggs lost plotted against mean distance to nearest neighboring nest, Dry Bay, 1977. A = 'A' Colony, B = 'B' Colony .

'A' and 'B' Colonies show quite similar tendencies indicating egg loss is little influenced by distance to nearest nest.

Table 3

Numbers of "Lost," "Infertile" and "Pipped" Eggs Which Did Not Hatch in the Study Areas: Egg Island (1975-1976); North Marble (1972-73); Dry Bay and Lake Louise (1977)

Colony & Year	Total Eggs in Study Area	Lost Eggs	Infertile Eggs	Pipped, but did not Hatch
Egg Island (1975)	386	114 (29.5%)	8 (2.0%)	1 (<1%)
Egg Island (1976)	447	104 (23.3%)	9 (2.0%)	1 (<1%)
North Marble (1972)	455	125 (27.5%)	22 (4.8%)	2 (<1%)
North Marble (1973)	566	150 (26.5%)	26 (4.6%)	1 (<1%)
Dry Bay (1977) 'A'	265	10 (3.7%)	8 (3.0%)	2 (<1%)
Dry Bay (1977) 'B'	63	7 (11.1%)	0	0
Lake Louise (1977)	211	N.A.	13 (6.2%)	2 (<1%)

Incubation Period

An incubation period is defined as the time span between the begining of incubation of an egg and the date of hatching. Gulls lay eggs spaced several days apart, but do not begin incubation until the clutch (usually three) is completed. Thus all the eggs in a clutch tend to hatch within a very short time of each other (1-2 days). Not only do eggs within the same clutch tend to hatch within a few days of each other, most of the chicks within a colony tend to hatch within a week. of each other, under undisturbed conditions.

Onset of incubation varies by several weeks at an individual colony between years (Fig. 20). The onset of incubation on North Marble ranged from 29 May 1973 to 10 June 1972. The beginning of incubation in colonies at Egg Island and Lake Louise fell within this time range, despite nearly

INCUBATION PERIODS BY COLONY

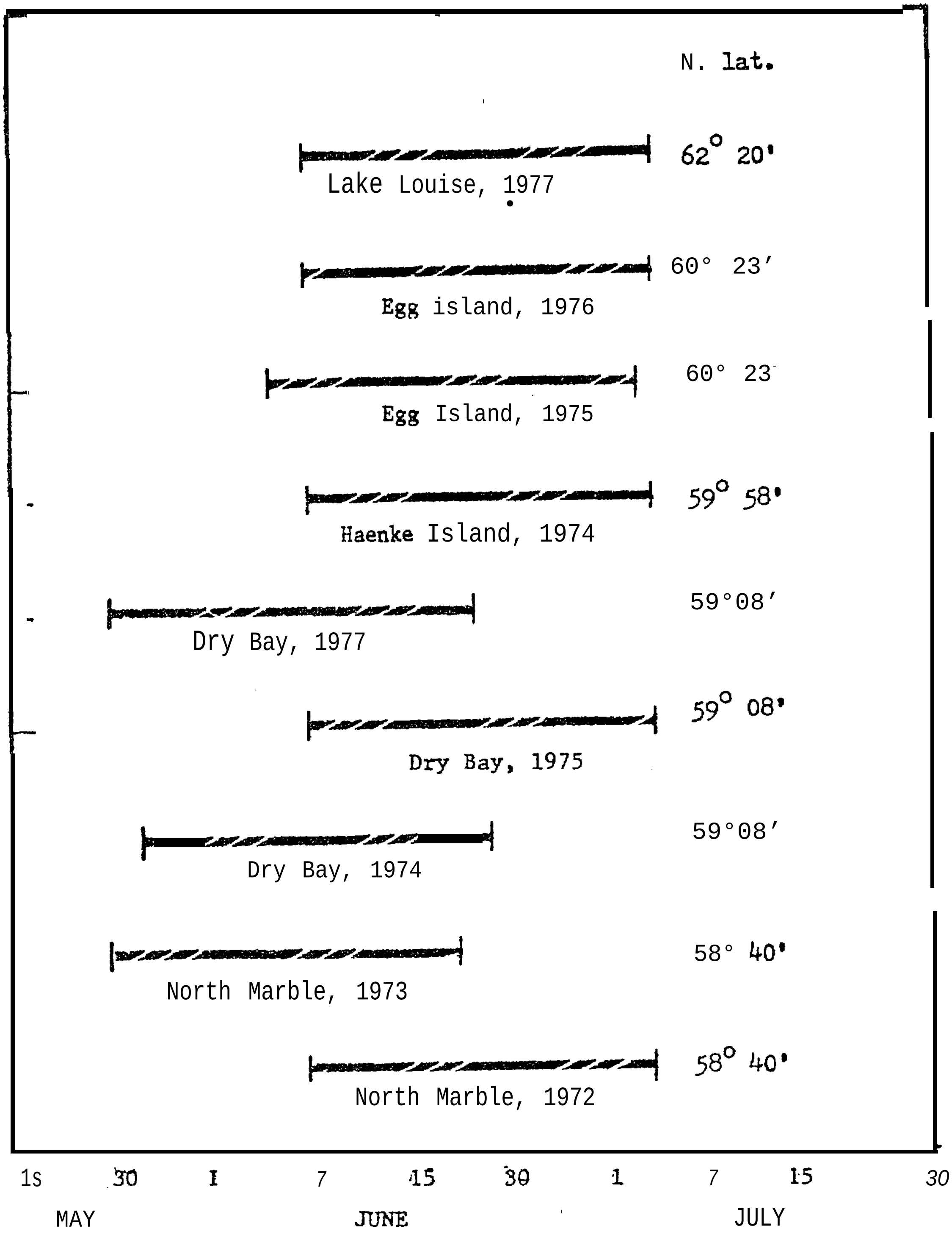


Figure 20

4° change in latitude. This suggests that gulls along this entire stretch of coastline and interior breed at the same time (Fig. 20).

The beginning of incubation was synchronized at North Marble, despite the somewhat larger spread of egg-dates from colony to colony. The abrupt synchrony of chick hatching both years of the North Marble study reflected the synchronized onset of incubation (Fig. 21). Median dates from onset of incubation to hatching established an incubation period of 24 to 27 days on North Marble.

The wider spread of chick ages on Egg Island reflected less synchrony in onset of incubation as well as greater spread of egglaying following egg-collecting by humans (Figs. 20, 23). However, in the study site at Egg Island, 50% of eggs were laid by June 5th, and 50% of eggs hatched by June 30th, demonstrating a median incubation period of 25 days.

At Dry Bay, 50% of eggs were laid by 24 May, and 50% of eggs hatched by 19 June~'demonstrating a median incubation period of 26 days. Similar incubation periods have been reported by Tinbergen (1960), Keith (1966), Schreiber (1970), Harpur (1971), and Vermeer (1963) for argentatus, occidentalis and glaucescens.

Chick Hatching

Synchrony is the tendency of a population of colonial birds to reproduce within a short period of time of each other. Synchrony is an adaptative anti-predator strategy.

Chick hatching was quite synchronous both years of the North Marble Island study. In 1972, 70% of the gull chicks hatched between 4 and 9 July; in 1973, 87% of the chicks hatched between 23 and 25 June. Chick hatching in 1973 at North Marble was two weeks earlier than 1972, a result

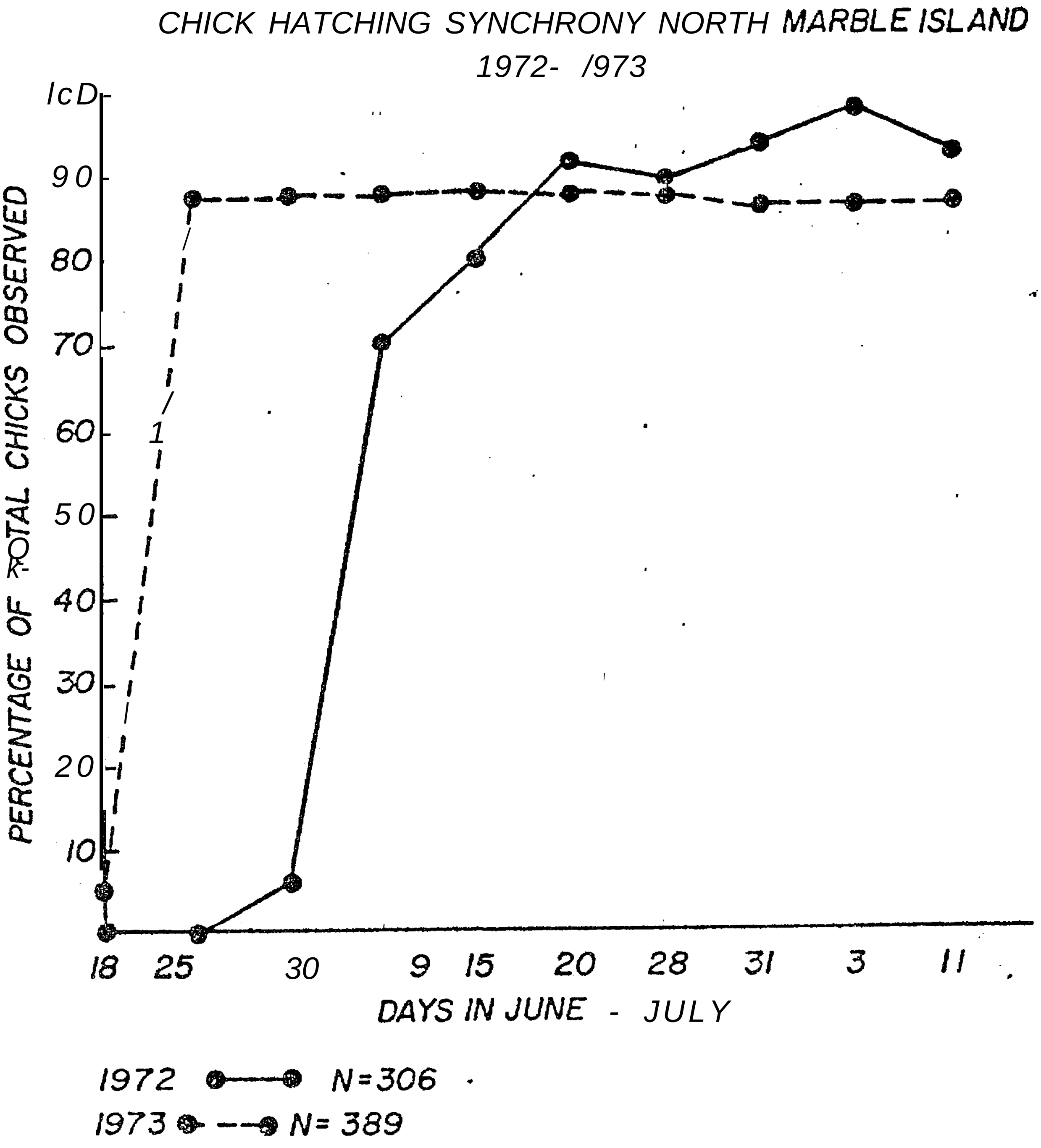

CHICK HATCHING SYNCHRONY NORTH MARBLE ISLAND
1972-1973
PERCENTAGE OF TOTAL CHICKS OBSERVED
100
90
80
70
60
50
40
30
20
10
18
25
30
9
15
20
28
31
3
11
DAYS IN JUNE - JULY
1972 ●——● N=306
1973 ●- - -● N= 389

Figure 21

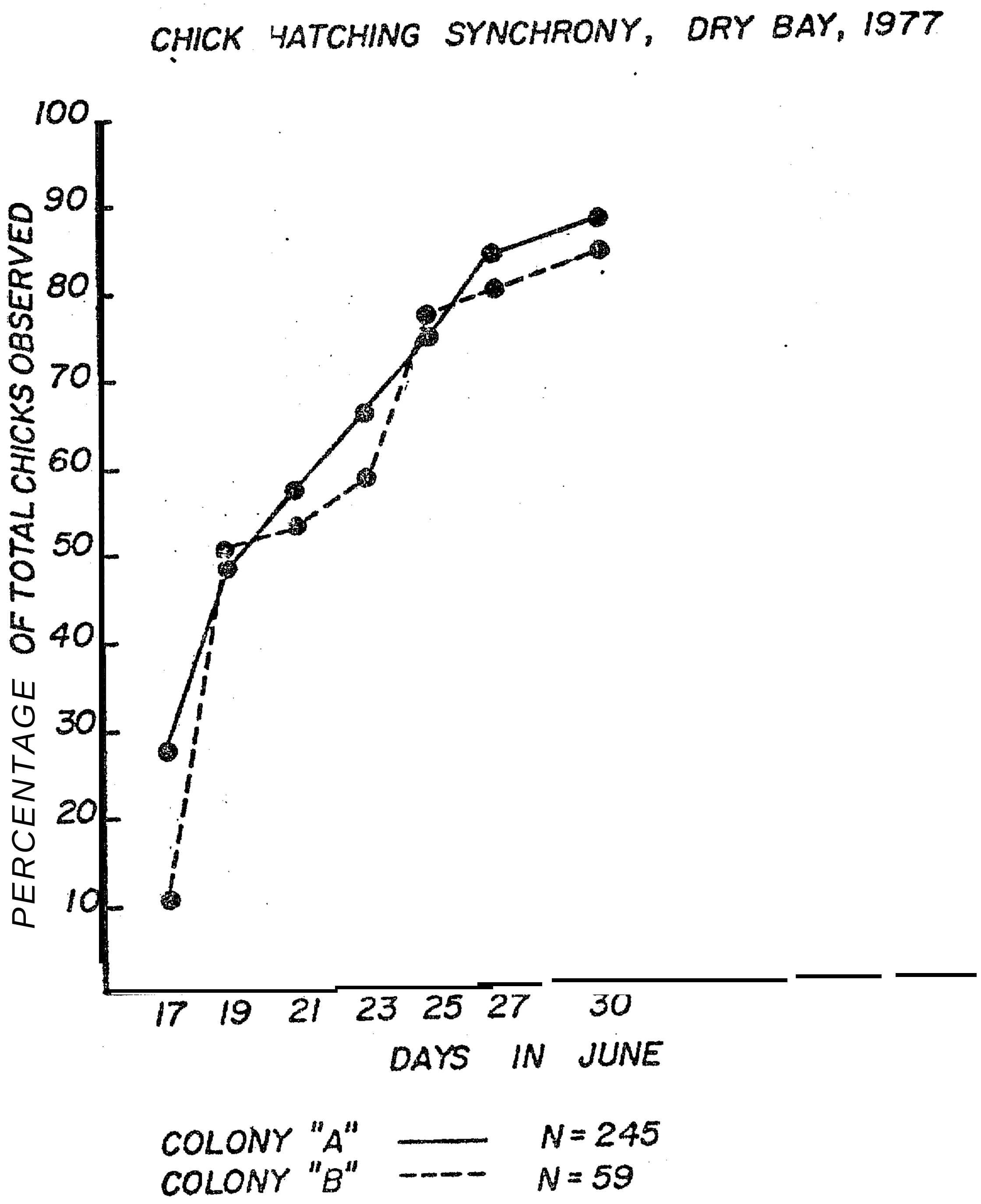

CHICK HATCHING SYNCHRONY, DRY BAY, 1977
PERCENTAGE OF TOTAL CHICKS OBSERVED
100
90
80
70
60
50
40
30
20
10
17
19
21
23
25
27
30
DAYS IN JUNE
COLONY "A" —— N = 245
COLONY "B" ---- N = 59

Figure 22

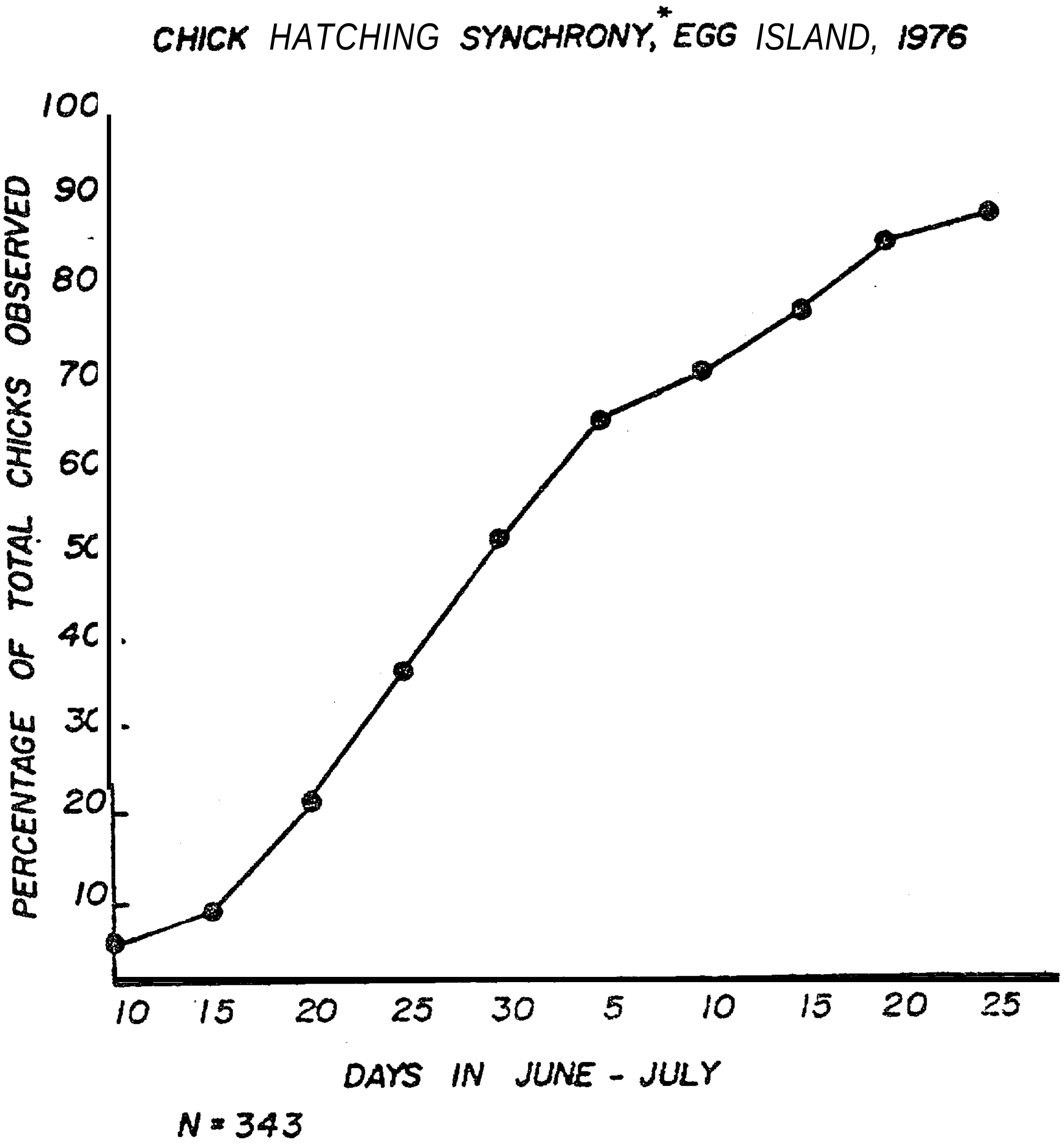


Figure 23

* The slope is nearly directly proportional to the. Therefore synchrony is technically not correct. "Phenology" would be correct. (See text for explanation.)

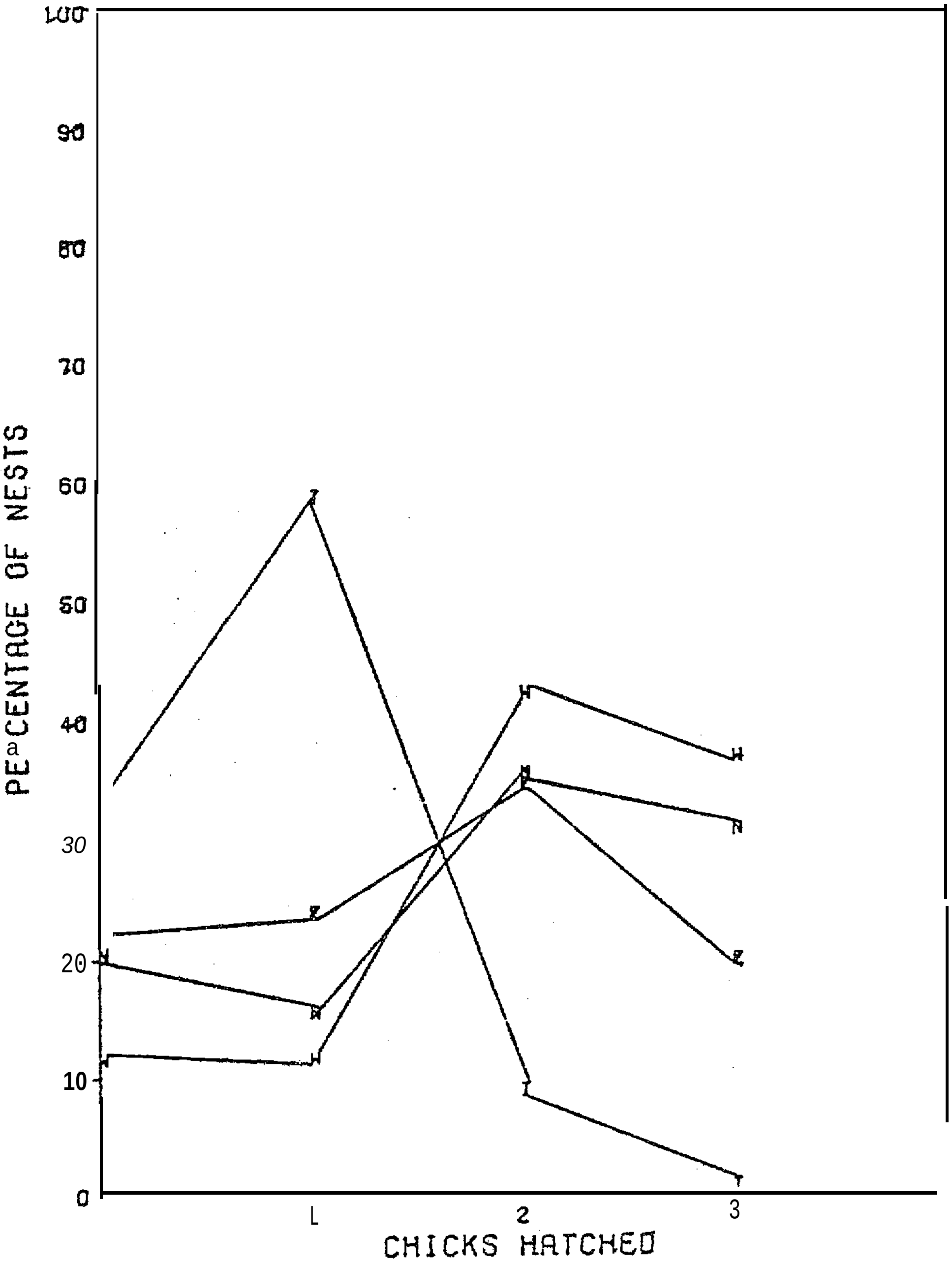


Figure 24. Chicks hatching plotted against percentage of nests. North Marble. 1972. E = East Colony, W = West colony, N = North Colony, T = Top Colony,

East, West and North Colonies are quite similar in number of chicks hatching per nest, The Top Colony, due to smaller mean clutch size, produced fewer chicks hatching in proportion.

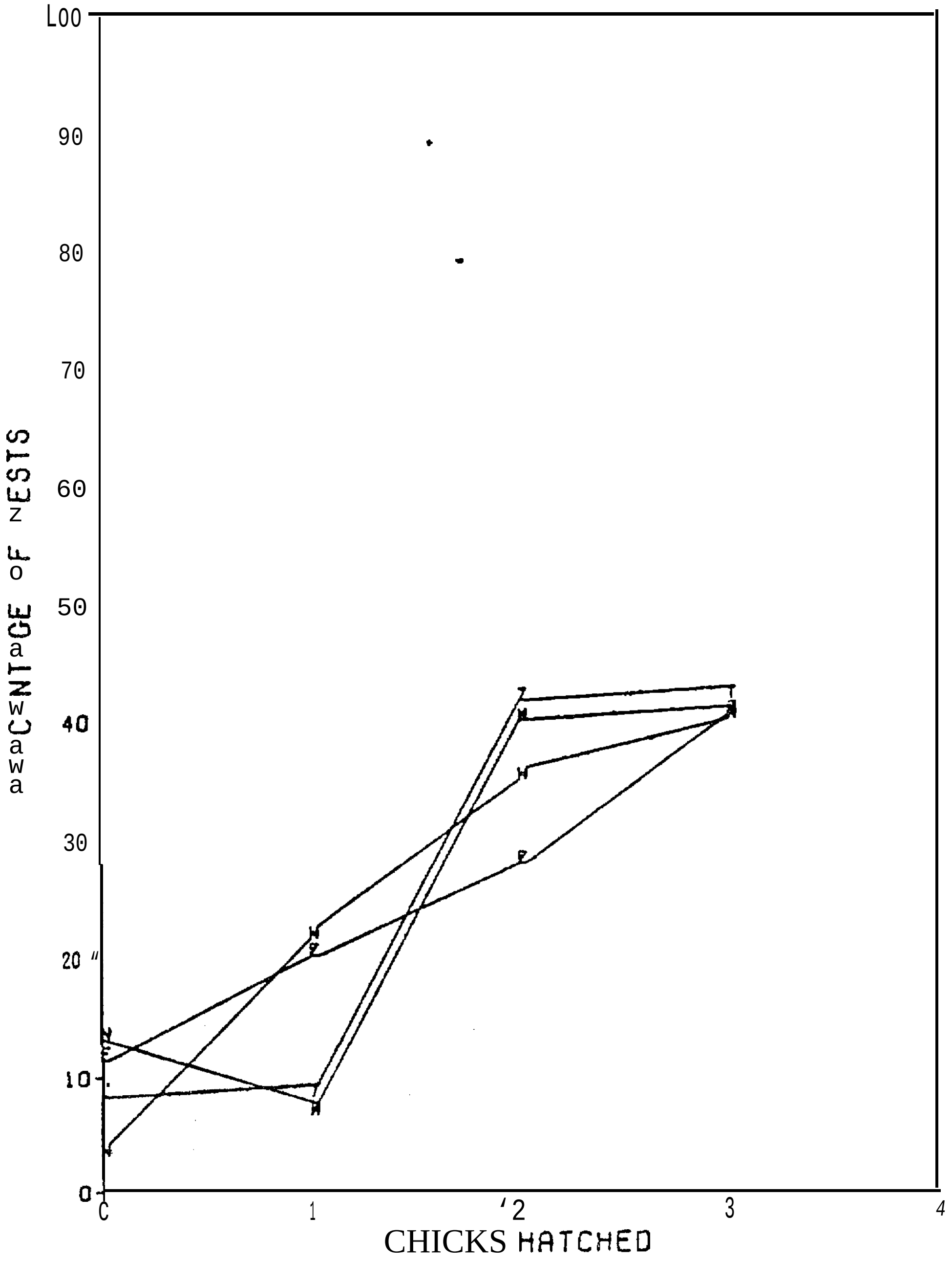


Figure 25 Chicks hatching plotted against *percentage* of nests, North Marble, 1973. E = East Colony, W = West Colony, N = North Colony, T = Top Colony.

All colonies show quite similar tendencies in proportion of chicks hatching due to similar mean clutch sizes and rate of predation.

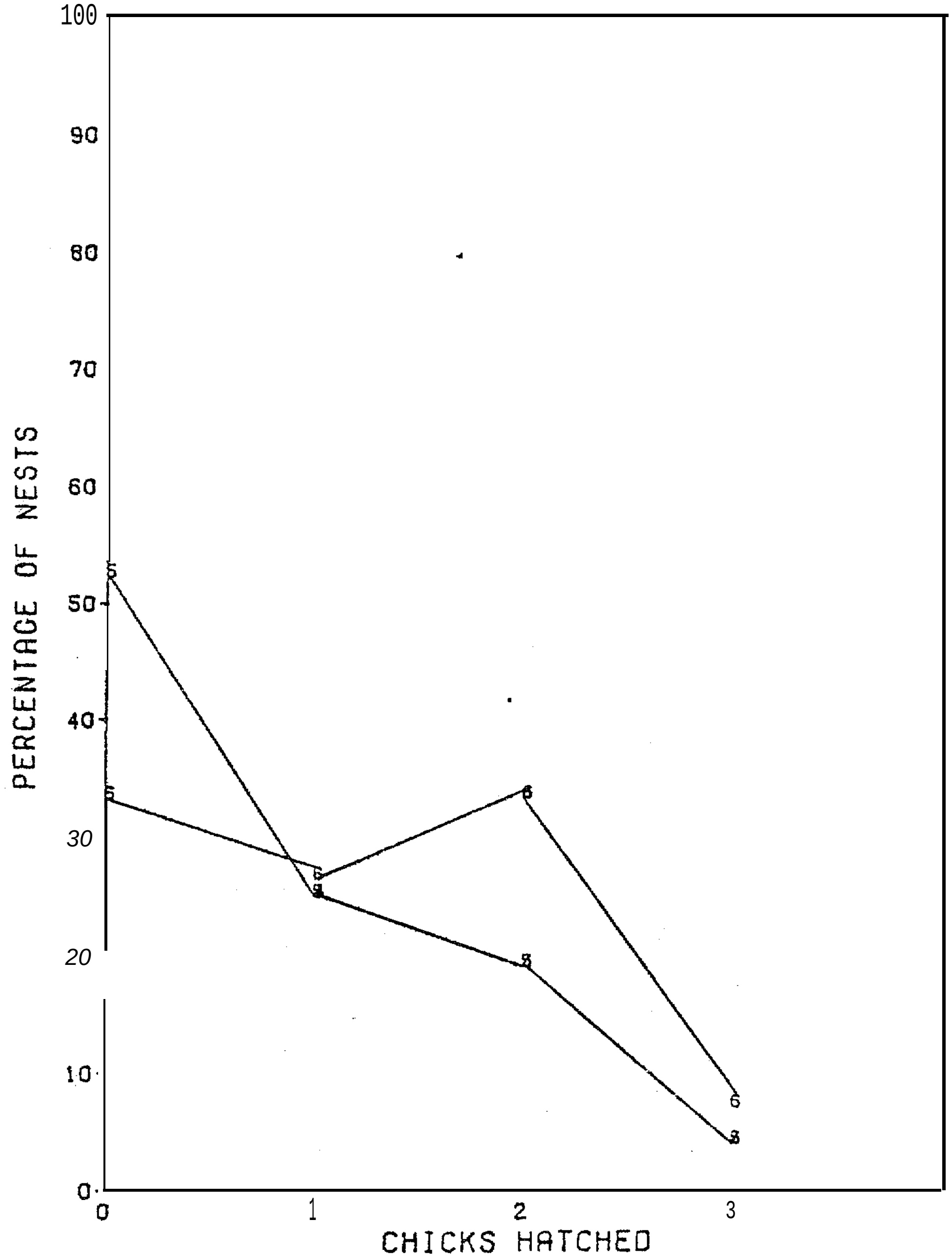


Figure 26. Chicks hatching plotted against percentage of nests, Egg Island, 1975 - 1976. 5 = 1975 survey, 6 = 1976 survey.

Egg Island, due to smaller mean clutch size, shows a reverse tendency in proportion of chicks hatching when compared to North Marble in 1973, but resembles the Top Colony on North Marble in 1972 (Figure 15), although not as extreme.

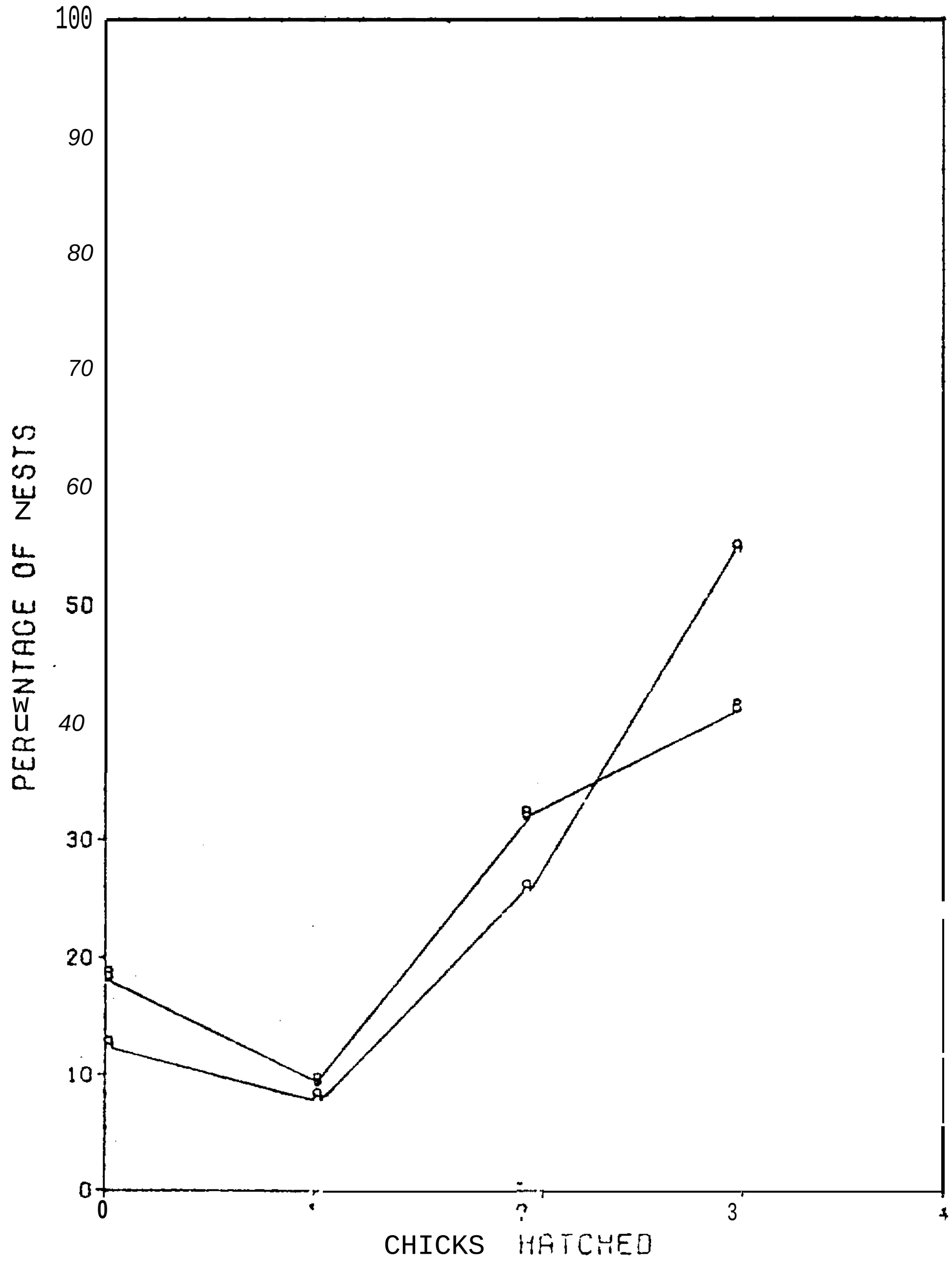


Figure 27. Chicks hatching plotted against percentage of nests, Dry Bay 1977.
A = 'A' Colony, B = 'B' Colony.

Dry Bay had the greatest percentage of chicks hatching in this study, due to largest clutch size and lowest rate of egg predation.

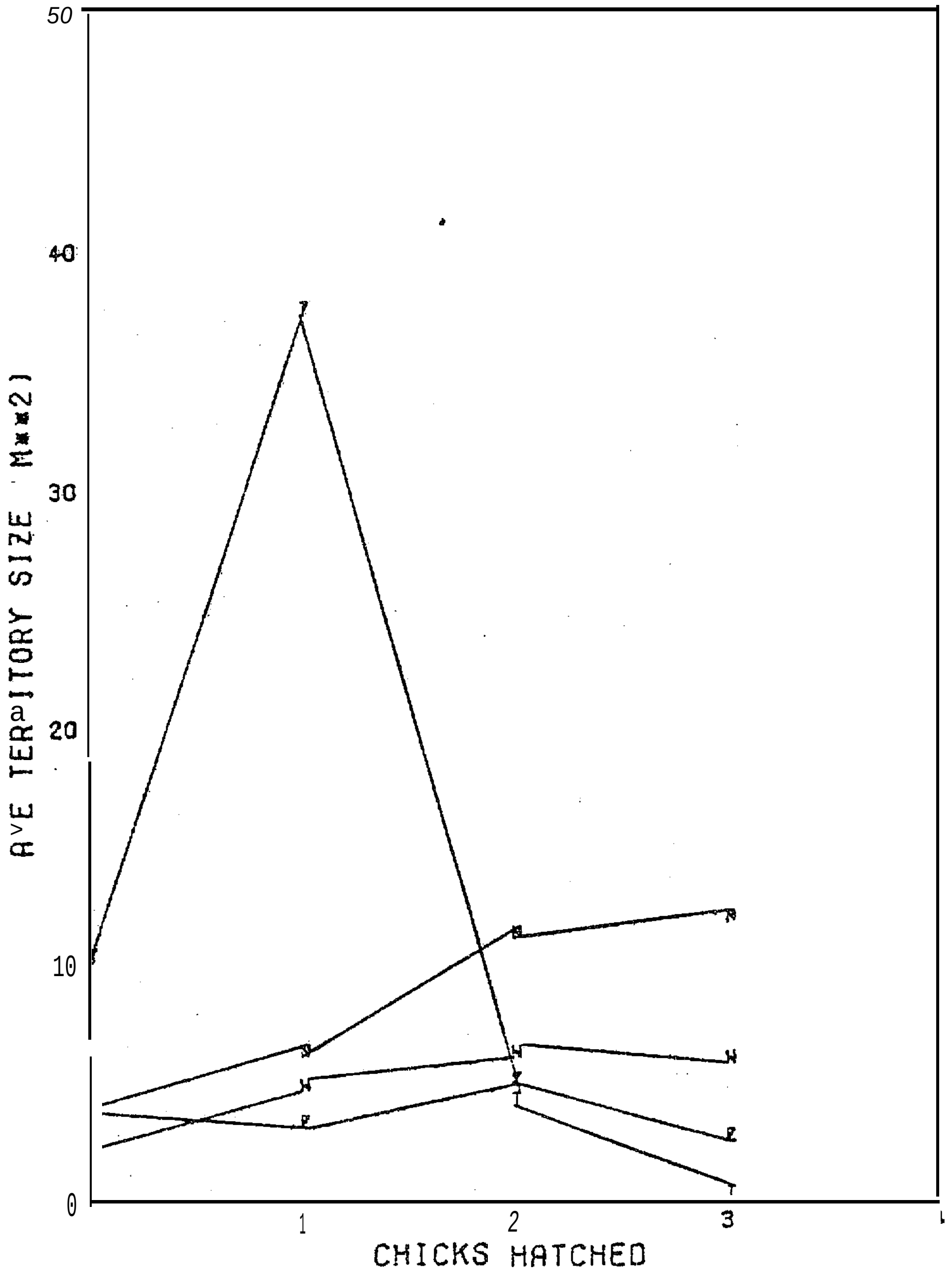


Figure 28. Chicks hatching plotted against average territory size, North Marble, 1972. E = East Colony, W = West Colony, N = North Colony, T = Top Colony.

East, West and North Colonies are quite similar in number of chicks hatching in relation to average territory size. Top Colony is significantly different, with large territory size, smaller mean clutch size, and fewer chicks produced.

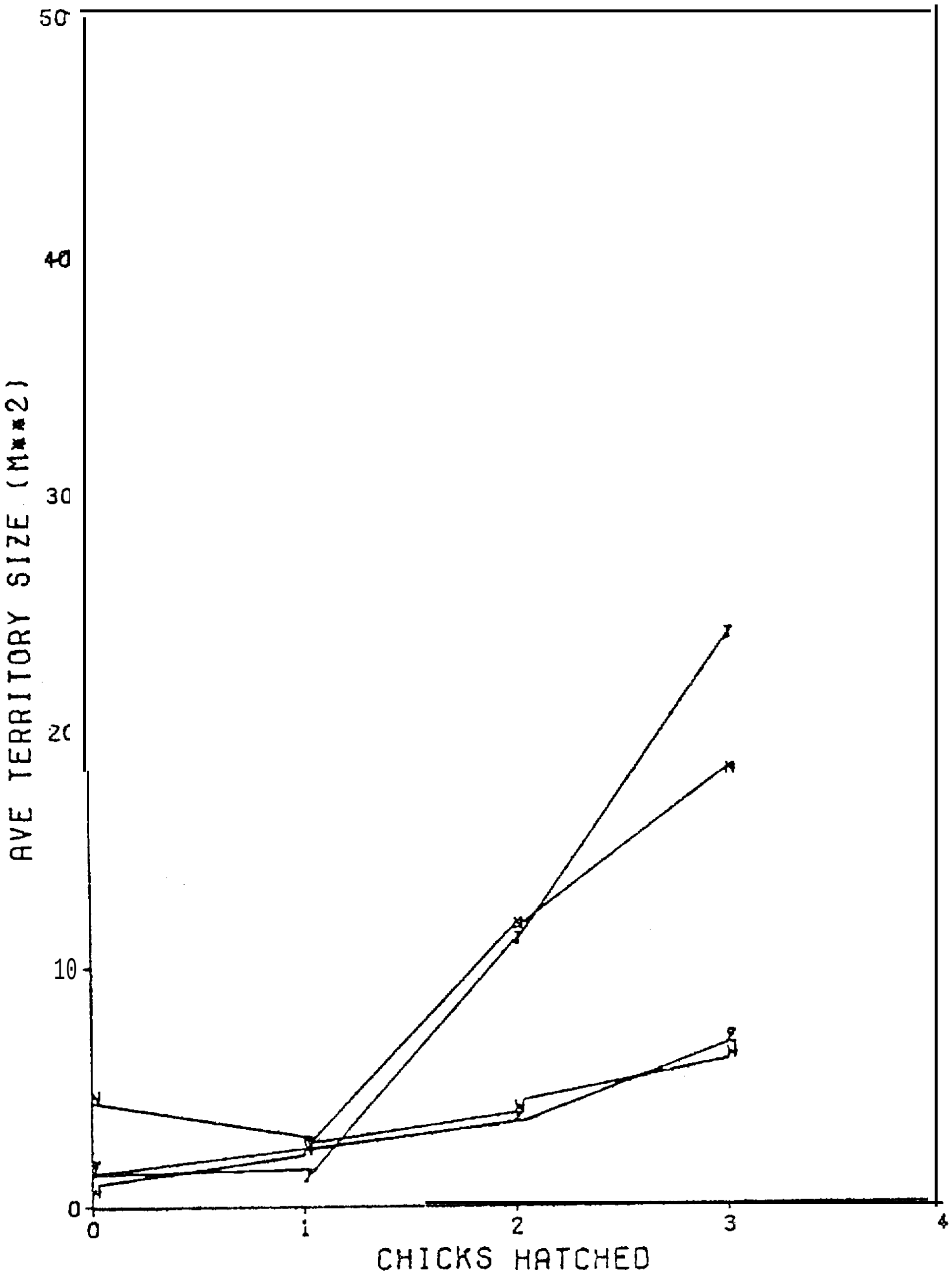


Figure 29. Chicks hatching plotted against average territory size, North Marble, 1973. E = East Colony, W = West Colony, N = North colony, T = Top Colony.

Top and North Colonies are similar in average territory sizes, as are East and West Colonies, but the two groups are different from each other, probably due to colony sizes. However, all colonies show similar tendencies in number of chicks hatched.

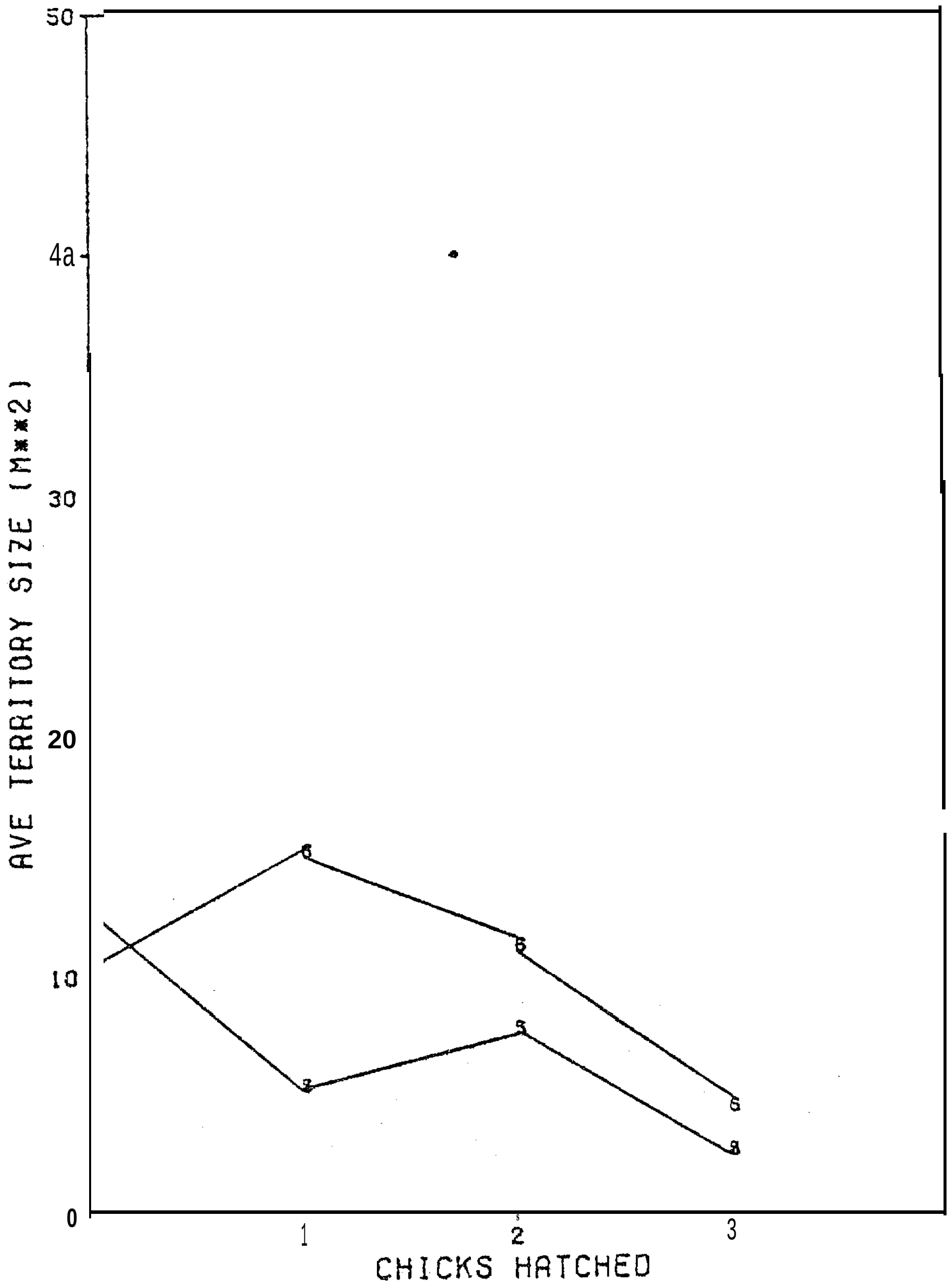


Figure 30. Chicks hatching plotted against average territory size, Egg Island, 1975 - 1976. 5 = 1975 survey, 6 = 1976 survey.

Average territory size on Egg Island in 1976 was larger than in 1975. Both years show a reverse trend from North Marble in 1%73 due to smaller mean clutch size,

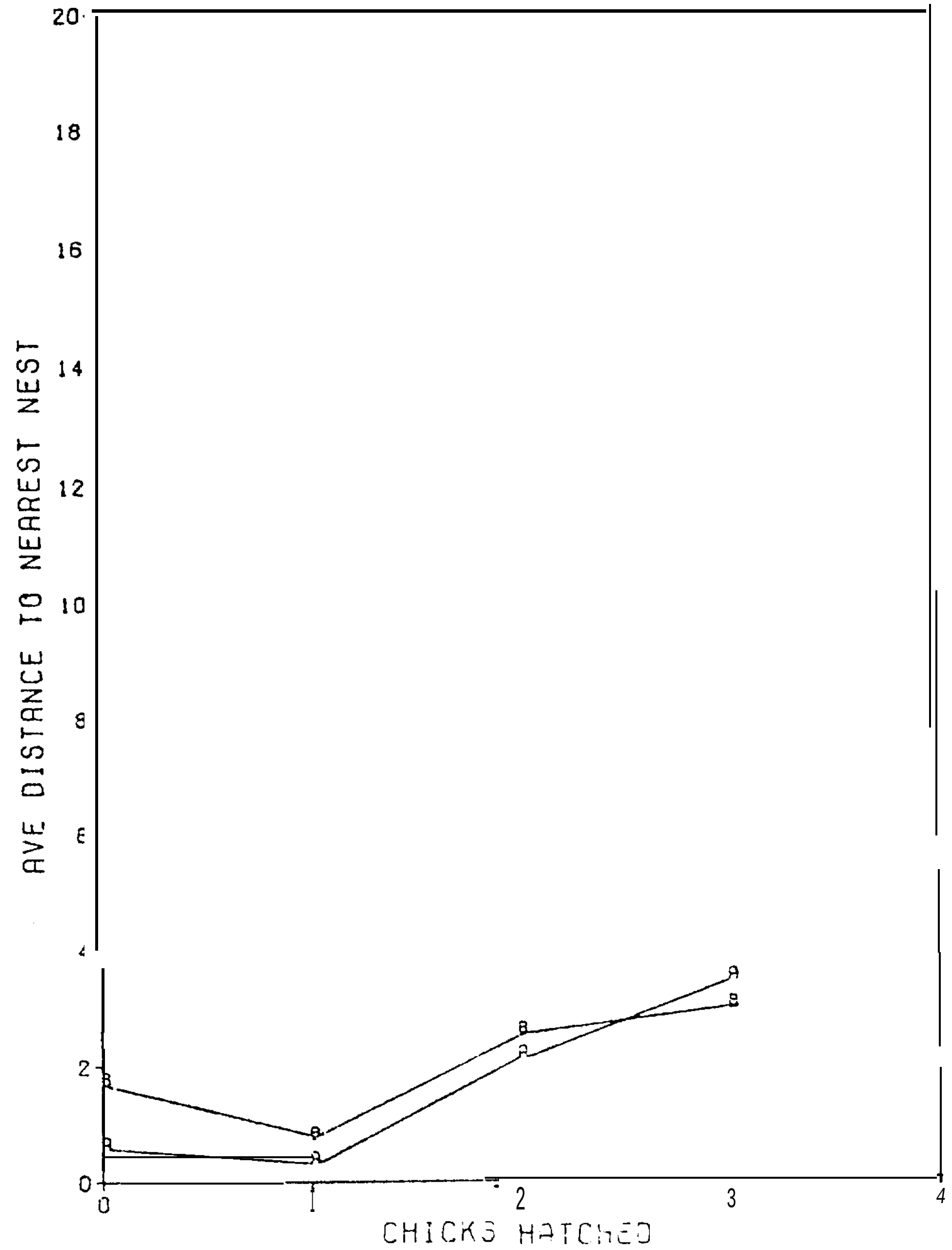


Figure 31. Chicks *hatching* plotted' against mean distance t-o nearest nest, Dry Bay,1977. A = 'A' Colony, B = 'B' Colony.

Mean distance to nearest nest influenced number of chicks hatching per nest only slightly.

of a generally earlier breeding season, related to milder weather. Chick hatching was also more synchronous in 1973 (Figs. 20, 21.).

Chick hatching was not synchronous at Egg Island in 1976. The increase in chick numbers was nearly directly proportional to time elapsed. Hatching for 50% of the eggs extended over 20 days, in contrast to the two to five day hatching period on North Marble. (Fifty percent of the eggs in the 1976 Egg Island study area were laid in one week.) Re-nesting "and clutch replacement following subsistence egging by fishermen in early June was the most likely explanation for this spread of hatching (Figs. 20, 23).

Dry Bay in 1977 was intermediate between Egg Island and North Marble in rate of chicks hatching over time. Chick hatching was more synchronous than egg-laying (Fig. 11, 22) at Dry Bay; 50% of the eggs were laid in an eight-day period in late May, but 50% of the chicks hatched in a three-day period between 17 and 21 June. This *suggests a* more synchronized onset of incubation than synchronized egg-laying.

North Marble and Dry Bay colonies contained roughly the same number of pairs (about 500) and both were relatively undisturbed areas. Egg Island was a huge colony with disturbance. There was a tendency for groups of birds to breed at the same time, but the synchrony was disrupted by human intervention (egging).

Chick Mortality

Chick mortality in southern Alaskan gull colonies was divided into two classifications: chicks which were observed dead, and chicks which disappeared, were not counted as fledged, and which were presumed dead.

Observed chick mortality in southern Alaskan colonies was low, ranging from 3 to 12% (Table 4). North Marble Island had the highest rate of hatching *failure,* which was due to egg predation, but the rates of observed chick mortality and disappearance were the lowest of colonies examined, except for Lake Louise, where we have limited data due to restricted time available for investigation (Table 3, part I).

Chicks which disappeared accounted for a high percentage of the chick loss at both Egg Island and Dry Bay. The figures ranged from 26% to 49% (Table 14). Egg Island, however, had the highest combined egg and chick mortality of coastal colonies studied (Table. 5). High egg and chick mortality, added to low clutch size, meant Egg Island had the lowest total reproductive success (in chicks fledged per nest) of the three major coastal colonies examined. Total chick mortality on Egg IsLand (mean of both seasons) *was* 38%. The Egg Island situation represented disturbed conditions, with access by boatmen, picnickers, and dogs, which may have accounted for the *large* number of chicks which disappeared.

Hatching successes at Egg Island and North Marble were within 8% of each other (Table 4). Dry Bay had *a* much higher rate of hatching, due to a low rate of egg loss, and larger clutch size. Thus Dry Bay had *more* chicks hatching in proportion to other colonies (Table .4). However, chick disappearance was the main factor influencing chick mortality at Dry Bay in 1977 (Table 4).

The few chicks found dead on the sparsely vegetated gravel bars at Dry Bay in 1977 showed injury due to attacks by adult gulls defending territory. We believe eagle predation (observed on a-n hourly basis in late June and July) was the main reason for chick disappearance, and thus was the major factor influencing reproductive success in the gullery at Dry Bay. When the

Table 4

Percent Chick Mortality, Egg Island 1975-76; North Marble Island 1972-73; Dry Bay, 1977

Study Area	% Hatching	% Observed Mortality	% Disappeared	Fledged as % hatched
Egg Island 197S (153 nests)	69	12	26	62
Egg Island 1976 (186 nests)	77	8	31	61
North Marble 1972 (162 nests)	67	5	2	93
North Marble 1973 (191 nests)"	69	8	4	88
Dry Bay "A" 1977 (90 nests)	92	6.5	39*	54
Dry Bay "3" 1977 (22 nests)	93	3	49*	47.5

* heavy eagle predation noted.

Table 5

Hatching Success, Mortality, Reproductive Success Egg Island, '1975-76; North Marble Island, 1972-73; Dry Bay, 1977; Lake Louise 1977

Colony	Hatching Success (%)	Egg and Chick Combined Mortality (%)	Total Reprod. Success (%)
Egg Island (153-1S6 nests)	73	65	44
Dry Bay (22-90 nests)	93	51	49
North Marble (161-192 nests)	68	34	61
Lake Louise (77 nests),	N.A.	N.A.	35

low rate of egg loss, and the high rate of chick loss were combined, Dry Bay had an intermediate rate of mortality compared to other coastal colonies. Total reproductive success at Dry Bay was better than Egg Island, but less than North Marble (Table 5).

Fledging Success

We determined the median length of the fledging period to be 40-45 days on North Marble, similar to Dry Bay, Egg Island, and Lake Louisa. Other investigators have reported similar fledging period for *argentatus* in Michigan (Keith, 1966), *occidentalis* in California (Schreiber, 1970; Harpur, 1971) and *glaucescens* in British Columbia (Vermeer, 1963) .

At the end of the fledging period at each major colony in this study, we made counts to determine fledging success. Fledging success, while a difficult measurement (Keith, 1966; Schreiber, pers. comm.), is crucial in understanding the reproductive biology of these gulls.

When the number of chicks fledged in 1972 at North Marble was plotted against percentage of nests for four colonies, the East, West, and North Colonies formed a pattern (Fig. 32,). The Top Colony was aberrant, with larger territory size (Table 2, Fig. 5), fewer chicks hatching Fig. 24), and fewer chicks fledging (Fig. 32). Territory size was not directly related to number of chicks fledging in the other colonies, since they were all within the same range (Fig. 32) .

The situation on North Marble in 1973 was different. The East, West, and Top Colonies formed a pattern.. Productivity was greater in the Top Colony; more chicks fledged. The increase in productivity was correlated with smaller internest distances, larger clutch sizes, and fewer eggs and chicks lost (Figs. 6, 13, 17, 33). The North Colony in 1973 exhibited the unusual, possibly artifactual, pattern. Disturbance associated with boat mooring may have caused nearly fledged chicks to emigrate earlier from the North Colony and not be counted as fledged.

At Dry Bay in 1977, both 'A' and 'B' Colonies fledged similar percentages of one chick per nest, but 'A' Colony had a greater reproductive output of two and three chicks per nest, which accounted for the better fledging success in Colony 'A' (Fig. 35). Mean distance to nearest nest showed little direct relationship to chicks fledging at Dry Bay in 1977 (Fig. 39).

Reproductive success (in chicks fledged per nest) was lower at Egg Island, compared to North Marble or Dry Bay, and was slightly higher than Lake Louise (Table 2). Egg Island exhibited a pattern similar to North Marble in 1972 when number of chicks fledged was plotted against percentage of nests (Fig. 34). On Egg Island, mean territory size was slightly, but not significantly, larger in 1976; productivity *was also* slightly, but not significantly, better than 1975. When territory size at Egg Island was plotted against number of chicks fledging per *nest,* the relationship was virtually the same for both study years (1975-76). Most nests fledged one chick (Fig. 38).

Summary of Fledging Rates

The fledging rate of 1.03 - 1.12 glaucescens chicks per nest on Egg Island is normal compared to other gull species (Table 6) but lower compared to a partially mixed argentatus - glaucescens colony at North Marble in post-glacial surroundings (1.77) due to the abundant natural food supply in the "unfilled" niche at Glacier Bay. The fledging rate of 0.95 argentatus chicks per nest at Lake Louise is sufficient to maintain a stable population, but also much lower than the highly mixed argentatus x

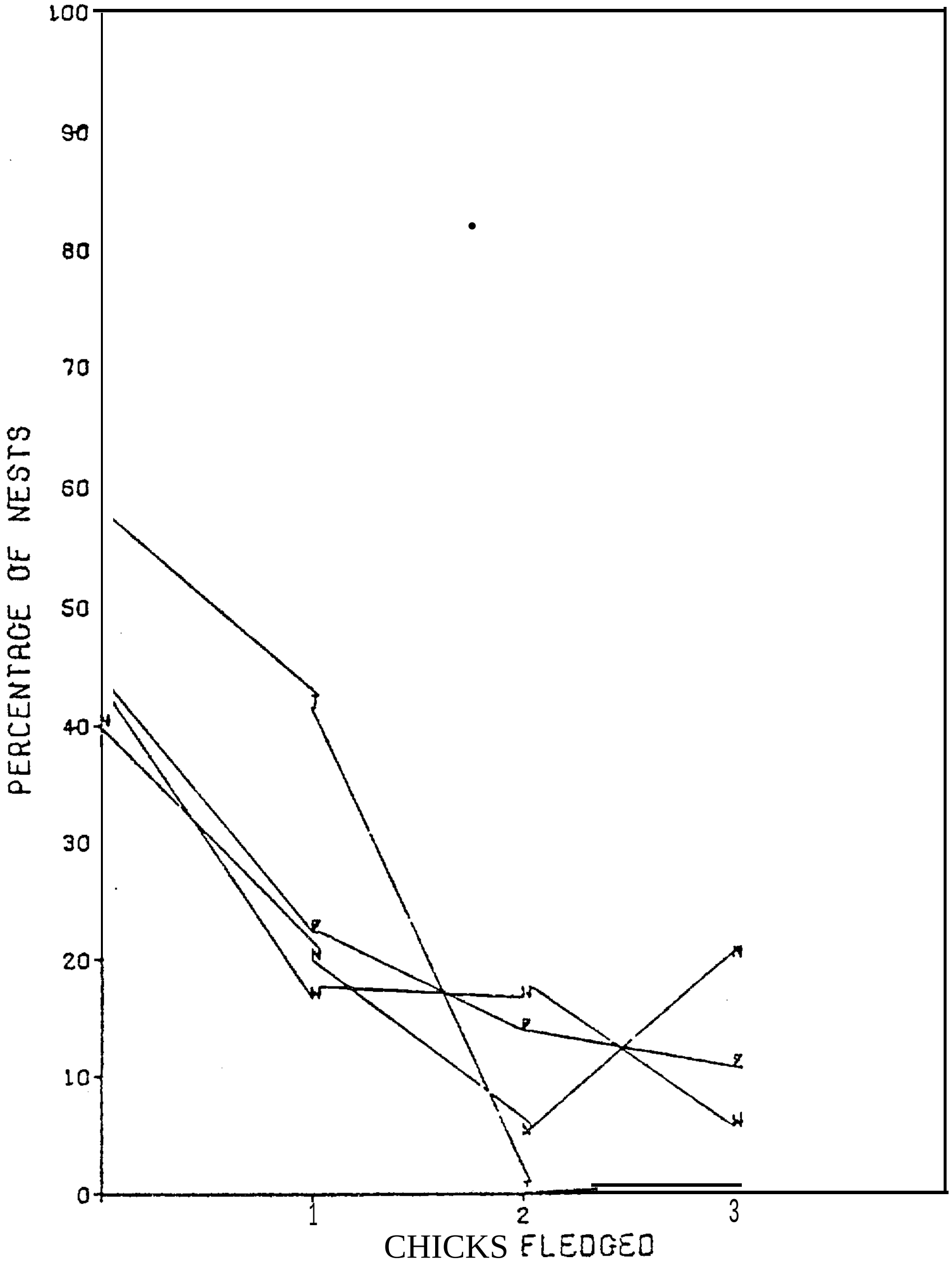


Figure 32. Chicks fledging plotted against percentage of nests, North Marble, 19?2.
E = East Colony, W = West Colony, N = North Colony, T = Top Colony.

Once again the East, West and North Colonies form a similar pattern and the Top Colony is aberrant, with large territory sizes, smaller clutches, fewer chicks hatching, greater chick loss, and fewer chicks fledging.

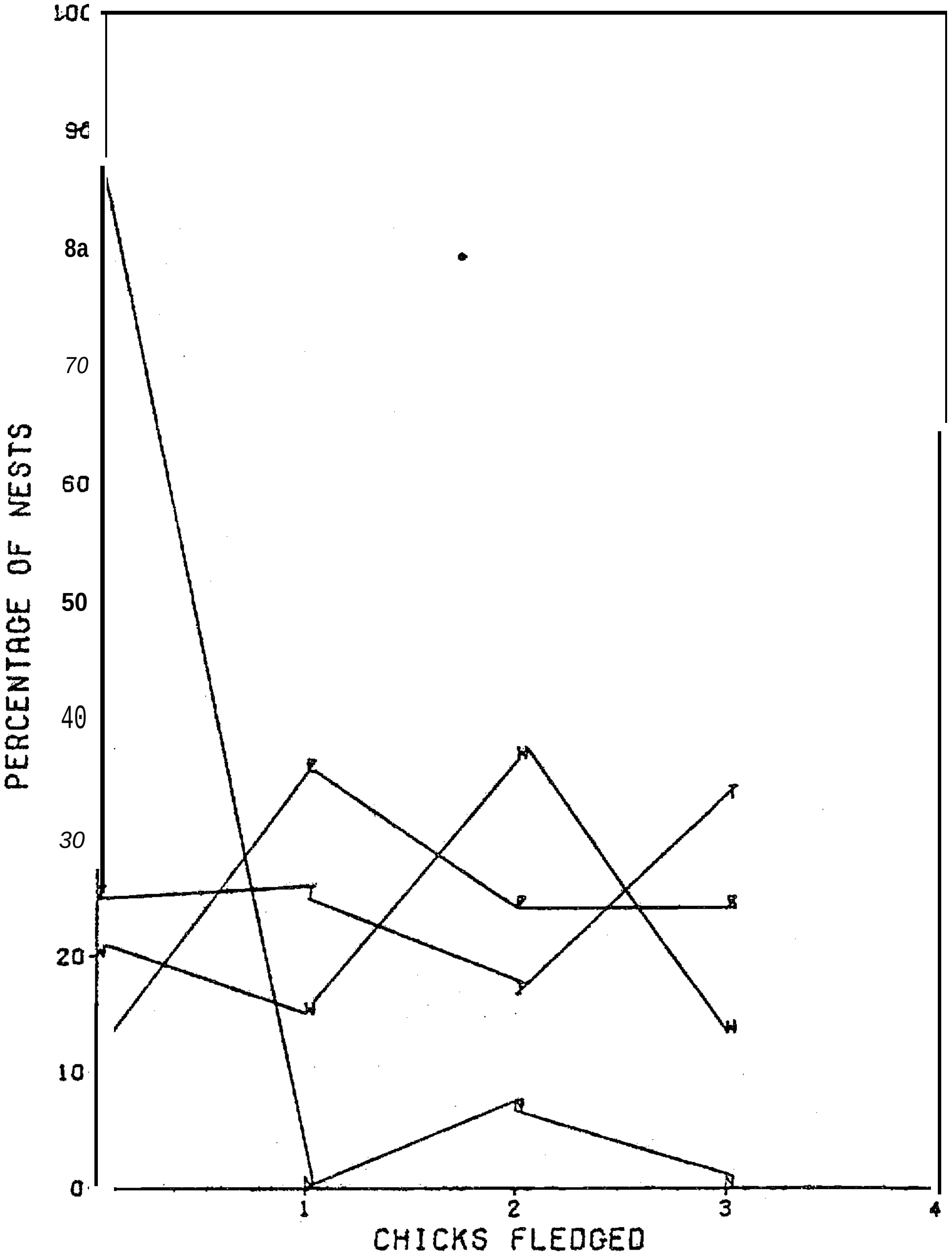


Figure 33. Chicks fledging plotted against percentage of nests, North Marble, 1973. E = East Colony, W = West Colony, N = North Colony, T = Top Colony.

The North Colony here presents an exception to the usual trend. The "East, West and Top Colonies closely fluctuate around a mean, while the North Colony breaks the pattern, with many fewer chicks apparently fledged. This may be due to disturbance due to boat mooring near the colony, causing chicks to emigrate early.

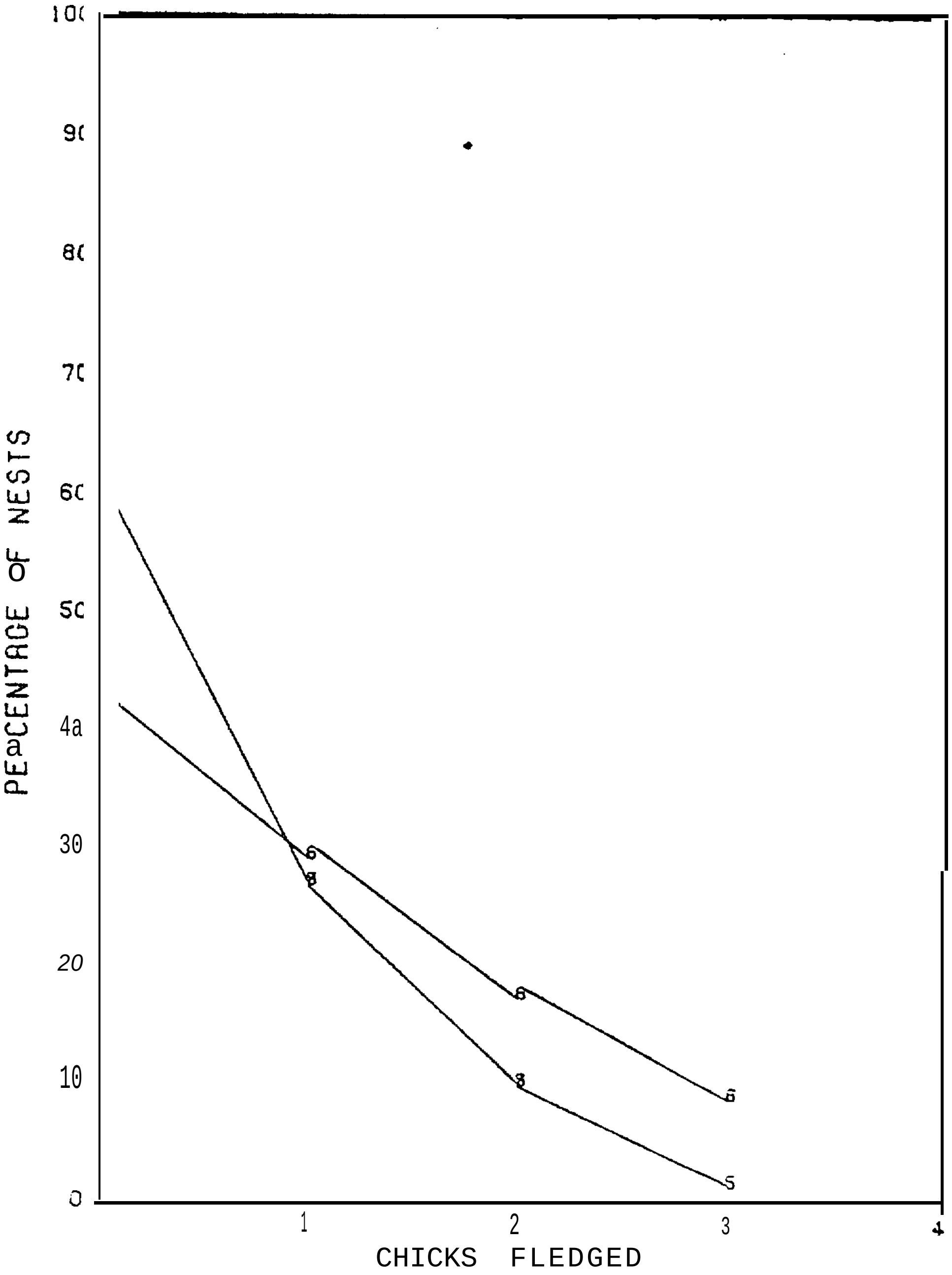


Figure 34. Chicks fledging plotted against percentage of nests, Egg Island, 1975-1976. 5 = 1975 survey, 6 = 1976 survey.

Egg Island gulls produce fewer chicks than those on North Marble, in proportion, but Egg Island resembles North Marble in 1972 in chicks fledged. The productivity on Egg Island is expected to increase as the proportion of experienced female breeders expands, given continued access to artificial food from human sources.

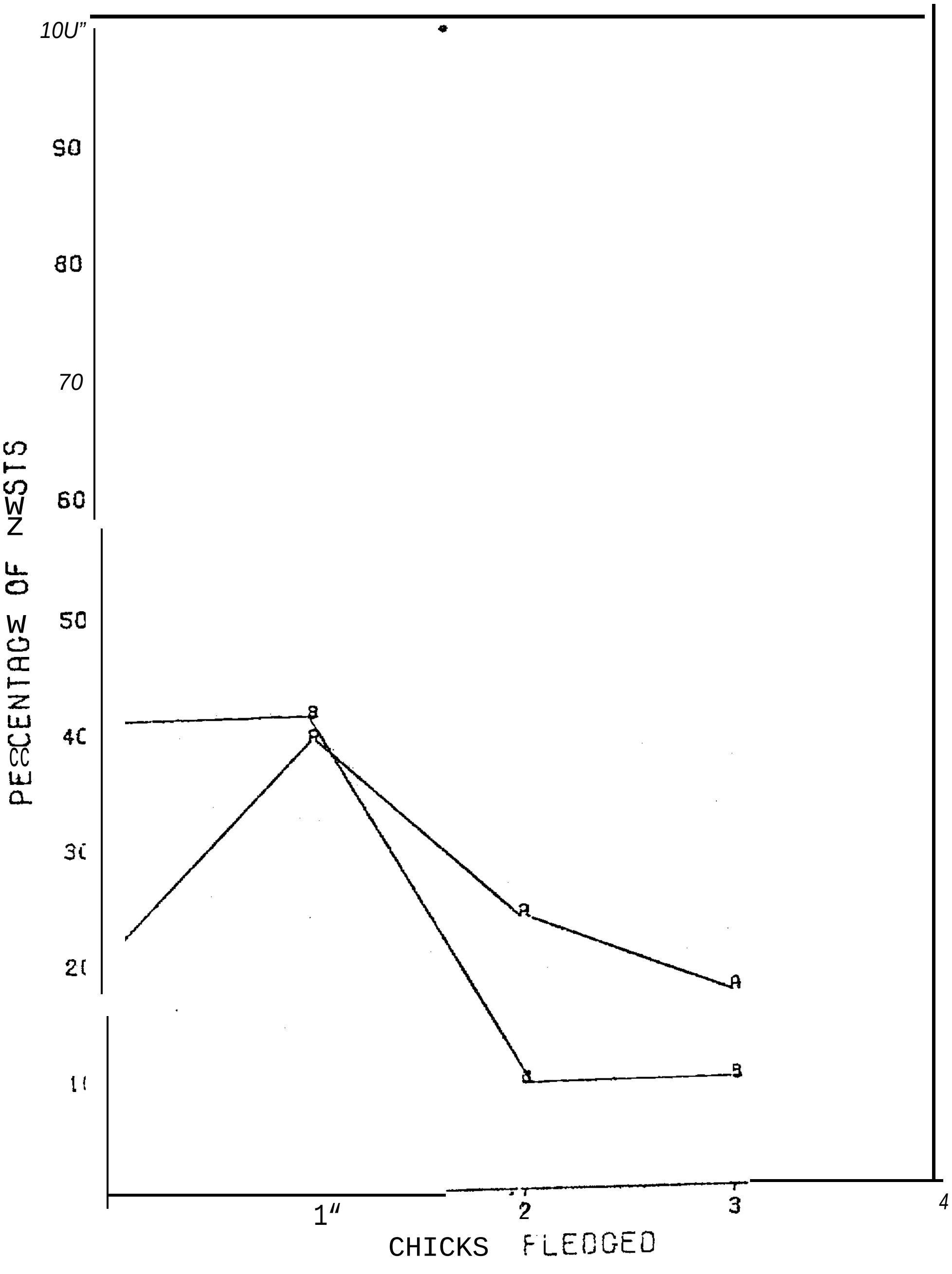


Figure 35. Chicks fledging plotted against percentage of nests, Dry Bay, 1977.
A = 'A' Colony, B = 'B' Colony.

Both 'A' and 'B' Colonies fledged similar percentages of one chick per nest, but 'A' colony fledged more two and three chicks per nest.

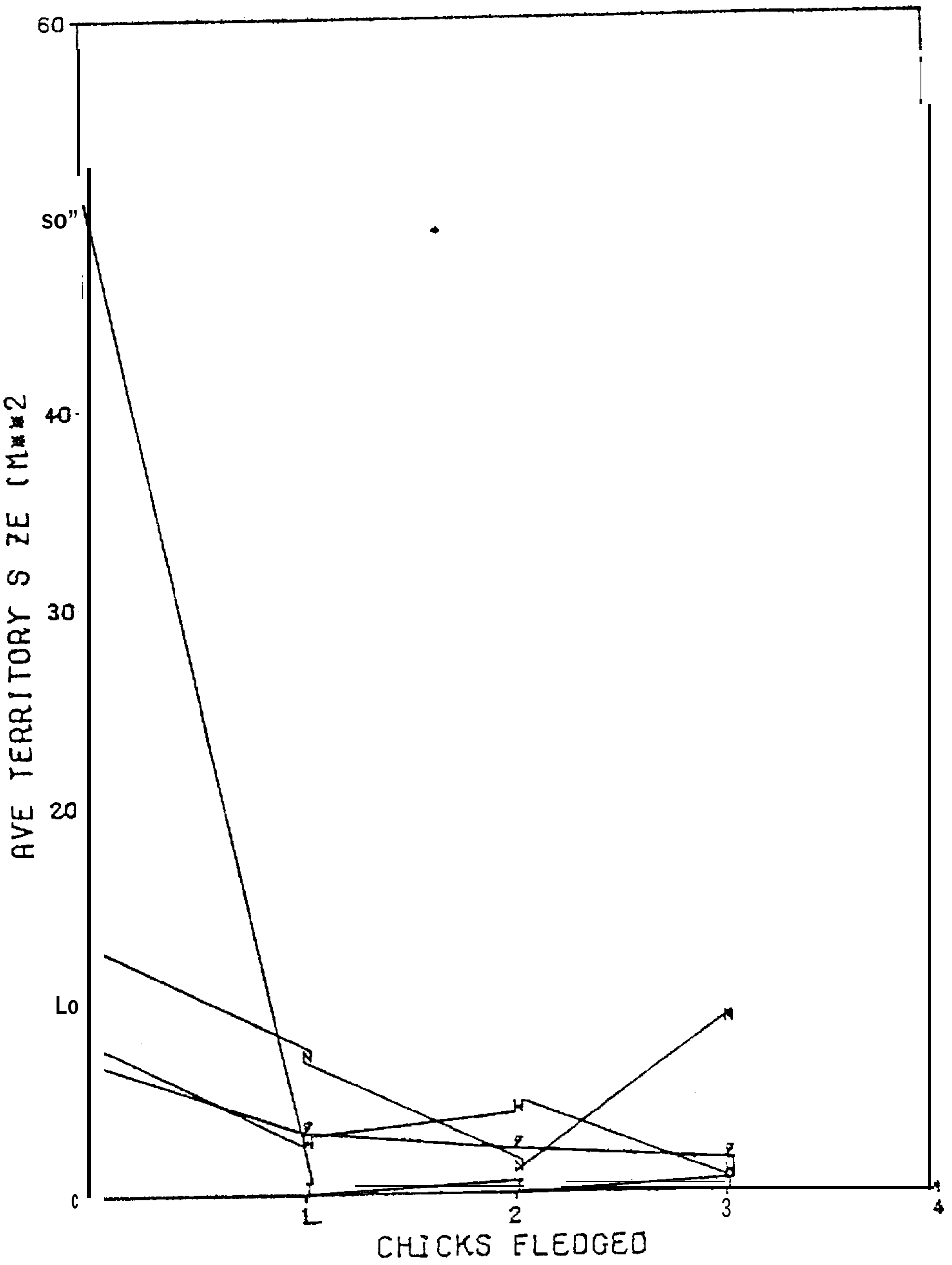


Figure 36. chicks fledging plotted against average territory size, North Marble, 1972. E= East Colony, W = West Colony, N = North Colony , T = Top colony.

Gulls with large territory sizes and small clutch sizes in the Top Colony fledged no chicks. Only a few chicks survived from this colony this season. Territory size played only a moderate influence in chicks fledging in the other colonies, since they were all within the same general. range.

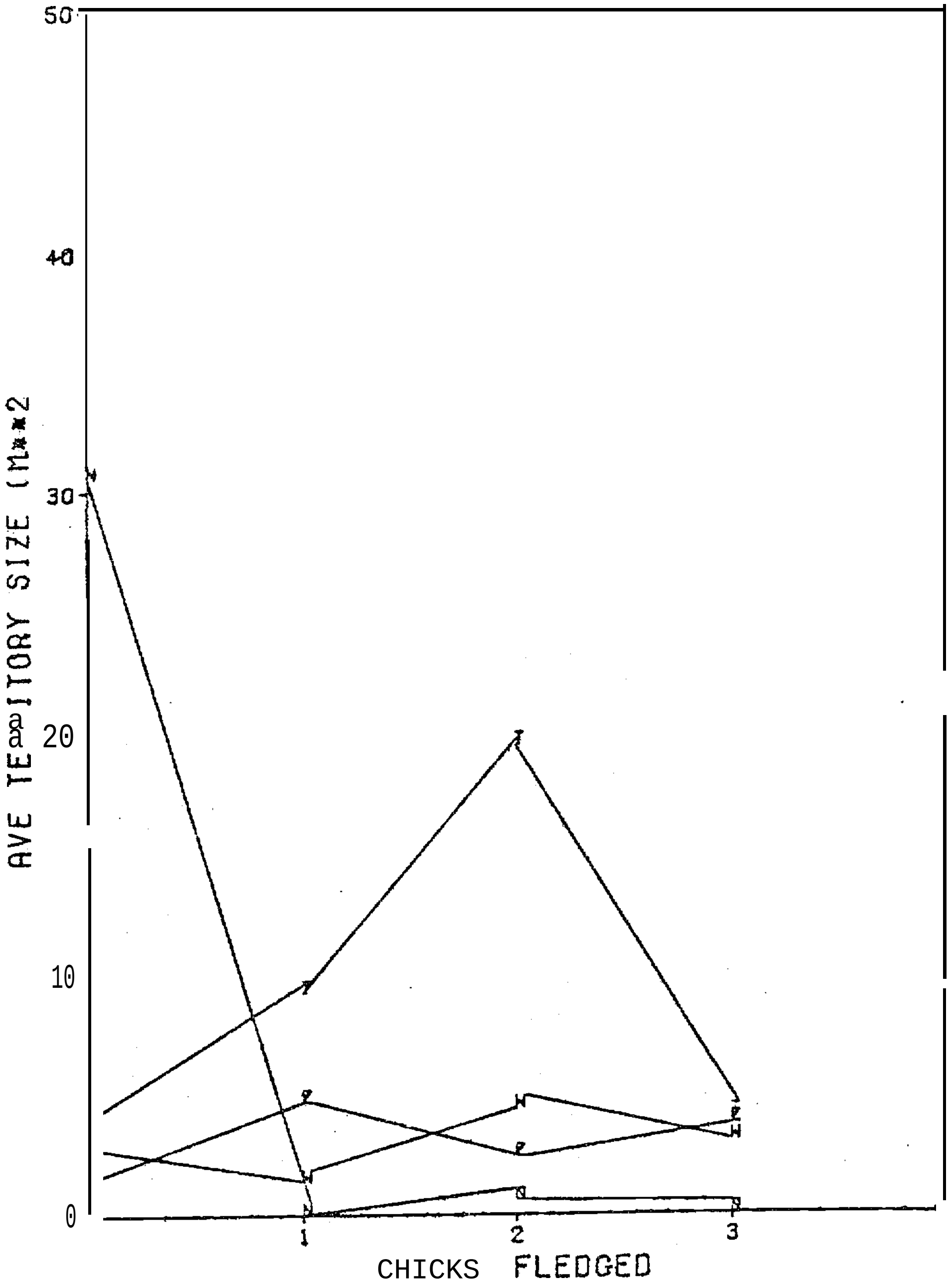


Figure 37. Chicks fledging plotted against average territory size, North Marble, 1973. E = East Colony, W = West Colony, N = North Colony, T = Top Colony.

Productivity was much greater in the Top Colony in 1973, with smaller average territory size, compared to 1972. The North Colony exhibits the unusual trend here, probably due to disturbance.

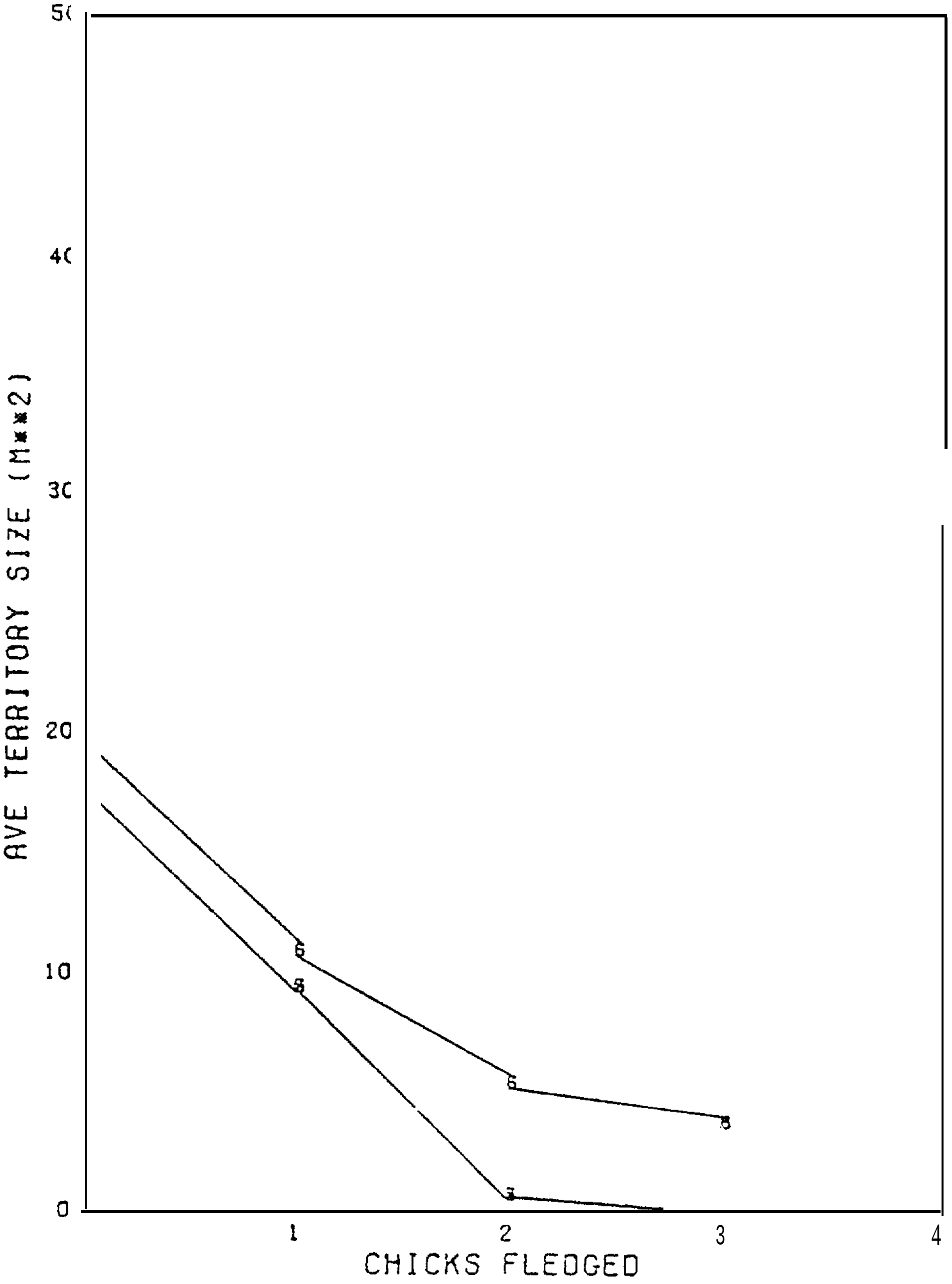


Figure 38. Chicks fledging plotted against average territory size, Egg Island, 1975 - 1976. 5 = 1975, 6 = 1976.

Territory size was slightly larger on the average in 1976, but productivity was also slightly better. However, both years the survey area shows a similar tendency, fledging mostly one chick per territory. Note larger territory size on Egg Island compared to North Marble (Figures 24, 25).

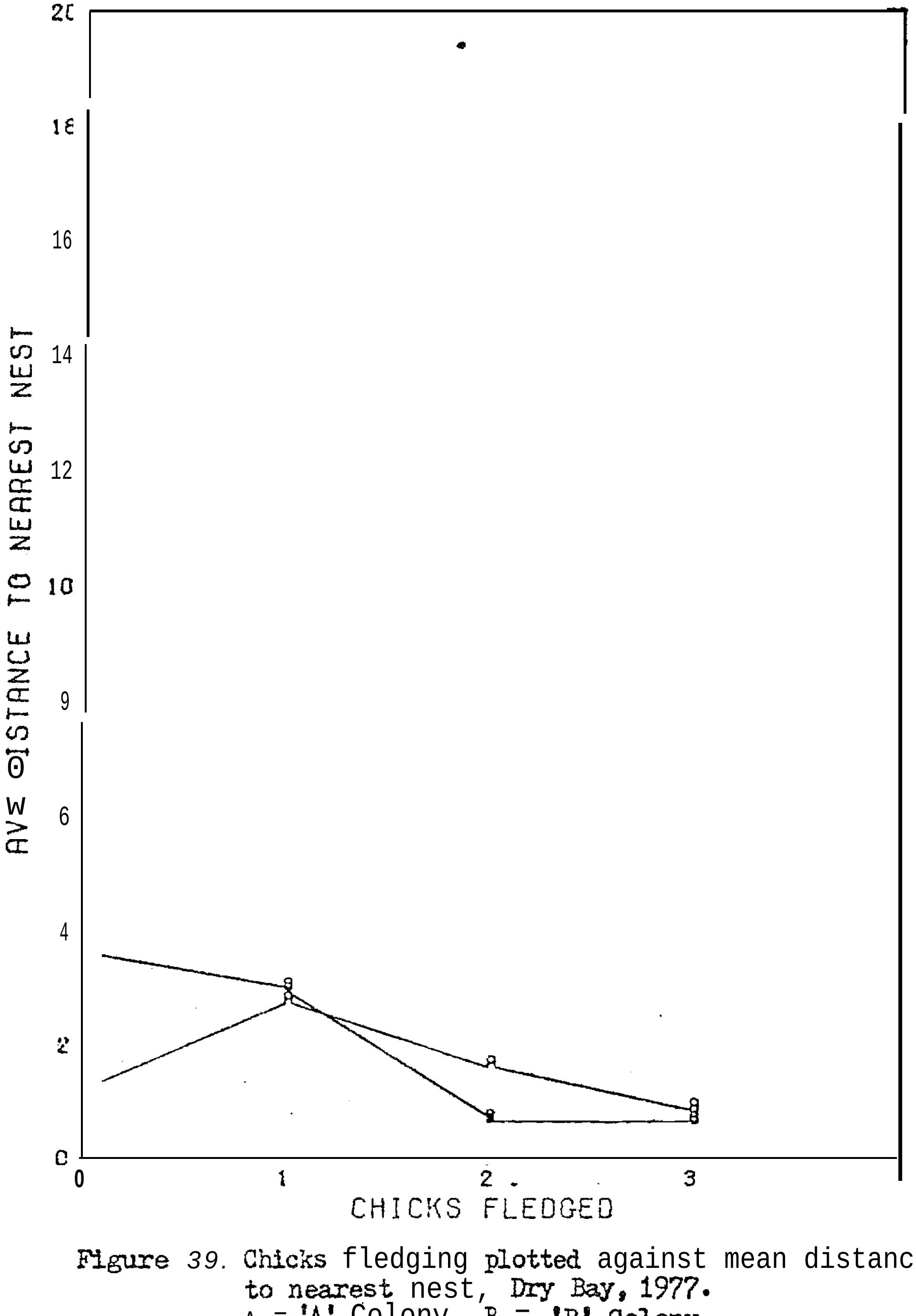


Figure *39.* Chicks fledging plotted against mean distance to nearest nest, Dry Bay, 1977.
A = 'A' Colony, B = 'B' Colony.

Mean distance to nearest nest had little effect on chicks fledging per nest at Dry Bay in 1977.

glaucescens colony at Dry Bay (1.44) (Table 6; Fig. 40).

The expanding coastal populations of *glaucescens* and *argentatus* x *glaucescens* hybrids encounter relaxed selection pressures due to unlimited nesting space and abundant natural food in recent-post glacial and river delta environments. *L. argentatus* genes are entering coastal populations at Glacier Bay, Dry Bay, and the Susitna Flats near Anchorage at the mouth of the Susitna River.

Paynter (1949) reported a production of 0.92 chicks per nest sufficient to maintain a stable population of *argentatus* on Kent Island, New Brunswick, very close to that we discovered at Lake Louise. Ludwig (1966) found a recruitment rate of 0.63 maintained a stable population of *delawarensis* on the Great Lakes. *L. argentatus* studied by Ludwig increased on the Great Lakes between 1960 and 1965 at an annual rate of 13% with a mean fledging rate of 1.47, quite close to the production at Dry Bay (*argentatus* x *glaucescens*). The population growth of *argentatus* on the Great Lakes was due to the abundance of the alewife (*Alosa pseudohargenus*), a major food source. Populations of *delawarensis* on the Great Lakes increased during the same period at 30% per year with a mean fledging rate of 1.74 (Ludwig, 1966), practically identical to North Marble. *L. glaucescens* studied by Vermeer (1963) produced 1.35 chicks per nest per year. Harpur (1971) published fledging rates of 1.33 and 0.96 per pair of *occidentals*. The highest mean fledging success in the literature is 2.00 chicks per nest reported by Coulter et al. (1971) for *occidentalis* on the Farallons. Other fledging successes, summarized by Keith (1966) ranged from 0.3 to 1.17.

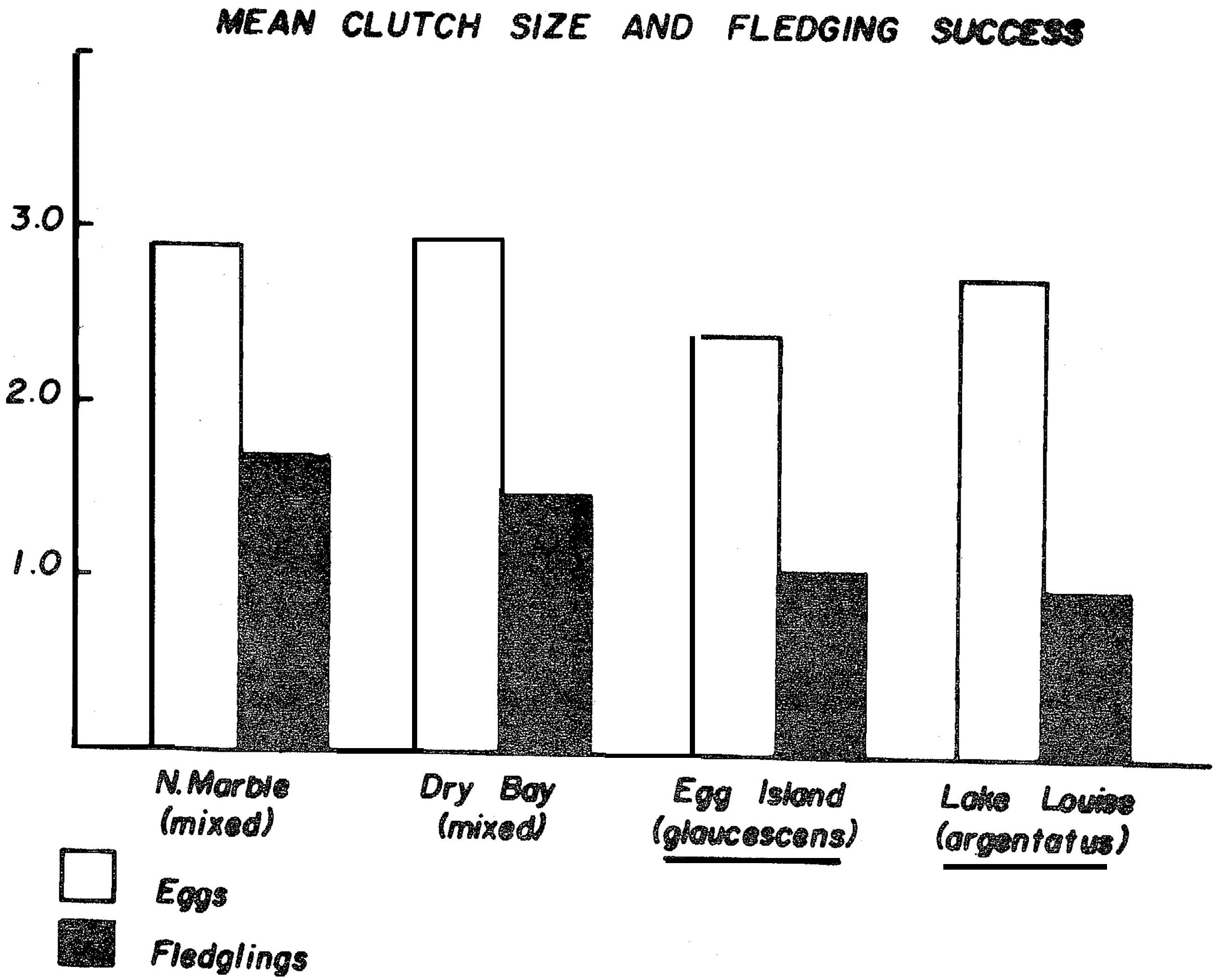
The above comparisons indicate the coastal populations of *glaucescens* and *argentatus* are reproducing well. North Marble has a very high reproductive rate, indicating a population expanding at 30% per year. Dry Bay has a high reproductive rate, suggesting expansion of 12% per year. The large glaucescens population at Egg Island, partially dependent upon artificial food in Cordova, is expanding at a rate of 4% per year, a "normal" pattern for gulls. For example, at this rate, in five years the 20,000 gulls breeding on Egg Island would number 24,333. This is over a 20% increase in five years, similar to conditions replicated in recent past in the eastern United States, due to the same reason, an increasing food supply due to man's activities. The Lake Louise population of argentatus, with limited nesting space and restricken food availability, is maintaining itself.

Table 6

Comparative Index of Gull Reproductive Success in Chicks Per Nest (Productivity)

Colony Location	Species	Chicks\ Nest	Reference
California	L. occidentals .	2.00	(Coulter et al., '71)
North Marble (1972-73)	mixed glaucescens/ argentatus	1.77	(Patten, 1974)
Great Lakes	L. delawarensis	1.74	(Ludwig, 1966)
Great Lakes	L. argentatus	1.47	(Ludwig, 1966)
Dry Bay (1977)	mixed glaucescens/ argentatus	1.44	(this paper)
British Col.	L. glaucescens	1.35	(Vermeer, 1963)
California	L. occidentals	1.14	(Harpur, 1971)
Egg Island (1975-76)	L. glaucescens	1.08	(Patten & Patten, 1977)
Lake Louise (1977)	L. argentatus	0.95	(this paper)
New Brunswick	L. argentatus	0.92	(Paynter, 1949)
Michigan	L. argentatus*	0.35*	(Keith, 1966)

* Population contaminated by DDT



MEAN CLUTCH SIZE AND FLEDGING SUCCESS

Figure 40

Banding Results

The temporal sequence of band recoveries from Egg Island juvenile gulls first suggested strongly migratory tendencies. Additional recoveries now support the emerging migratory pattern of juvenile gulls originating on sandbar barrier islands off the Copper River Delta. Indications are that recently fledged juvenile gulls from Egg Island disperse explosively to Prince William Sound salmon streams within a month of fledging (cf. Moyle, 1966) , and reach as far as Anchorage and Valdez before beginning migration south along the Pacific Coastline (Table 7; Fig. 41; Pearse, 1963). Band recoveries in January, from young gulls originating off the Copper River Delta, extend from Ketchikan, AK, to Puget Sound, WA. Several Egg Island juveniles, just over one year old, have been found in their second summer at Valdez. A color-dyed three-year old gull demonstrated lateral movement in July between Egg Island, off the Copper River Delta, and Middleton Island in the Gulf Of Alaska (Fig. 42.). More band recoveries of young gulls banded at Egg Island are from Valdez (25%) than any other location. Whether this represents environmental disturbances capitalized by gulls or simply concentration of human observers remains to be determined.

Table 7

Banding Recoveries of Juvenile Gulls from Egg Island

Location	Date	Reason
1. Valdez AK	22 Aug 75	aircraft strike
2. Valdez AK	22 Aug 75	aircraft strike
3. Valdez AK	29 Aug 75	dead on road
4. Anchorage AK	30 Aug 75	found dead
5. Copper Delta AK	1 Sept 75	eaten by eagle
6. Yakutat AK	- Oct 75	found dead
7. Juneau AK	4 Ott 75	shot by boy
8. Ketchikan AK	20 Jan 76	oiling
9. Vancouver BC	- Jan 76	found dead
10. Valdez AK	19 Jul 76	injury
11. Valdez AK	19 Jul 76	found dead
12* Cape Hinchinbrook AK	28 Jul 76	collected
13. Seward AK	5 Sept 76	found dead
14. Yakutat AK	8 Ott 76	found dead
15. Juneau AK	31 Ott 76	entangled
16. Olympia WA	23 Nov 76	no information
17. Petersburg AK	10 Dec 76	caught by dog
18. Harris Harbor AK	15 Jan 77	found dead
19. Prince Rupert BC	23 Jan 77	found dead
20. Rivers Inlet BC	-- Feb 77	found dead
21. Lake Tapps WA	• Feb 77	shot
22. Ketchikan AK	3 Mar’ 77	hit by car
23. Valdez Arm AK	24 Aug 77	found dead
24. Cordova AK	31 Aug 77	trapped & released

Table 8

Banding Recoveries of Juvenile Gulls From Strawberry Reef. Copper River Delta

	Location	Date	Reason
1.	Vancouver BC	3 Feb 77	found dead
2.	Bainbridge Island WA	16 Feb 77	found dead

Note: Tables 7 & 8. Radiation to Prince William Sound region after breeding seasons and then strongly migratory tendencies exhibited by N - S chronological sequence of banding recoveries.

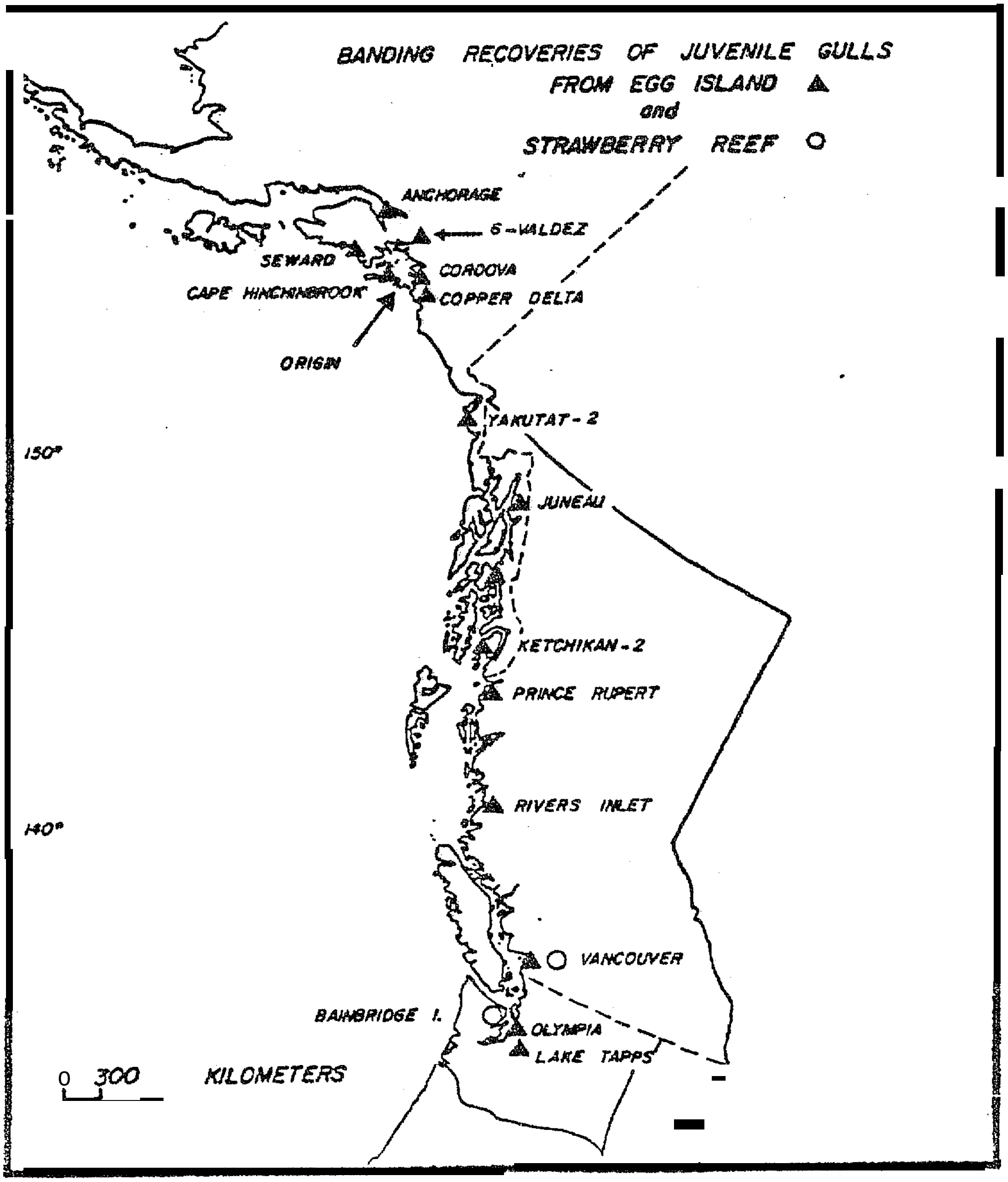

BANDING RECOVERIES OF JUVENILE GULLS
FROM EGG ISLAND ▲
and
STRAWBERRY REEF ○
ANCHORAGE
6 – VALDEZ
SEWARD
CORDOVA
CAPE HINCHINBROOK
COPPER DELTA
ORIGIN
YAKUTAT - 2
150°
JUNEAU
KETCHIKAN - 2
PRINCE RUPERT
RIVERS INLET
140°
VANCOUVER
BAINBRIDGE I.
OLYMPIA
LAKE TAPPS
0 300
KILOMETERS

Figure 41

Table 9

Observations of Color-dyed Gulls (Adults)

	Location	Date	Activity
1)	Cordova docks-canneries	July-Aug 75 Sept-Ott 75	feeding
2)	Cordova dump	July-Aug 75 Sept-Ott 75	feeding
3)	Egg Island	July-Aug 75	breeding
4)	Eyak River, Copper Delta	Aug 75	resting
5)	Hawkins Island, Prince William Sound	Aug 75	flying
6)	Juneau	Sept 75	resting
7)	Cordova docks-cannieries	March 76	resting
8)	Egg Island	June 76	breeding
9)	Middleton Island,* Gulf of Alaska	July 76	resting
10)	Hartney Bay, Orca Inlet	Aug 76	feeding
11)	Cordova City Airport	Aug 76	resting
12)	Cordova dump	July-Aug 76 Sept-Ott 76	feeding

<u>Note</u> artificial food sources, winter absence, suggestion of migration pattern.

* third-year juvenile

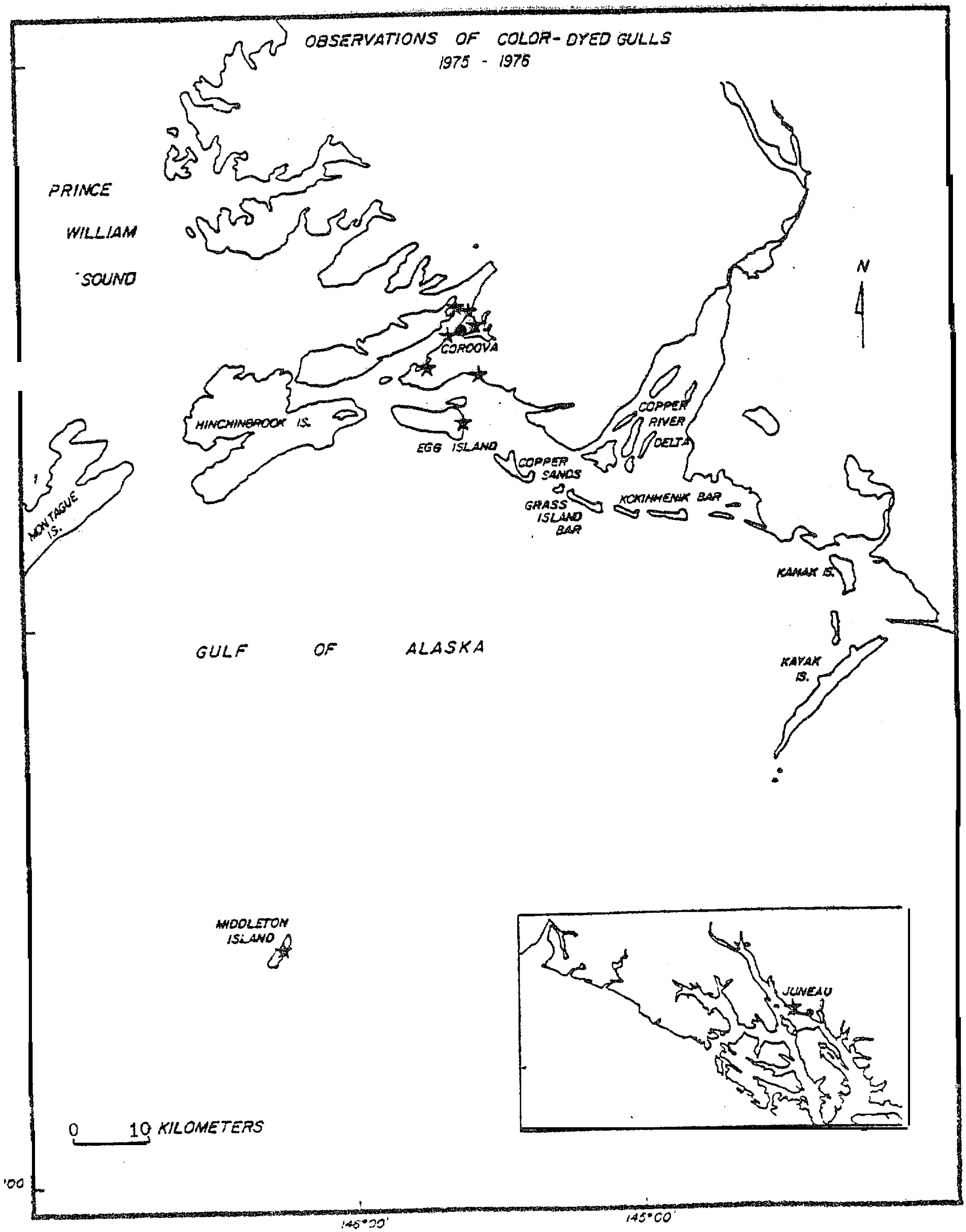

OBSERVATIONS OF COLOR-DYED GULLS
1975 - 1976
PRINCE
WILLIAM
SOUND
N
CORDOVA
HINCHINBROOK IS.
EGG ISLAND
COPPER
SANDS
GRASS
ISLAND
BAR
KOKINHENIK BAR
COPPER
RIVER
DELTA
KANAK IS.
KAYAK
IS.
MONTAGUE
IS.
GULF OF ALASKA
MIDDLETON
ISLAND
JUNEAU
0 10 KILOMETERS
'00
145°00'
145°00'

Figure 42

Wintering Areas of argentatus and glaucescens

A review of recent literature on wintering areas and F&WS observations of large gulls in the northeast Gulf of Alaska (Lensink, pers. comm.) amplifies banding and color-dyeing studies.

Isleib and Kessel (1973)* suggest part of the northeast Gulf of Alaska glaucescens population winters offshore on the continental shelf. Isleib (pers. comm.) reports argentatus, glaucescens and other hybrids are common in the winter in the Cordova area, where argentatus and hybrids are quite uncommon during the summer. Hoffman (pers. comm.) also finds glaucescens, argentatus and hybrids offshore between Yakutat and Kodiak in November. These observations, with the results of color-dyeing studies showing Egg Island-Cordova adult glaucescens departing the Cordova area and returning in March, indicate major pelagie population shifts and migratory movements southward in fall. and winter, (Table 9; Fig. 42).

The Fish & Wildlife Service / NOAA winter cruises (18 Jan - 13 Feb) find highest densities of seabirds in association with trawling operations 65 - 200 km east of Kodiak Island in waters over the continental shelf, or shelf break. Mean density in birds/km^2 for outer continental shelf *regions is:* British Columbia Shelf: 6.3; Southeast Alaska Shelf: 6.3; Northwest Gulf of Alaska 47.4; and Kodiak Basin: 35.2 (Lensink, 1977).

Larus glaucescens is among the most abundant species on NOAA/F&WS patrols (14-21 Feb; 7 Feb-4March). High numbers are consistently correlated with trawling operations of foreign-flag factory ships on the continental shelf. Larids occur in low but regular numbers in off-shelf areas. Apparently pure *glaucescens* predominate but a few *glaucescens* x *argentatus* hybrids and a very few typical *argentatus* are sighted off Canada and in the Gulf and Kodiak basins (Lensink, 1977).

Sanger (1973) and Barrington (1975) report pelagic *argentatus* and *glaucescens* 80 - 640 km off. southern California from January to April. *L. argentatus* increase until mid-February, and then rapidly decrease from mid-March to mid-April. Gulls collected in April have enlarged gonads in near breeding condition. Further north, F&WS ship surveys in the northeast Gulf of Alaska find marked shifts in relative abundances of gulls indicating migration from more southern regions:

Table 10

Large Gulls Observed on Transects in the Northeast Gulf of Alaska (Lensink, pers. comm.)

Species	Number/km^2			
	Feb.	Apr.	May	June
Unidentified Gull	0	.08	.05	.07
Glaucous Gull	.02	.23	0	0
Glaucous-winged Gull	3.33	1.69	1.89	.19
Herring Gull	.03	.21	3.23	.41

The sharp increase and then decline in May of argentatus per km^2 represents a migration from more southern regions (e.g., off California) towards interior breeding localities in Alaska, B.C., and the Yukon (Table 20). Herring Gulls appear on interior lakes across Alaska" in May just before spring break-up. Non-breeding argentatus may summer at sea, since inland lakes are not especially productive. Breeding pairs on inland lakes are more scattered than colonial and clutch size is smaller than coastal gull populations (Anderson, viva vote). Post-breeding adult gulls depart abruptly from interior lakes in late August or early September. Major rivers (Copper, Alsek, Taku, Stikine) provide migratory pathways to the sea.

The more gradual decline in glaucescens per km^2 from Feb. to June represents coastal breeders returning to colonies. From February to April pelagic glaucescens decrease by 50%. Gulls from Mandarte Island, B.C., are on site in February; gulls are present at North Marble in Glacier Bay in March (Streveler, pers. comm.) and appear on territories at Egg Island in April (Isleib, pers. comm.).

F&WS standing stock estimates of pelagic gulls exceed known breeding pairs in the NEGOA (Lensink, pers. comm.). Non-breeders and gulls originating from other than coastal NEGOA colonies comprise a large portion of the pelagic population. Offshore gull populations utilize food resources (including offal from foreign fisheries) , reducing corn-petition with onshore breeding populations.

Gull Food Habits

Continued access to food resulting from human activities will increase gull numbers in Alaska. This food supply is not likely to decrease with further industrial development in Alaska. Gene flow among gull populations will follow increasing numbers. Gulls exploit artificial. food due to natural plasticity of food selection and. dichotomy of foraging' pathways. Gull populations in Alaska currently exhibit both food selection under natural. conditions, and response to artificial food supply.

Glacier Bay

Alaskan gulls of the *argentatus* group under natural conditions show two major foraging pathways: first, gulls scavenge the intertidal in areas such as Glacier Bay, from the lowermost to the uppermost regions. The rise and fall of the strong tides in Glacier' Bay exposes up to ten meters of a rocky, algae-covered zone. Gulls take a wide variety of food items, including cast-up larger fishes such as Gadidae, Scorpaenidae, Cottidae and *Theragra*, and invertebrates such as *Mytilus*, *Thais*, *Balanus*, and *Pagurus* (Table 11). Invertebrates are broken, dropped, pried open, or swallowed whole. Secondly, strong tidal currents in Glacier Bay cause upwelling of soil nutrients deposited in the waters by glaciation (Streveler and Paige, 1971). The nutrients support food chains producing small fishes. Gulls dive for small fishes, stooping from several meters to well beneath water surface, in areas of tidal disturbances, at river mouths, near surfacing whales (Jurasz, pers. comm.; Divoky, 1976), taking

Osmeridae, Clupea harengus, Thaleichthys pacificus, and small shrimp (Pandalus). Gulls take other small fishes (Pholidae) from rocky intertidal pools by stalking. Glacier Bay, representing the natural environment, a recently deglaciated "unfilled niche," provides excellent feeding for gulls.

Dry Bay

Gulls feed on outer sandy beaches and at river mouths between Yakutat and Cape Fairweather (cf. Patten & Patten, 1975, for similar observations at Dixon River in Glacier Bay National Monument). Dry Bay is an important feeding area for gulls, cormorants, mergansers, and seals. Eulachon (Thaleichthys pacificus), fed heavily upon by gulls, normally spawn in clear rivers in March and April, but a prolonged, late and heavy run continued until the end of May 1977 south of Yakutat, including Williams Creek, a tributary of the Alsek. Gulls also feed heavily on Pacific capelin (Mallotus villosus) spawning in the surf during summer high tides. Other gull foods include small crabs (Cancer magister) ≤ 4 cm, blackfin poacher (Bathyagonus nigripinnis), herring (Clupea hargengus) spawning on kelp in April and May, Pacific sandlance (Ammodytes hexapterus) and razor clams (Siliqua patula). The abundant 1977 eulachon may have accounted for the high clutch size and resultant good reproductive success in the gull colony at Dry Bay.

Salmon offal from Dry Bay Fish Co., a small processing plant, is currently a minor food source for gulls, bears and wolves. Dry Bay supported much heavier commercial fishing earlier this century and the resulting offal may have then supported more gulls . A railroad hauled fish from the Akwe River to a cannery at Dry Bay (Ak. Geo., 1975). The Alsek fishery included both drift and set gill nets (Brogle ADF&G, pers. comm.). Nothing is left of the cannery except pilings. An indian village existed at Dry Bay long before the cannery (Ak. Geo., 1975). Only a dozen fishermen now live along the lower Alsek from late May to October. Their impact upon the biota other than salmon is minimal.

Haenke Island

Alaskan gulls also exploit marine mammals under natural conditions (Divoky, 1976; Tuck, 1960). Seals, for instance, give birth on pack ice at Haenke Island near Yakutat and in Muir Inlet in Glacier Bay. Gulls (both argentatus and glaucescens nesting on nearby fjord cliffs) scavenge seal feces, stillborn pups, other carcasses, and placentae (Streveler & Paige, pers. comm.). Remains of seal placentae, lanugo hair, and ordinary seal hair form the most common item in gull castings and stomach specimens collected at Haenke Island in June (identification courtesy Mr. T. Eley, ADF&G).

The affinity of gulls for sewage has been previously discussed (Patten & Patten, 1977) . This behavior may have originated from following marine mammals.

A long stretch of exposed, sandy beaches connects the fjordlands of Glacier and Yakutat Bays with prince William Sound on the north.

Egg Island

The gull colony at Egg Island, at the end of the chain of sandy beaches between Glacier Bay and Prince William Sound, exhibits parameters of an expanding population as discussed above. The population is expanding for two reasons: a result of increase in nesting space, as plant succession follows earthquake uplift of island colonies, and availability of artificial food in Cordova in the form of offal. and garbage.

Fish and crab processing plants in Cordova in 1972 discharged <u>2.6 million pounds of seafood waste</u> into Orca Inlet (USDI, 1976; underlining mine). EPA regulations require dumping of waste where material is not visible but in summers 1975-76-77 the gulls found the material highly visible, attracting huge foraging flocks (10,000 individuals per hour), notably during salmon-packing season (July-August). This is precisely when gulls feed young on Egg Island 20-30 km away. Color-dyed breeding birds from Egg Island join in these flocks with non-breeding adults and second and third-year juveniles. Gulls constantly interchange from Eyak Lake, Eyak River, and Orca Inlet to the colonies on sandbar islands at the mouth of the Copper River (Fig. 72) . The gulls feed on circling swarms on the effluent hosed from the floors of the seafood processing plants, ground up and dumped from pipes at the ends of the wharves. Gulls also feed on detritus in the harbor and on fishing boats.

Newly fledged juveniles appear at the seafood plants in late July and early August. Fewer gulls are found in the area when the seafood plants are not processing, e.g. , when ADF&G closes the season or when commercial fishermen strike. The Cordova municipal dump provides a more limited but more constant food supply and is used by fewer birds when effluent is available from seafood plants.

Lake Louise

Lake Louise, across Prince William Sound and 160 km into the interior from Cordova (Fig. 13)*, supports a small, now relatively stable population of argentatus. Fish, including lake trout (Salvelinus namaycush), greyling (Thallymus arcticus), burbot (Lots iota) and suckers (Catostomidae), form the most important part of the gull diet at this interior lake, since invertebrates are few in numbers and species. Gulls also scavenge fish scraps, refuse from State campgrounds, and garbage from a dump three km from the lake. Armed Forces recreation centers were located at Lake Louise until the mid-1960's, at which time the lake received heavier fishing pressure than at present. Poe (viva vote) stated his impression that gull nesting density on Bird Island is less now than a decade ago, when refuse and fish scraps were more readily available.

Gulls identified as argentatus are absent from the Cordova seafood plants during the summers, but Isleib and Kessel (1973) indicate they are common in the winter around the wharves. Most certainly these gulls originate from interior lakes such as Lake Louise, frozen in the winter.

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*(Part I).

Table 11

Known Gull Food Items

Colony/ Foraging Area	Glacier Bay	Dry Bay	Strawberry Reef	Copper Sands	Egg Island
Food items:					
Phylum Mollusca Class Pelecypoda					
	Mytilus edulis	*Siliqua patula*			*Siliqua patula* *Mytilus edulis* *Clinocardium nuttallii*
Gastropod					
	Fusitriton oregonensis *Neptunea lyrata*				
Cephalopod					
					octopus sp.
Phylum Arthropods Class Thoracica					
	Balanus glandula				
Decapoda	*Pagurus beringanus* *Hyas* lyratus *Chionoetes bairdi*	*Cancer magister*	*Pandalus borealis*		
Insecta					
					Tipulidae sp.
Phylum Echinodermata Class Echinoidea					
	Strongylocentrotus drobachiensis				

DISCUSSION

The rapid expansion of coastal settlements with their associated production and accumulations of sewage and refuse, the development of offshore oil fields, the discharge of industrial effluents into the ocean, the development of commercial fisheries with their attendant production of fish offal, and the steady increase of coastal recreational facilities, all have had, and continue to have, an impact on the distribution and number of seabirds (Cramp et al., 1974). Certain species show marked changes associated with the rapid industrial expansion and resource development occurring around the Northern Hemisphere. The large gulls (Larus) in particular, are rapidly reproducing "weedy" commensal species, highly adaptable to changing circumstances and able to withstand and often take advantage of changes in the environment. Commensal species inhabit ecological niches that are directly or indirectly the result of human interference. The most important artificial niches for gulls are garbage piles, sewage outfalls, and fish offal. The brown rat, European Starling (Sturnus vulgaris) in America, and various native "blackbirds" are examples of dramatic population increases that have had effects on other ecologic processes.

Gulls have increased sufficiently on both sides of the North Atlantic to become a major threat to other seabirds, by direct predation on adults and young, by robbing adults of food destined for young, and by usurping vital nesting areas. The rapid increase in Atlantic gull populations in recent years has caused both disquiet to civic authorities and alarm to conservationists.

Recently, we have noticed a marked increase in reproductive rate of Alaskan populations of Glaucous-winged Gulls (*Larus glaucescens*) and similarities in age structure of the arctic Alaskan populations of Glaucous Gulls (*L. hyperboreus*) to expanding populations of North Atlantic species of *Larus*, principally *L. argentatus*, the Herring Gull.

Herring Gulls have increased their numbers and expanded their breeding range since the turn of the century. The New England population has increased by a factor of 15 to 20 (Kadlec and Drury, 1968; Drury and Kadlec, 1974). The breeding range has extended south to North Carolina (Hailman, 1963; Parnell and Soots, 1975). Explanations offered for this increase include a reduction of direct human depredations (e.g. egging and shooting) since the turn of the century, and changes in factors such as availability of food. In recent years, the impact of traditional subsistence upon seabirds in the Atlantic has been minimal, and there have been vast increases in availability of artificial food (offal and garbage).

The expansion in breeding range has been followed by expansion of nesting habitat into salt-marshes (Parnell and Soots, 1975; Burger 1977). Consequently, Herring Gulls now nest in habitats used by other larids such as Common Terns (*Sterna hirundo*) and Laughing Gulls (*L. atricilla*) and increase in Herring Gull colonies has been associated with a decrease in populations of Laughing Gulls and Common Terns (Drury, 1965; Nisbet, 1971, 1973), Recently Burger and Shisler (1978) have studied nest site selection and competitive interactions of Herring and Laughing Gulls in New Jersey, and suggest continued displacement of breeding Laughing Gulls from sites colonized by Herring Gulls, as Herring Gull populations continue to expand.

There has been a general tendency for a decrease in numbers of both Arctic Terns and Common Terns all along the coasts of the Eastern United States and Canada over the last 30 years as gull populations have expanded (Nettleship and Lock, 1973; Nisbet, 1973; Drury, 1973, 1974). Tern populations are particularly vulnerable to harassment by gulls. The continuing increase in gull numbers along the Atlantic seaboard poses a considerable threat to tern productivity (Nettleship, 1977).

Recently the impact of disturbance by large gulls on the breeding performance and distribution of other birds has become of such magnitude that it is now considered to be quite serious (Nettleship, 1977).

The Herring Gulls and the Great Black-backed Gull (*L. marinus*) have done so well (increasing in numbers and expanding in range) that they now cause substantial damage to certain specialized species (terns, Atlantic Puffin (*Fratercula arctica*, among others) by taking eggs and young, by cleptoparasitism (*i.e.*, robbing parents taking food to young) and by physical displacement from optimal nesting locations (Nettleship, 1972, 1975; Nisbet, 1973; Drury, 1973, 1974).

Gulls in Britain have assumed their role as the modern urban scavenger since the late 1800's, accepting cities as safe refuges after protection by law from indiscriminate shooting (Cramp et al., 1974). In urban areas, gulls have increased enormously in the last 50 years and currently exhibit a doubling time of 6-15 years. The Herring Gull has shown steady increases on both sides of the Atlantic. In general, the Herring Gull in Britain has increased around developed parts of the mainland wherever nesting conditions are suitable; even nesting on buildings in populated areas reflect pressures on normal breeding sites caused by population growth. The increasing numbers of Herring Gulls have led to drastic control measures, which have been only partially successful.

The documentation of early signs of an impending explosive growth phase in local *Larus* population in the northeast Gulf of Alaska has been part of the results of an OCS project supported by BLM/NOAA over the past four years. There now is little question that the potential for explosive increases in the Alaskan populations of large gulls exists. In one week in July 1978, Patten with a field crew provided by the Forest Service, banded over 5,400 gull chicks in one location in southern Alaska. Over " 1,000 gulls have been banded in the last four field seasons.

In stable populations of large gulls on the east coast of the United States, the annual chick production rate averages 0.5 chicks/nest and the proportion of subadults in the population averages under 12% (Drury, pers. comm.). Surveys from Juneau, Alaska to Prince William Sound indicate much higher rates (1.08-1.77 chicks/nest]. George Divoky (pers. comm.) reporting preliminary 1978 census data from the Beaufort Sea estimated subadult plumaged birds made up 20% of the population and near Barrow, which has a sizeable human population (over 3,000), and with a dump appealing to Glaucous Gulls, the subadult population made up an astounding 40% of the population.

William Drury (pers. comm.)surveyed 1,500 miles of northwestern Alaska coast and concluded that Glaucous Gulls may be in Or entering a period of rapid growth of their population. The percentage of subadults in the population are the same as or above those of Herring Gull populations which are known to be rapidly expanding on the east coast of North America, *i.e.*, above 14%. The figures given to us by Drury from 1975 to 1978 are 15, 21, 7, and 23% for populations from Cape Spencer on southern

Seward Peninsula to Tolstoi Point in Norton Sound. The low figure in 1977 resulted from missed age group counts in part of the survey. Comparing northwestern Alaska populations to the east coast populations, the averages are both 18% subadults. The assumption is therefore, that both populations are expanding. If stable populations consist of 12% or less subadult birds, an increase of 6% per year in that category is highly significant.

SIGNIFICANCE

The ecological history of man's relationship to other species has only partially been a recitation of direct extirpations - as exemplified by the Bison, Passenger Pigeon, Carolina Parakeet, California Condor, Snail Darter, and the like. The other side of ecological history demonstrates how man enhances the carrying capacity of the environment for weedy, or nuisance species, which are adapted to disturbed environments and utilize artificial food. This aspect of population change is at least as serious as direct extirpations, both in total historic importance, and in the implications for future impact to man and other species of wildlife. A series of comparisons will be enlightening. Next to the Passenger Pigeon, consider the European Starling. Next to the Bison, consider the Brown Rat. In Alaska, next to the Sea Otter (a history of near extinction) consider the growth OF the large gull populations. All signs point to an explosive increase in 'sea gulls' in Alaska, similar to the unfortunate pattern of gull population explosions along the East Coast of North America and in the North Atlantic.

There are at least three serious aspects of unnaturally inflated gull populations in Alaska as elsewhere. First, gulls are a public health hazard, since they have been demonstrated as vectors of human pathogens in an outbreak of Salmonella poisoning at Ketchikan, in which over 100 persons sought medical treatment (Wilson and Baade, 1959). Secondly, gulls are opportunistic, efficient predators on other seabird and shorebird species, threatening, for example, the population stability of Alaskan marine bird species such as Horned (Fratercula corniculata) and Tufted Puffins (Lunda cirrhata), and having a significant effect on nesting by displacement of more abundant species such as the Murres (Uris spp.) (Drury, pers. comm,). In certain areas of the North Atlantic, as gull populations have expanded, the Common Puffin has disappeared from much of its former breeding range. Large gulls, which survive winters in unusually high numbers due to availability of garbage and fish offal, harass puffins during the breeding season, robbing the parent puffins of fish destined for the young, and actually by preying upon the starving puffin chicks which come from their burrows in search of food (Nettleship, 1975).

Geometric population expansion such as observed in Herring Gulls in Britain requires only a total annual increase of about 10%. The total annual increase is accelerated by slightly enhanced survival among juvenile gulls. Survivorship in young gulls is aided by availability of artificial food, such as garbage and commercial fish wastes. A typical demographic profile of a gull population in an explosive growth phase shows 18% of the population to be 0-3 years old, juveniles and subadults. This is excellent survivorship at the most vulnerable part of the age structure. Once adults, past age four, gulls are very long-lived species. Gulls at age four typically have a life expectancy of ten more years, all of which can be reproductively active.

Domestic and industrial onshore and offshore development activities generate large volumes of solid comestible waste in unnatural settings, precisely what may trigger explosive increases in survivorship in juvenile gulls. The aesthetic sight of large flocks of gulls above garbage barges is an example of the third aspect of unnaturally inflated gull populations. Secondary effects of development will without a doubt include spreading onshore garbage dumps, precisely the sort of environment that facilitates increased gull survivorship. Sufficient knowledge of the situation is not yet available even to measure the true dimensions of the coming gull problem. North of the Alaska Peninsula the coastal environment becomes radically different from the Gulf of Alaska, with winter minimal daylight, shore-fast ice, small tidal fluctuations, diminished intertidal life, and low temperatures. These factors require different foraging strategies by gulls. Conditions which may limit the growth of gull populations north of the Alaska Peninsula probably do not come into effect during the breeding season, but during the winter, about which we have little or no data.

Alaska could be on the sill of a major ecological disruption. Coastal towns such as Kodiak, Dutch Harbor, Nome, and Kotzebue represent an unknown potential for facilitating increases in gull populations like those witnessed in the North Atlantic. Offshore oil and gas operations in frontier areas, as well as fisheries, also have the potential of widening and extending the basis for commensalism bygulls.

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PART 111

Pathobiology

Table of Contents

page

List of Tables

- A Review -

The Role of Gulls (Larus argentatus & Larus glaucescens) in the Transmission of Human Parasitic and Enteric Diseases in Alaska

Human Parasitic Diseases and Gulls

The exposure of untreated or poorly treated sewage to gulls in Alaska may lead to human health hazards from bacterial and helminth infections (cf. Coulson and Monaghan, 1978; Crewe and Owen, 1978). One of the traditional safety factors relied upon for prevention of dispersal of pathogens which may be present in sewage has been the dilution of the effluent with an abundance of river or sea-water (Silverman & Griffiths, 1956). Overloading, however, or construction of new sewage plants with outfalls into already heavily polluted waters, i.e., the Cordova dockfront area (USDI, 1976), reduces the dilution factor, and certain organisms such as gulls may actively concentrate human pathogens through their foraging behavior (Crewe & Owen, 1978). For instance, in primary sewage treatment plants there is little evidence that continuous aeration adversely affects helminth ova, nor is rapid sand filtration an effective means of removing helminth ova from *sewage* effluent (Silverman & Griffiths, 1956). Varying percentages of viable helminth eggs (Ascaris, Trichurus, Enterobius, Diphyllobothrium and Taenia - all human pathogens) have been found in sludge of primary sewage treatment (Silverman & Griffiths, 1oC. cit.). Eggs may persist in a viable state in the sludge for years.

The role of birds in the dissemination of helminth ova is difficult to evaluate, but is highly suggestive (Silverman & Griffiths, 1oC. cit.; Crewe & Owen, loc. cit.). Götzsche (1951) suggested that gulls might be responsible for dissemination of tapeworm eggs from. sewage outfalls. Gulls may come into contact with sewage at every stage of treatment, and it is well known that gulls frequent canneries, fish-packing houses and garbage dumps in Alaska in addition to roosting on municipal water supplies, *i.e.*, Ketchikan and Cordova (Wilson & Baade, 1959; USDI, 1976). Dumping of raw sewage from coastal towns in Alaska attracts gulls, which, as natural scavengers, forage on the fecal matter, e.g. at Valdez (Bayliss, pers. comm.) and Juneau (Williams, pers. comm.) and Ketchikan (Wilson & Baade, 1959) (Fig. 43,44). Silverman and Griffiths (1956) found gulls attracted to sewage outfalls especially in winter (see Ketchikan epidemic below). These authors reported that feeding experiments with Herring Gulls revealed that tapeworm eggs (*Taenia* spp.) can pass through the digestive tract of gulls and still retain infectivity. The eggs appear in the feces about an hour after ingestion. Mature eggs may hatch in the gut of the gull, and the activated hexacanth embryo may be found in the droppings.

Sewage treatment and disposal problems in isolated areas are varied and complex (Silverman & Griffiths, *loc. cit.*). Pollution from inadequate disposal of human excreta is a potential source of health problems along the Alaskan coast, and is complicated by the scavenging nature of abundant Alaskan gull populations.

Naturally Occurring Human Helminth Infections Associated with Gulls in Alaska

Eskimos in western Alaska depend upon several species of fish for much of their food. These fishes are often eaten raw and thus transmit certain species of *Diphyllobothrium* tapeworms for which the fish are intermediate hosts (Rausch *et al.*, 1967). Kuskokwim Eskimos eat raw or partially frozen smelt (*Osmerus*), blackfish (*Dallia*), and stickle'backs (*Pungitus*) which often contain larval tapeworms (Rausch *et al.*, 1967).

Rate of tapeworm infection reached highest level in winter and early spring, after greatest consumption of blackfish and sticklebacks (Rausch et al., loc. cit.). Uncooked fish comprises over a third of the diet of these Eskimos (Heller & Scott, 1967). Levels of infection with Diphyllobothrium tapeworms ranges from 16% to 30% (Rausch et al., loc. cit.).

One of the most frequently found tapeworms in this region was identified by these authors as D. dalliae; the adult stage is in humans and dogs. Early life stages inhabit the blackfish, Dallia pectorals, an abundant and economically important species in the Kuskokwim River region (Rausch et al., loc. cit.). Rausch (1956) obtained infectious tapeworm plerocercoid larvae from blackfish trapped on the lower Kuskokwim, and raised adult tapeworms from these larvae at the Anchorage laboratory in Glaucous-winged Gulls, which had been hatched in an incubator and maintained parasite-free until the experimental infection. Rausch (1956) stated that the occurrence of the tapeworm Diphyllobothrium dalliae is to be expected in gulls in Alaska. Gulls are implicated in the dissemination of this parasite, transporting eggs to various aquatic areas where the eggs develop through several life stages to plerocercoid larvae in fish infective for humans.

Another cestode commonly found in man in Alaska is a Diphyllobothrium species undetermined. This type appears identical with a tapeworm reared experimentally in humans, dogs, and Glaucous-winged Gulls from plerocercoids (infectious larvae) encysted on the stomach of salmonid and coregonid fishes (Rausch et al., loc. tic.). We report salmon gurry from the Cordova canneries frequently contains large numbers of tapeworms and this gurry is scavenged by gulls. Rausch et al. found Glaucous-winged Gulls naturally infected with the above Diphyllobothrium in Alaska. The presentation of fish gurry harboring tapeworms to gulls provides ample opportunity for parasite dissemination.

Rausch (1956) collected other adult cestodes morphologically resembling *D. dendriticum* from various species of gulls in Alaska. Kuhlow (1953)* established infections by feeding encysted tapeworm plerocercoids from the stomach of *Osmerus eperlanus,* *a smelt.* Chizhova (*in* Rausch, 1956) observed a tapeworm parasitizing Herring Gulls, humans, and dogs at Lake Baikal; similar cross-parasitism is expected in Alaska. Rausch (1954) observed specimens of still another *Diphyllobothrium* species in dogs, foxes, cats, and gulls in Alaska after feeding plerocercoids from infected steelhead (rainbow) trout. Rausch (1954) experimentally infected Glaucous-winged Gulls with the tapeworm *Diphyllobothrium ursi,* a parasite of brown bears. It is readily apparent that tapeworms associated with gulls infect a variety of hosts including humans.

Thomas (1938) reported the life cycle of the tapeworm *Diphyllobothrium oblongatum* involved Herring Gulls, herring (*Leucichthys* sp.), and copepods. Tapeworm eggs were deposited in the feces of the gulls. Thomas (1938) reported that freezing the tapeworm eggs solid in ice for a month did not destroy their ability to hatch normal coracidia (early developmental stages). This suggests tapeworm ova survive through the Alaskan winter to continue their life cycle in the spring.

Although the pernicious-like anaemia associated with human *Diphyllobothrium* tapeworm infection in Eurasia has not been observed in Alaska, the potential for such disease has been examined by Rausch *et al.* (1967). These authors reported that there was no evidence that infection of Alaska

***In* Rausch, 1956.

natives by diphyllobothriid tapeworms contributed to the development of microcytic anaemia. However, in view of the often poor nutritional level of these people, the infection may be detrimental due to tapeworm absorption of B-vitamins (Rausch et al., 1967). Caucasians, however, especially those descended from northern European stock, may be genetically susceptible to anaemia associated with Diphyllobothrium tapeworm infections (Tötterman, 1947).

In addition to fish tapeworms, gulls have been demonstrated as part of the marine cycle of trichinosis, a roundworm which typically infects Eskimos in arctic Alaska. Marine"mammals may become infected through consumption of encysted trichinae in the feces of carrion feeding birds such as. gulls (Schwabe, 1964). Eskimos become infected with trichinosis upon consuming raw flesh of marine *mammals,* including polar bears, seals, walrus, and beluga whales, all of which carry Trichinella spiralis (Rausch et al., 1956).

Summarizing Parts I & II: Alaskan gulls associated with cannery effluent and sewage outfalls are implicated with the dissemination of human cestode and nematode parasites.

Gulls and Enteric Disease in Alaska

Reports originating from all parts of Alaska of human gastroenteric diseases associated with high fever, marked diarrhea, and dysentery have been received by Alaska Department of Health and Social Services on occasion {Williams, 1950). Outbreaks of intestinal diseases occur in Alaska where water supplies are unprotected *(Foster, 1954).* Alaska Public Health Laboratories have conducted studies indicating improper sewage disposal, Herring and Glaucous-winged Gulls, and public water supplies in the spread of the pathogenic bacteria Salmonella manhatten. First, a definition:

salmonellosis is the term applied to infections caused by any of a group of more than 1,100 microorganisms (Steele & Galton, 1969). Salmonellosis usually occurs as an intestinal infection resulting in enteritis, or may terminate in septicemia and death (Steele & Galton, 1969).

Technically, the bacterial genus *Salmonella* is composed of gram-negative, aerobic, non-spore-forming microorganisms that grow well on artificial media and reduce nitrate to nitrite (Edwards & Galton, 1967). All members of the genus are potentially pathogenic for man and animals. Salmonella inhabit most species of warm-blooded animals (Steele & Galton, *loc*. cit.). *Salmonella typhimurium* has been recovered from gulls found dead near a cannery (Nielson, 1960). *S. paratyphi* B has been discovered in Herring Gulls (Wilson & MacDonald, 1967) as well as *S. derby* (Faddoul & Fellows, 1966, *in* Steele & Galton, 1969). Gulls carry many other kinds of *Salmonella* (Steele & Galton, 1967). Enteritis in gulls may be the only sign of infection, increasing the probability of disease transmission (Nielson, 1960).

Herring and Glaucous-winged Gulls became suspect in the Ketchikan *Salmonella* epidemic at Ketchikan because of scavenger feeding habits at the city sewer outfall (Foster, 1954). Gulls leave the Ketchikan waterfront with the advent of winter storms and fly approximately four km to Ketchikan Lake, the municipal wasupply (Wilson & Baade, 1959). Epidemics of gastrointestinal disease have occurred at this time of year. Subsequent epidemiological investigation indicated a common vehicle (the community water supply) for the etiological agent. Literally thousands of gulls roosted on the lake at the time of the 1953 epidemic, and the water showed gross contamination not explainable by any other source (Wilson & Baade, 1959).

Specimens from gulls collected at the lake proved positive for Salmonella manhatten (Paratyphoid C group). Cultures from gulls as well as patients hospitalized with gastroenteritis were verified by CDC, Atlanta, GA. Over 100 persons in Ketchikan were treated by physicians. At the time of the outbreak, drinking water was not purified by *any* method. Subsequent chlorination of the water supply *drastically* reduced the incidence of this disease in Ketchikan, but the situation must be monitored to assure constant levels of chlorination. Similarly, gulls roost on the lake forming the Cordova water supply and the chlorination is monitored (Morley AEH, pers. comm.).

The city of Valdez in September 1976 was still dumping raw sewage below waterline in that harbor (Bayliss, pers. comm.). Photographs show gulls at Valdez foraging directly *at* the sewage outfall with slick extending some hundred of meters downwind. Bayliss (pers. comm.) informs us Valdez will soon complete sewage treatment facilities..

Pollution of reservoirs by aquatic birds has been recorded from Massachusetts, New York City, San Francisco, Los Angeles, Vancouver, B.C., and London, England (Wilson & Baade, 10C. cit.). Typhoid bacillus has been isolated from gull excreta collected in the vicinity of *a* town in Scotland where typhoid epidemics had first occurred (Wilson & Baade, 10C. cit.). Salmonella were recovered from 78% of gull droppings collected near sewage disposal works at Hamburg, Germany. Samples taken from sewage-free areas were consistently negative (Muller, 1965).

According to Pauls (1953), providing *safe* and adequate water supply and sewage disposal is intricately linked with prevention of enteric disease outbreak. The role of gulls is an added phase to the study of both enteric and parasitic diseases in Alaska. The Ketchikan *Salmonella* outbreak underlines the need for proper, adequate sewage disposal systems preventing gull contamination with disease organisms transportable to public water or food supplies. Sewage disposal in many smaller communities in Alaska is accomplished by single premises or *scavenger systems* (underlining mine) (Pauls, in Alaska's Health, 1954). Contaminated water supplies and improper sewage disposal have historically (since 1807, the first reporting date) been major causes of gastrointestinal disease outbreaks in Alaska (Pauls, 1953).

The influx of people to Alaska will increase health hazards since carriers of typhoid and parasitic infections are undetected within this group (Pauls, 1953). The present explosive immigration to Alaska and projected rapid industrial growth of offshore oil operations may lead to conditions where gulls act as vectors for rapidly spreading human diseases.

Influenza in Avian Populations - A Review

Interactions between human and gull populations will increase with the development of coastal oil resources in Alaska. We include here under Task A - 28 a discussion of another potential aspect of the increase in gulls in Alaska as it relates to oil development.

Animals can be important as potential reservoirs or contributors to new pandemic strains of influenza virus (Kaplan and Beveridge, 1972). Pandemics of type-A influenza are caused by "new" strains of virus appearing suddenly in human populations. These new strains may arise by genetic recombination with animal or avian influenza viruses. For instance, Hong Kong virus (A/Hong Kong/1/68) probably arose as a genetic recombinant formed as a result of a mixed infection of an animal or bird with an animal or bird influenza virus and a human A/Asian (Asian flu) strain (Kaplan and Beveridge, 1972).

Individual influenza viruses contain two different virus-coded surface antigens, known as the haemaglutinin and the neuraminidase. Webster and Laver (1972) suggest that because the haemaglutinin of Hong Kong virus is completely different from the preceding Asian strains, such a great difference is not likely to have arisen by mutation. It seems more likely that the new Hong Kong virus arose by recombination. An animal or avian virus could have donated the haemaglutinin of A/Hong Kong/1/68 and the neuraminidase could have come from the human A/Asian strain. This sort of genetic recombination can be produced in live animals under experimental conditions. Since this kind of recombination can *occur* in laboratory animals it could occur in nature.

Avian influenza is caused by type-A viruses and infects both wild and domestic species around the world. Depending upon the virus strain, host species, and age of bird infected, avian influenza produces symptoms ranging from a drop in egg production to extraordinarily high mortality (Beard, 1970). The virus A/tern/South Africa/61 caused very severe disease in terns, with mortality running into the millions (Becker, 1966). The epizootic in terns was first noted because of the high mortality, but high mortality rates are probably an exception. Becker (1966) suggested that wild birds might act as unapparent carriers of avian influenza viruses. This *has* since been demonstrated by Homme and Easterday (1970), who showed that exposed ducks were infected for two weeks, long enough to carry the virus long distances and transmit the infection to wild and domestic birds along the way.

Antibodies specific for type-A influenza viruses have been demonstrated by serological surveys of wild birds in the U. S., Australia, and the USSR (Slemons et al., 1974). At least 100 distinct types of avian influenza virus have been isolated from various bird species with signs of respiratory illness or from flocks showing mortalities of unknown origin. Influenza viruses in birds not only affects the upper respiratory system, but also causes a drop in egg production, fertility, and matchability. Experiments have indicated that strains of avian influenza have a marked effect upon the reproductive systems of birds (Samadieh & Bankowski, 1970). Kleven et al. (1970) reported chalky-white, unpigmented, soft-shelled eggs increased up to 30% when breeding flocks are struck by influenza. The effect of influenza upon wild bird population reproduction is completely unexplored (see above discussions of egg pathologies, in Egg Loss section)

Environmental factors can play a very important role in infection and disease, and it is here we relate influenza and offshore petroleum development. Studies have revealed that more severe manifestations of influenza result from interactions of virus and other factors, particularly cold stress. For instance, apparently recovered birds stressed by chilling show further infection as measured by virus isolations and rises in antibody titers (Homme et al., 1970). There was a consistent correlation between coldstress and disease; birds subjected to low ambient temperatures developed much more severe, chronic virus disease. Petroleum exposure is known to lead in hypothermia in birds (McEwan & Koelink, 1973). Logically petroleum exposure could lead to the onset of virus disease. We point out the complete lack of information concerning the interactions between petroleum exposure, hypothermia and disease, especially in seabird populations in northern seas. (See above Chick Mortality section for a discussion of weather factors on survivorship).

Avian influenza viruses can be dispersed by migrating birds. Becker (1966) suggested that some species of seabirds carry virus in a latent state. Under stress, such as stormy weather, or oil exposure, the viruses become active, resulting in epizootics. During migrations, seabirds with active virus infect susceptible species with which they come into contact. Rosenberger et al. (1974) isolated type-A influenza viruses from migratory waterfowl. In this study, the cloaca appear to be a better site than the trachea for isolations of the virus. If the cloaca or feces are a prime site of influenza isolations> this is an important implication for dissemination of these viruses.

Sera collected from seabirds in the northern USSR, among which were Herring Gulls, have shown antibody activity not only to avian influenza virus but also to A/Hong Kong/1/68 (Zakstel'skaja et al., 1972). Webster and Laver (1972) found sera from Australian pelagic birds specifically inhibited the neuraminidase of Asian/57 strain of human influenza, in addition to the neuraminidase of A/Hong Kong/1/68, indicating presence of specific antibodies to these viruses. The antibodies to A/57 neuraminidase were found in sera of Short-tailed ShearWaters (Puffinus tenuirostris) and several other species. Webster and Laver (1972) suggest that these birds exchange avian influenza virus from areas in the Northern Hemisphere with Australian coastal waters. The Short-tailed Shearwaters possessing antibody to A/57 neuraminidase are known to migrate around the Pacific from Australia to the Bering Strait off Alaska (underlining mine), returning to Australia (Webster & Laver, 1972).

Slemons *et al* (1974) showed that ducks in the California Flyway, which includes Alaskan birds, are involved in the natural history of type-A influenza viruses, and that the migration patterns and daily foraging flights provide one mechanism by which the viruses can be transported over long distances and be disseminated at each stopping place. Multiple strains of virus circulating simultaneously in bird populations provide excellent conditions for genetic recombination in nature. Thus wild birds play an important role in the dissemination of type-A influenza viruses, and may provide conditions for genetic interaction of type-A viruses of both human and animal types, resulting in new hybrid strains.

Experimental Challenge of Gulls with Human Influenza

To test susceptibility of partially immune and non-immune gulls to human influenza virus, Messrs. J. Klein, M.Sc., J. Markowitz, M.Sc., and S. Patten, M.Sc., under the direction of I.L. Graves, DVM, inoculated two species of gulls (*Larus argentatus* and *Larus delawarensis*) with the virus Influenza A/Port Chalmers/1/73 (H3N2) , a recent human strain. Both test animals had been caught in the wild and maintained in captivity in Johns Hopkins Animal Facilities. The Herring Gull showed a weak antibody titer in serum (1:16) *prior* to laboratory challenge; the Ring-hilled Gull showed no such titer. The presence of antibodies specific to Port Chalmers influenza in the Herring Gull set-urn was confirmed by Radial Diffusion (Ouchterlony) test, and replicated three (3) times. The gull could have been exposed previously to the influenza strain in the wild or in captivity.

Under experimental conditions, both gulls were inoculated intranasally and into the trachea with .2cc undiluted stock virus. Under normal circumstances influenza is spread by droplet (respiratory) transmission.

Incubation period is one to three days. Characteristically an abrupt onset of disease follows, indicated in humans by chills, fever, headache and myalgia. Recovery of uncomplicated cases begins three to four days after onset of symptoms. Immune-competent individuals should be able to mount a response to an influenza infection within five days. Passage of the test virus used in this experiment through embryonated chicken eggs showed the strain to be very infectious *to* the 10" dilution.

Four days after the initial challenge with the virus, the non-immune gull was found dead. The first day post-challenge, the gull showed a slight rise in temperature. On the third day the gull still exhibited good reactions and normal behavior. Gross pathology observed in autopsy was consolidation of the lower left lung (evidence of a pneumonia-like infection). Heart, brain, kidneys, lung and liver were cultured for bacteria with mostly negative results. Only the brain evidenced presence of a slight bacterial growth, likely a post-mortem occurrence.

Five days post-challenge with the *virus, the* partially immune - Herring Gull showed poor behavior, with nyctitating membrane fibrillation (CNS symptom), loss of weight, cyanotic soft-parts (pneumonia-like symptoms), and died with *a very* acute illness on the evening of the fifth day. Autopsy revealed no lung consolidation, air sacks asymptomatic, no tracheal blockage or other gross pathology other than infestation with mallophaga. Bacteria were cultured on nutrient agar plates from several organs, indicating possible bacteremia.

Tissue specimens from trachea, pharynx and internal organs were cultured for viruses and passed again through egg and tissue culture to determine which organs were virus-positive. Virus recovery was confined to specimens from the upper respiratory tract of both birds, suggesting a response similar to the course of fulminating human influenza infections.

Influenza Virus Antibody Assay

To answer the question of whether gull populations in the northeast Gulf of Alaska have been exposed to Type-A influenza viruses, we performed a series of tests on gull sera collected during the course of this investigation.

Methods involved the use of multiple-well Single Radial Diffusion Plates supplied by WHO with the following antigens in gel medium: 1) Bel RNP (all influenzas); 2) A/Chick "N" Ger RNP (all avian influenzas); and 3) A/Hong Kong/68 (a human influenza).

Results are as follows: 1) Adult gull sera (n=19) ran against Bel RNP (all influenzas) showed 5% exposure to influenza virus of unspecified nature. Positive serum was from an adult gull breeding at the Alsek River (Dry Bay) in 1975. 2) Gull chick sera (n=56) collected from the large population at Egg Island in 1976 and ran against A/Chick “N” Ger RNP (all avian influenzas) gave positive antibody response in 7% of the cases and a weak response in 1.7% of the cases. 3) In the initial run against the A/Hong Kong/68 antigen (human influenza), 16% of the adult gull sera (n=19) showed positive antibody response. These reactive sera were from adult gulls collected at Egg Island and Dry Bay. However, on the second run against the HK antigen, the previous positives did not react , giving equivocal results. On the third run, 9.5X of sera collected from adult gulls breeding at Egg island in 1975 (n=21) indicated some response to the Hong Kong antigen, forming precipitin rings around the wells in which the sera had been deposited. These precipitin rings were not as strong as the positive control, suggesting either a weak antibody response, exposure at some time in the past with subsequent decreasing antibody titer, or cross-reactivity with another influenza antigen.

These results to date indicate avian influenza is present in the NEGOA gull populations and some exposure to a Hong Kong or similar antigen.

Newcastle Disease Virus Antibody Assay

Newcastle disease virus (NDV) is considered a pathogen for most avian species (Hanson, 1972). Newcastle disease can be a mild illness with *transient* respiratory signs or it can be fatal with severe respiratory and neurological symptoms (Beard and Brugh, 1975). It can also cause hemorrhage and necrosis of the intestinal tract (Beard and Brugh, loc. cit.). Bradshaw and Trainer (1966) gave evidence of NDV infection in wild ducks and Canada geese by demonstrating hemaglutination-inhibiting (HI) antibody in 14-17% of birds tested. Palmer and Trainer (1970) reported 31% of Canada goose sera contained antibody to NDV. Rosenberger et al. (1974) described isolation of NDV from several species of migratory waterfowl. The cloaca or feces may be a prime site of virus isolations in migratory waterfowl, with implications for dissemination (Rosenberger et al., 1974).

We observed three dead or dying immature Black-legged Kittiwakes and many Glaucous-winged Gull chicks in the meadows on Egg Island; the kittiwakes and some gull chicks showed no external injury (see Chick Stage and Mortality Factors, above). The kittiwakes were totally unexpected in the meadows since they are cliff-nesters and pelagic feeders. In the Hopkins laboratories we are examining an adequate sample (250) of sera from Egg Island gull chicks for evidence of common virus diseases, among whicl is NDV. We are using the HI test, which is the most convenient, rapid and economical method for evaluating antibody titer to NDV (Beard and Brugh, 1975).

Our procedures are as follows: all sera are heat-treated at 56°C for 30 minutes to remove non-specific inhibitors; positive control is NDV hyperimmune chicken antisera; negative control is normal chicken serum (both controls heat-treated 56°C, 30 min.). HI tests are performed on microtiter plates using 0.5 or 1.0% chicken red blood cells in buffered saline. In the initial screening antibody activity has been detected in 8 of 125 sera (6.47.). We are continuing our examination of these sera and suggest an NDV strain in this gull population.

Botulism, Toxoplasma. and Q Fever Antibody Assays

Gull sera from the Northeast Gulf of Alaska, collected as part of the NOAA OCSEAP RU96 research program, were further examined for antibody titers against botulism, toxoplasma and Q Fever, animal-borne diseases which can be transmitted to humans. The antibody testing was conducted on a cooperative basis by the Department of Epidemiology and Preventative Medicine of the School of Veterinary Medicine, University of California, Davis.

All Alaskan gull sera examined were negative for antibodies *against* botulism. Investigators in Denmark reported isolating botulism bacteria from gulls that fed in brackish waters of the North Sea. However, the Danish researchers failed to find antibodies to the botulism bacteria. The lack of antibodies with the bacteria present is an unusual situation. More work needs to be done on the resistance of gulls *to* botulism toxins (Behymer, pers. corm.).

The Davis group tested 61 Alaskan gull sera, both chick and adult, for antibodies against toxoplasma and Q Fever. All 31 chick sera were negative to both antigens. However, of 30 adult gull sera tested, 4 (13%) were positive for toxoplasma.

The sera identification numbers, location of collection, titers and dates of *collection* are presented in Table 1 .

Table 1 . Toxoplasma Titers in Alaskan Gulls

Site	Sera ID #	Titer	Date
Egg Island	EI *40*	(1:64)	July 10, 1975
Egg Island	EI 44	(1:256)	"
Egg Island	EI 44 (duplicate)	(1:4096)	"
Dry Bay	AR 37,	(1:2048)	June 30, 1975
Cordova clocks	CO 50″	(1:128)	July 12, 1975

*Note: gull CO 50, collected on the Cordova Ocean Docks, Cordova, Alaska, at the canneries and fish-processing plants . had antibody titers to both toxoplasma and Q Fever.

There were also low titers against Q Fever in 7 of 30 adult gulls (23%) as follows in Table 2 .

Table 2. Q Fever Titers in Alaskan Gulls

Site	Sera ID#	Titer	Date
Egg Island	El 45	(1:2)	July 10, 1975
Egg Island	EI 46	(1:2)	"
Egg Island	EI 47	(1:2)	"
Dry Bay	AR 33	(1:2)	June 30, 1975
Dry Bay	AR 34	(1:2)	"
Dry Bay	AR 40	(1:2)	"
Cordova docks	co 50*	(1:4)	July 12, 1975

*See previous table for note regarding CO 50.

Here follows a brief discussion of toxoplasmosis and Q Fever.

Toxoplasmosis is a sytemic protozoan disease. A primary infection in human females *during* the early gestational period of pregnancy may lead to death of the fetus; later infection to chorioretinitis, brain damage with intracerebral calcification, hydrocephaly, microcephaly, fever, jaundice, rash, hepatomegaly and splenomegaly. The occurrence of this disease is worldwide in animals and man. Infection in man is common but clinical disease exceptional. The infectious agent is *Toxoplasma gondii*, an intracellular coccidian parasite belonging to the *Sporozoa* and closely related to the *Isosporoa*. The taxonomy and complete life cycle of this parasite are uncertainly known. Birds and mammals appear to be intermediate reservoir hosts of ‘1’. *gondii* (APHA, 1975).

Q Fever is an acute febrile-rickettsial disease; onset may be sudden. A pneumonitis occurs in most cases, with cough and chest pain. Chronic endocarditis, hepatitis, and generalized infections have been reported. This disease is endemic in many areas. The infectious agent is Coxiella burneti, an organism with unusual viability in the free state. Wild and domestic animals are the reservoir hosts, with infection unapparent. The mode of transmission is commonly by airborne dissemination of ricketssiae in dust or near premises contaminated by placental tissues, birth fluids and excreta of infected animals. The disease is also contracted by direct contact with infected animals" or other contaminated materials. Susceptibility of humans is general (APHA, 1975). The scavenging of seal placentae by gulls may link these birds to the natural cycle of this disease.

SUMMARY

Alaskan gulls, associated with sewage outfalls and cannery effluent, are implicated with the transmission of Salmonella, an enteric disease, and in the dissemination of human cestode and nematode parasites. The Ketchikan Salmonella epidemic, in which over 100 persons sought medical treatment, emphasizes the need for proper and adequate sewage disposal systems preventing the contamination of gulls with disease organisms transportable to public water or food supplies. Gulls are demonstrated to be susceptible to human influenza strains, and to display antibody titers to avian influenzas, Newcastle Disease virus, toxoplasma, and G--fever. A review of the Literature on avian influenzas indicates a complete lack of information concerning interactions between petroleum exposure, hypothermia, and onset of virus disease, particularly in seabird populations in northern seas.

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PART IV

Effects of Petroleum Exposure on the Breeding Ecology of Gulls and Kittiwakes

Table of Contents

List of Tables

List of Figures

Objectives and Rationale of Petroleum Exposure

This research is addressed to the following task: an analysis of the effects of petroleum exposure on the breeding ecology, including incubation behavior and hatching success, of the Gulf of Alaska Herring Gull group (*Larus argentatus* x *Larus glaucescens*) and on Black-legged Kittiwakes (*Rissa tridactyla*).

The devastating effects of massive oil spills on seabird survival are widely reported, but little is known of the effects of low--level oil pollution on avian reproduction (Grau *et al.*, 1977). Previous studies of petroleum effects on seabird eggs suggest matchability is markedly reduced (Gross 1950; Birkhead *et al.*, 1973; Patten & Patten, 1977). Rittinghaus (1956) and Hartung (1963, 1964, 1965) reported that marine birds contaminate eggs with oil from the environment and hatching success of eggs thus exposed to petroleum was markedly reduced even after extended periods of incubation. Abbott, Craig and Keith (1964) suggested that oil interfered with normal respiratory exchange through the eggshell, while Szaro and Albers (1976) found hatching success of eider (*Somateria mollissima*) eggs was significantly reduced by microliters of petroleum exposure, that is, very small quantities. Patten and Patten (1977) have recently found unweathered North Slope Crude Oil 22 times more toxic than equivalent amounts of mineral oil under field conditions. Grau *et al.* (1977) have confirmed in laboratory experiments that small amounts of bunker C oil significantly depress bird reproduction. Indeed, oil exposure has been used in the past to control gull populations along the Eastern Seaboard of the United States and in several western U.S. wildfowl refuges (Gross, 1950; R. King, USF&WS, pers. comm.).

In summary, literature on the effects of oil exposure on the reproduction of marine birds is limited. Studies that do exist suggest high toxicity of petroleum to eggs, and marked effects upon the reproductive productivity of females. Complete knowledge of the effects of petroleum exposure in various forms is needed to evaluate and predict the full impact of oil pollution on the annual productivity of marine bird populations.

This current research is to provide information on the effects of both weathered and "raw" North Slope Crude Oil on the hatching success and incubation behavior of key seabird species nesting on Alaskan islands in proximity to Valdez tanker lanes and offshore oil lease areas.

Species examined are Herring Gulls (*Larus argentatus*) and Glaucous-winged Gulls (*Larus glaucescens*), which are common inshore and marine scavengers nesting in colonies and Black-legged kittiwakes (*Rissa tridactyla*) common pelagic feeders nesting on cliffs. The study sites are the largest gull colony in the northeast Gulf of Alaska, Egg Island, located 10 km SE of Point Whitshed and 20 km south of Cordova (60° 23′ N, 145° 46′ W) Dry ‘day, 75 km SE of Yakutat (59° 10' N, 138° 35′ W), and Middleton Island, 130 km S of Cordova (58° 24′ N, 146° 19' W).

Our research objectives are thus defined as:

(1) to determine threshold levels of petroleum effects to gull and kittiwake reproduction under field conditions, including both "raw" and weathered oils,

(2) to test alteration of incubation behavior and ability to

produce second (replacement) clutches following experimental mortality due to petroleum exposure,

(3) to analyze gull and kittiwake population ecology in order to determine factors influencing “normal” reproductive success in other colonies in the northeast Gulf of Alaska.

NOTE : Study areas and itinerary are discussed in Part I {Evolution Section) with the exception of Middleton Island (see below).

Materials and Methods of Petroleum Exposure

Our methods include analysis of reproductive productivity at a series of nest sites marked with survey flags. Petroleum exposure to eggs is by drops from microliter syringes with repeating dispensers, with equivalent amounts of non-toxic mineral oil applied to a control sample. Reproductive success/mortality is compared to further controls of "normal" (unexposed) colonies adjacent to the experimental areas. The use of microliter syringes allows for precise manipulation of tiny amounts of petroleum exposure, which is in 20, 50, and 100 microliter doses at three (3) stages of incubation. Petroleum used is North Slope Crude Oil provided by NMFS Auke Bay Laboratory, with commercially available mineral oil as the control.

Experimental results are compared to the standards previously established for "normal" Alaskan gull reproduction (Patten, 1974; Patten & Patten, 1975, 1976, 1977). Egg loss through nonspecific predation has been the principal factor influencing hatching success and fledging rate in previous studies.

Results of Petroleum Exposure to Eggs

To determine threshold levels of petroleum exposure to gull reproduction, we conducted an oiling experiment in a colony at Dry Bay, mouth of the Alsek River, 75 km SE of Yakutat, Alaska. The oil experiment was carried out in an experimental area adjacent to controls known as 'A' and 'B' colonies. Receptors were a mixed group of Glaucous-winged x Herring Gulls (Table 4).

Table 1

Petroleum Exposure Parameters

Sample size		Dose	Date	Approx. Day of Incubation
10 nests	30 eggs	20ul	24 May	1
20 nests	60 eggs	50ul	1 June	8
20 nests	60 eggs	100U1	4 June	11

Petroleum Exposure Results

Table 2

Nests 1 - 10 Time: Onset of Incubation

Dose: 20µl 30 eggs Date: 24 May

9/30	=	30%	hatch
6/30	=	20%	"lost" (predated)
15/30	=	50%	failed to hatch

Table 3

Nests 11 - 30 8th day of Incubation

Dose: 50µl 60 eggs Date: 1 June

16/60	=	27%	hatch
14/60	=	23%	"lost"
30/60	=	50%	failed to hatch

early (1-2 days) chick mortality

3/60 eggs	=	5%

Table 4

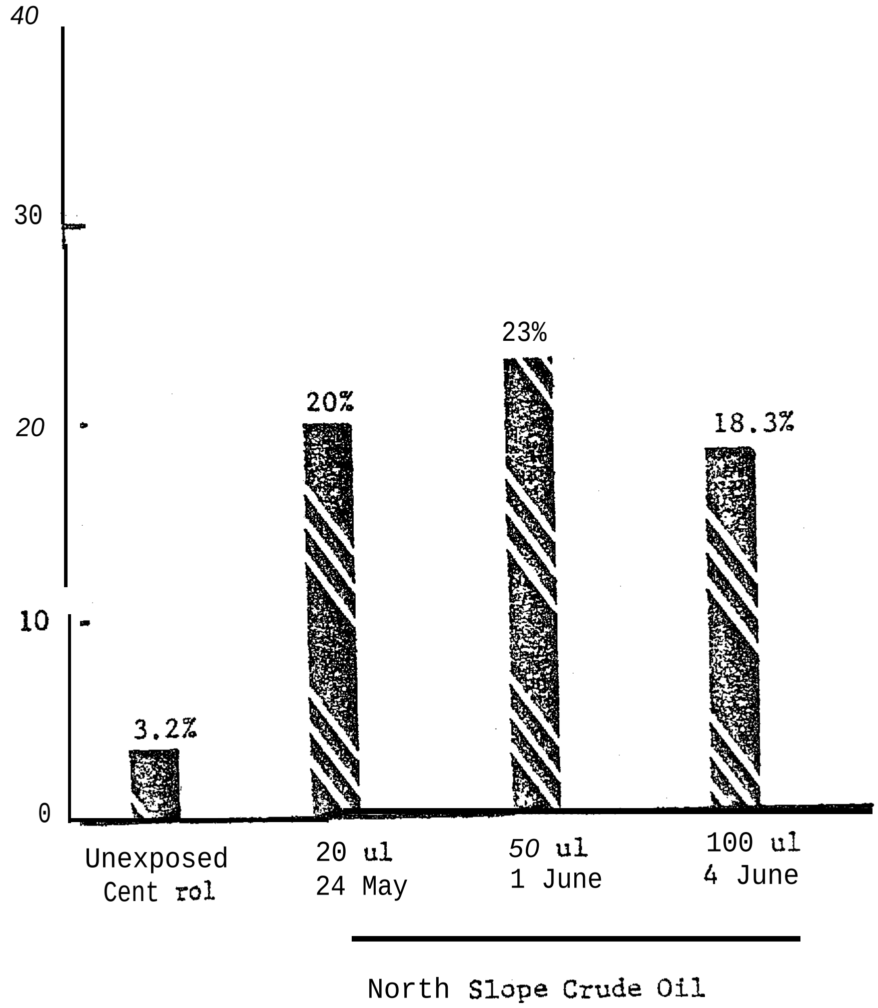
Nests 31 - 50 11th day of Incubation

Dose: 100µl 60 eggs Date: 4 June

41/60	=	68.3%	hatch
11/60	=	18.3%	"lost"
8/60	=	13.3%	failed to hatch

early (1-2 days) chick mortality

2/60 eggs	=	3%



KNOWN EGG LOSS , DRY BAY 1977
EXPERIMENTAL AND CONTROL COLONIES

Figure 1

PERCENTAGE EGGS REMAINING IN NESTS (FAILED TO HATCH)
IN EXPERIMENTAL AND CONTROL COLONIES, DRY BAY, 1977

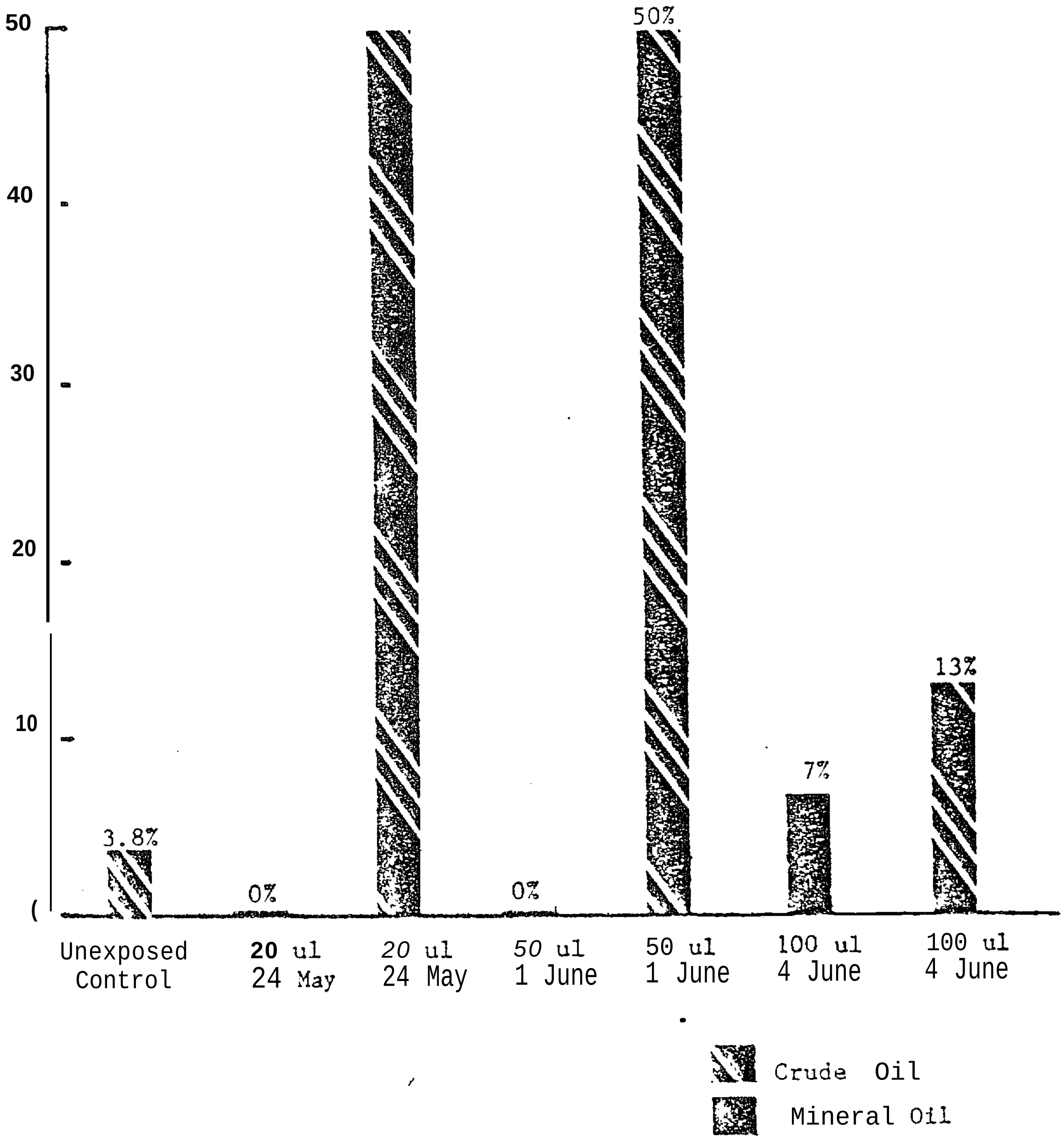
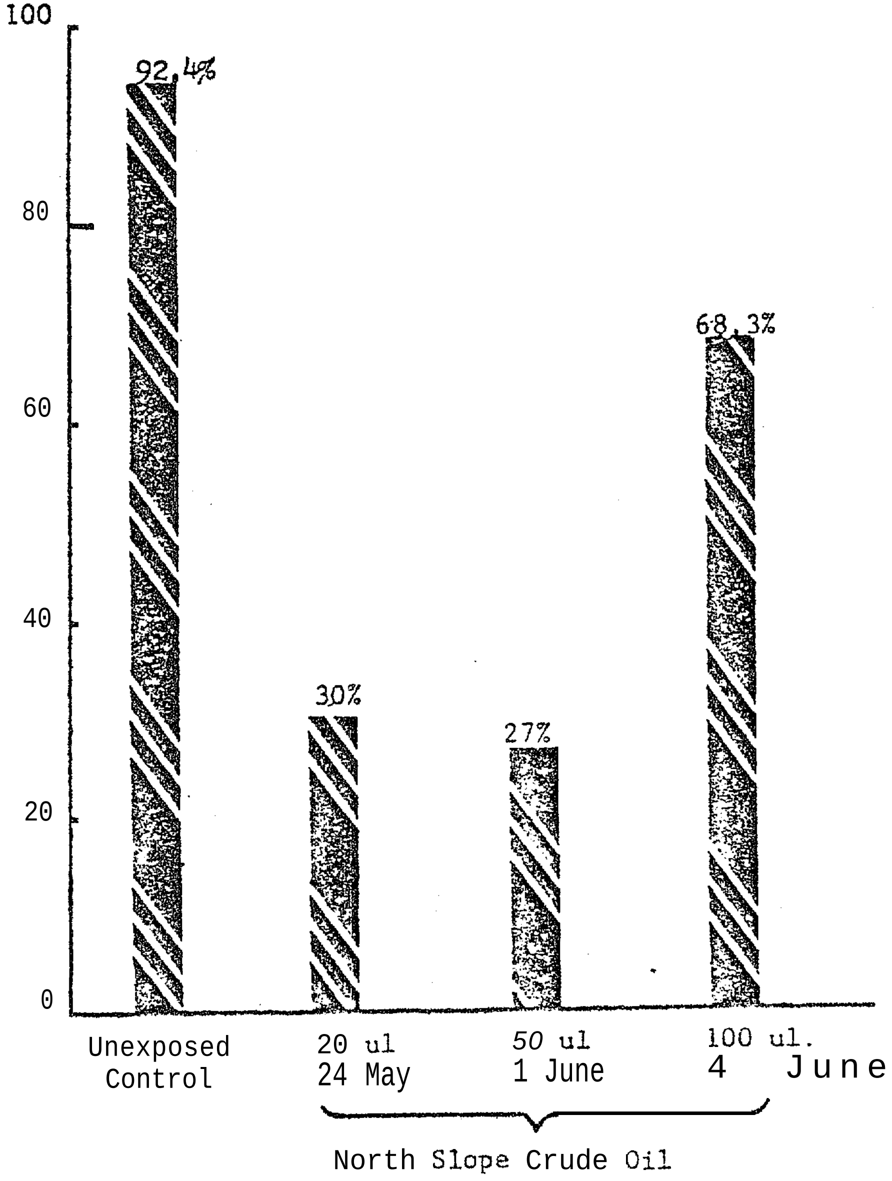


Figure 2



HATCHING SUCCESS, DRY BAY 1977
EXPERIMENT AND CONTROL COLONIES

Figure 3

Table 5

Mineral Oil Experiment

7th day of incubation

Nest #	# Eggs	Dose in ul	Failed to Hatch (Eggs Remaining)	Chick Mortality (Known)
51	3	20	0	
52	3	20	0	
53	3	20	0	
54	2	20	0	
55	3	20	0	
56	3	50	0	
58	3	50	0	
59	2	50	0	
60	2	50	0	
61	3	100	0	
62	3	100	0	
63	2	100	0	
64	2	100	0	
65	3	100	1 died pipping	1 dead chick (5 days)
15 nests	40 eggs	3 different doses	mortality not significant	

Our conclusions from the above experiments are: very small amounts of North Slope Crude Oil exposure to gull eggs in the field, at early stages of incubation, lead to high embryonic mortality (Tables 5, 6). Embryonic resistance to petroleum exposure increases with the duration of incubation (Table 7). Mineral oil in equivalent microliter doses causes no significant mortality (Table 8).

Results of Egg Petroleum Exposure on Incubation Behavior

To test alteration of incubation behavior and ability to produce second (replacement) clutches following experimental egg mortality due to petroleum exposure, we conducted the following experiment: at Egg Island, the largest gull colony in the northeast Gulf of Alaska, located 20 km south of Cordova, we chose our experimental and control areas to coincide with our established study site (RU #96 - 76). There were "75 nests in the experimental area, compared to 186 in the adjacent "normal" control colony. The experimental and control areas are located on the ocean slope of stabilized meadow-covered dunes at the east end of Egg Island in proximity to the U.S. Coast Guard Light Tower (Figures 9,10, 11).

Oil was delivered to completed clutches of three eggs at the tenth day of incubation. Fifty clutches (150 eggs) received 1 cc/egg surface application of North Slope Crude Oil, and 25 clutches (75 eggs) received the identical does of mineral oil. Both treatments were delivered by drops from calibrated syringes. The initial dose was selected to be well below the lethal level of oiling for adult waterfowl (7.0 - 3.5 gins) reported by Hartung (1963), but is nearly completely lethal *for* eggs. Most evidence of petroleum exposure disappeared the next day except for slight petroleum odor.

Observed clutch size in the oiling experimental area initially declined at a rate compatible with normal predation from other gulls (Fig. 23), but in July egg loss accelerated.

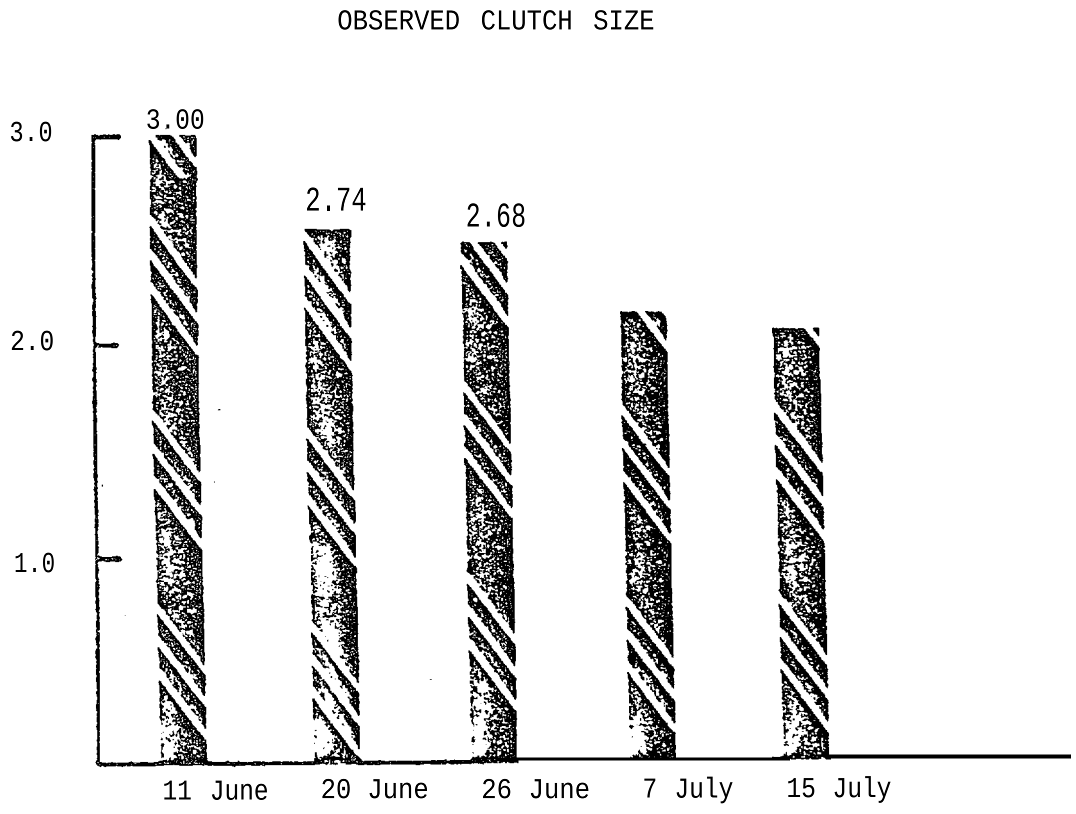


Figure 4. Observed clutch size in-the oiling experimental area initially declined at a rate compatible with normal predation from other gulls.

due to adult gulls abandoning unhatched clutches after incubation prolonged 100% longer than normal. At this time we terminated the experiment. A month after hatching began in the adjacent control colony, 33% of eggs oiled with North Slope Crude and 24.4% of eggs to which mineral oil had been applied remained in the nests on 15 July. These figures can be compared to 2% of eggs in the adjacent control area remaining in nests at the end of incubation, a "normal" infertility rate (Figs. 24, 25).

Hatching success in eggs exposed to this nearly completely lethal dose of North Slope Crude was 0.67% (Fig. 26). Mineral oil applied in equivalent amounts to gull eggs led to a hatching rate of 14.6%. North Slope Crude Oil is thus calculated to be 22 times more toxic than equivalent amounts of mineral oil. Hatching success in the adjacent "normal" control colony was 77%; the normal range for these gulls in Alaska is 67% - 77%. Adults continued to incubate almost all unhatched clutches at least 20 days longer than normal. Eggs opened at the close of the experiment were highly decomposed and no living embryos were found. Adult gulls nesting in the oiling area produced no more replacement clutches than the neighboring control colony (4.0% vs. 4.8%) (Figs. 28 , 29).

Gull behavior is thus altered by the continued incubation of dead eggs. Adults fail to respond with the normal production of replacement clutches, which normally follow clutch loss to natural causes. The combination of high egg mortality and alteration of adult behavior virtually eliminated gull reproduction. in the experimentally oiled area.

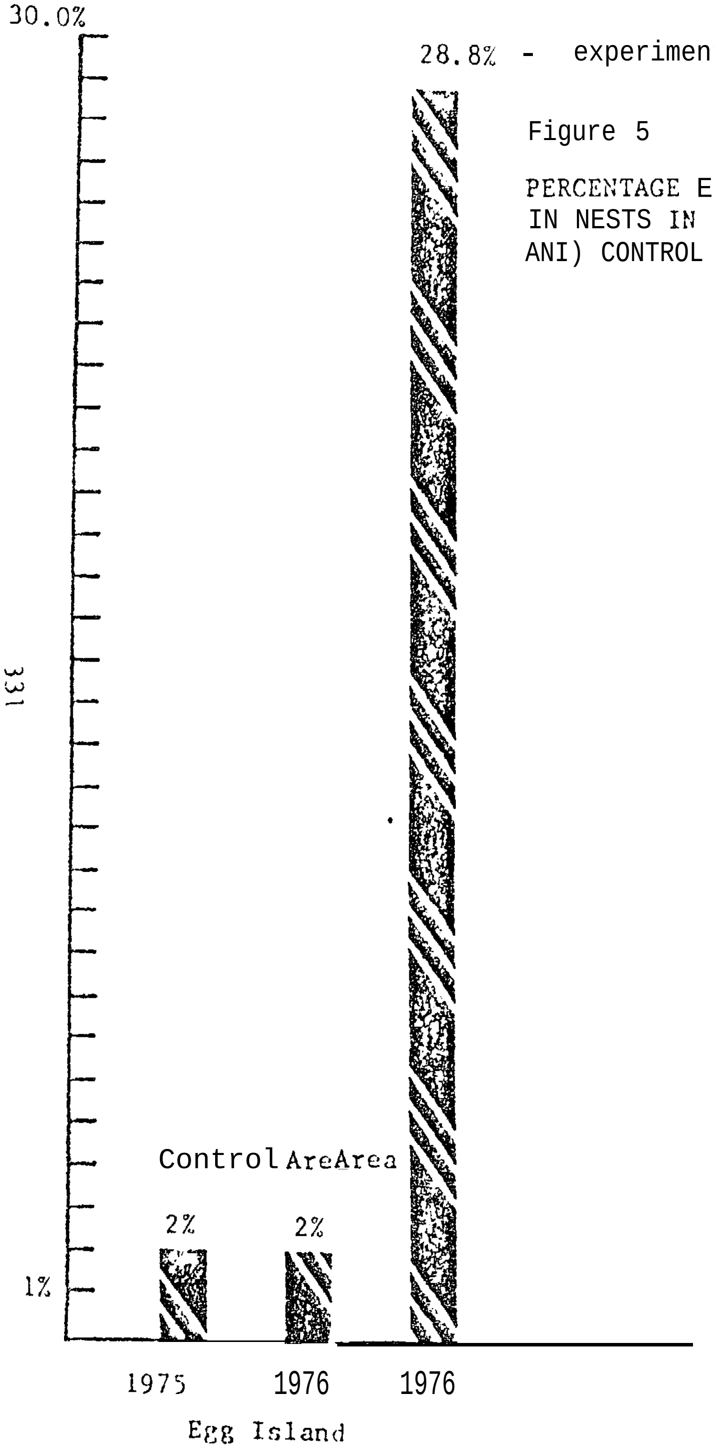


Figure 5

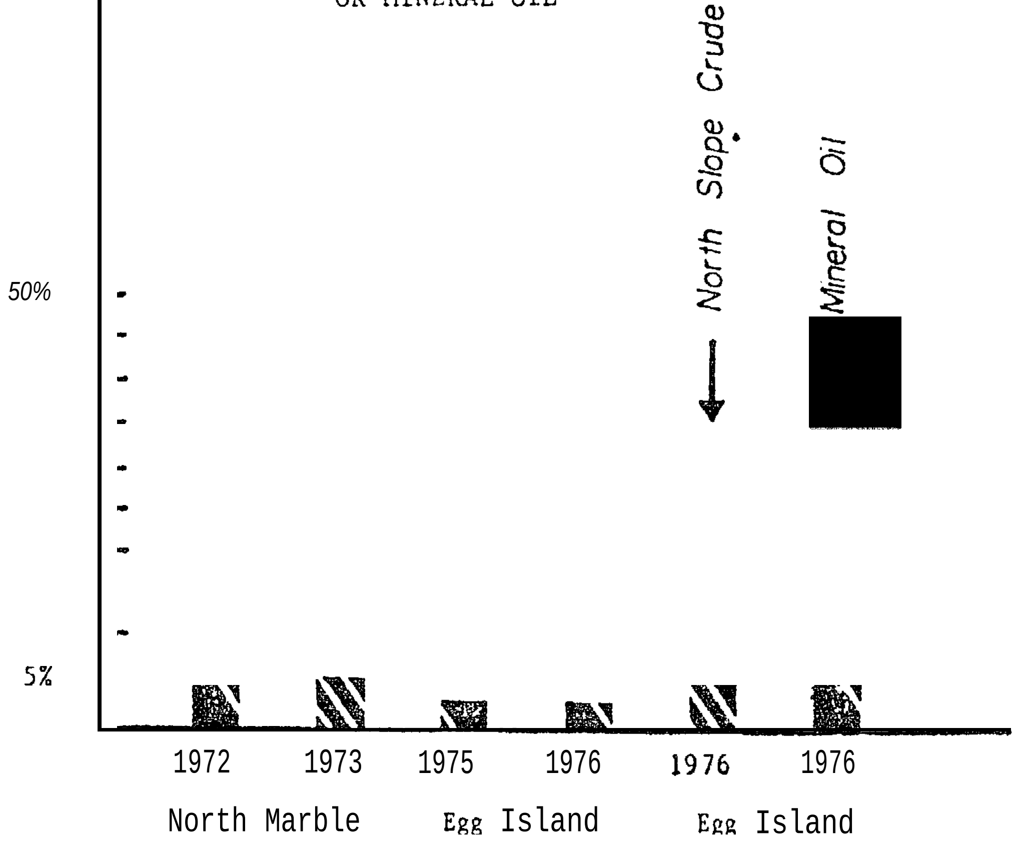
PERCENTAGE EGGS REMAINING IN NESTS IN EXPERIMENTAL AND CONTROL COLONIES

Figure 5. , Percentage eggs remaining in nests at close of incubation or experimental period, experimental and control colonies, Egg Island, 1975-76.

Figure 6. A month after hatching began in the adjacent control colony, 33% of eggs oiled with North Slope Crude and 24.4% of eggs to which mineral oil had been applied remained in the nests.

Figure 6

PERCENTAGE EGGS REMAINING IN NESTS WITH NS CRUDE OR MINERAL OIL



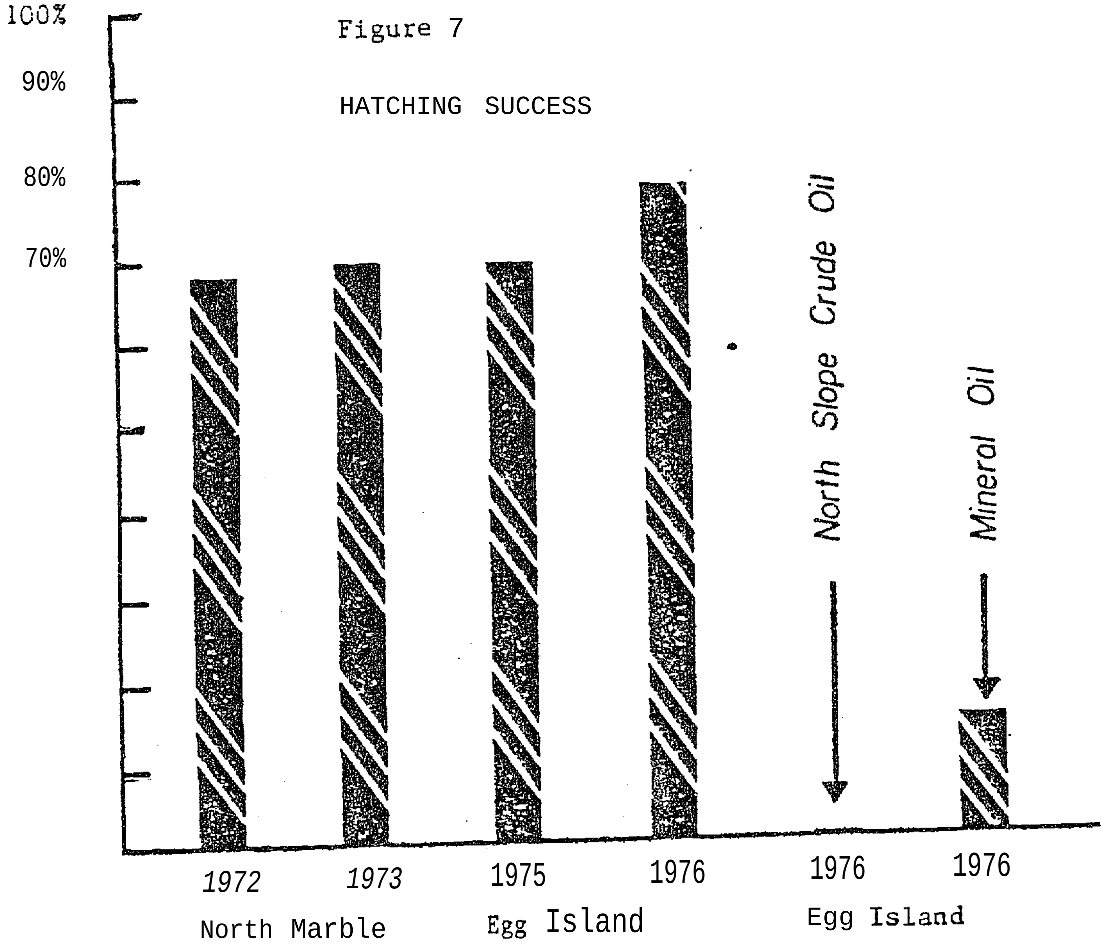


Figure 7

HATCHING SUCCESS

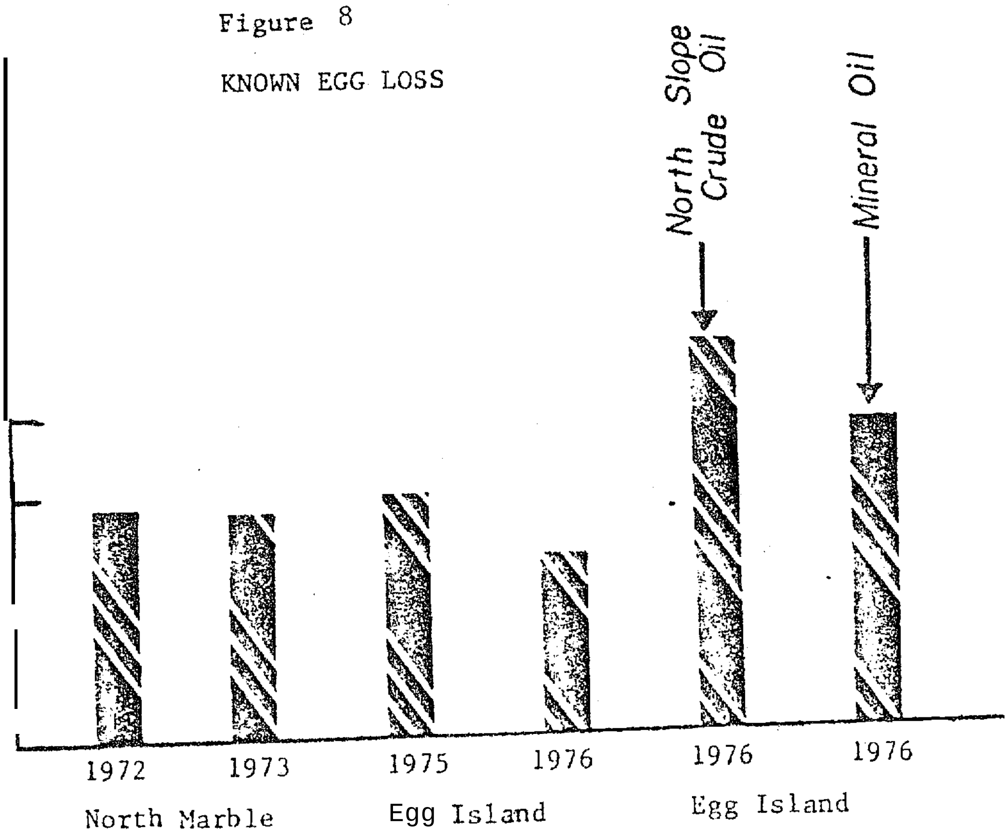


Figure 8

KNOWN EGG LOSS

Figure 9

MEDIAN INCUBATION PERIODS,
EXPERIMENTAL AND CONTROL COLONIES

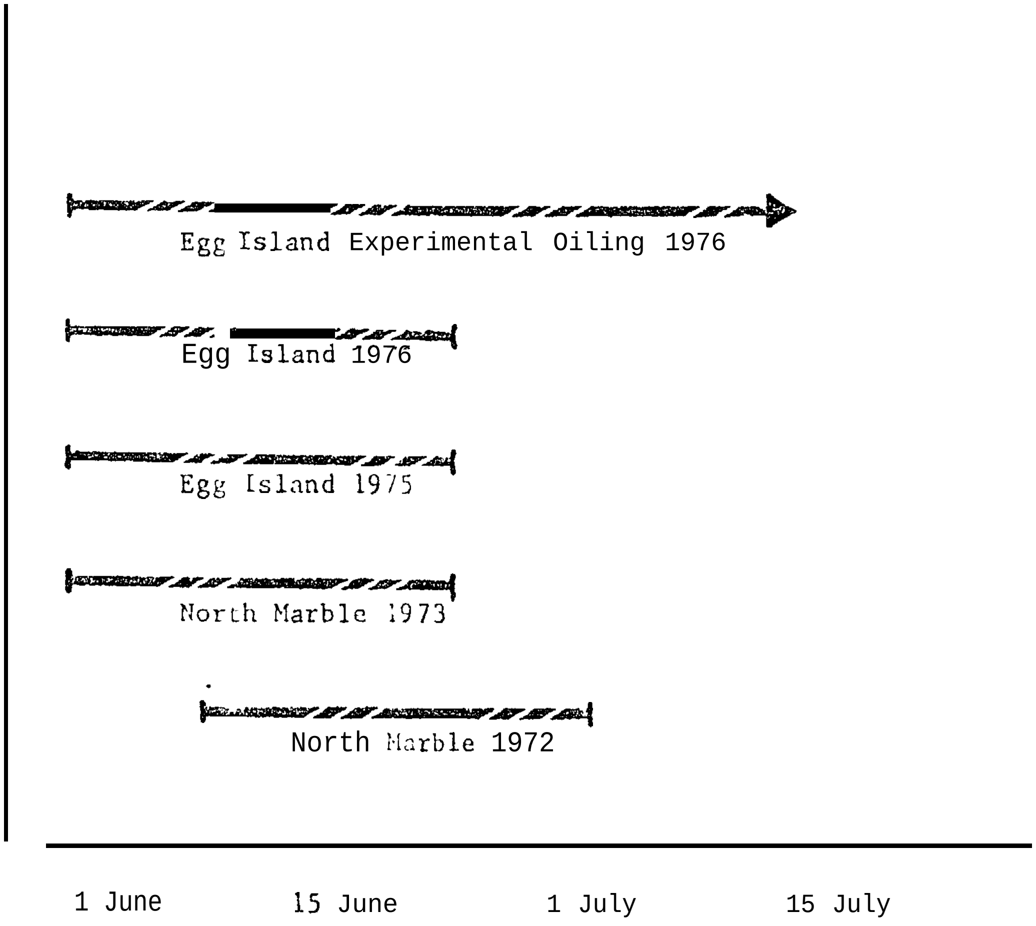
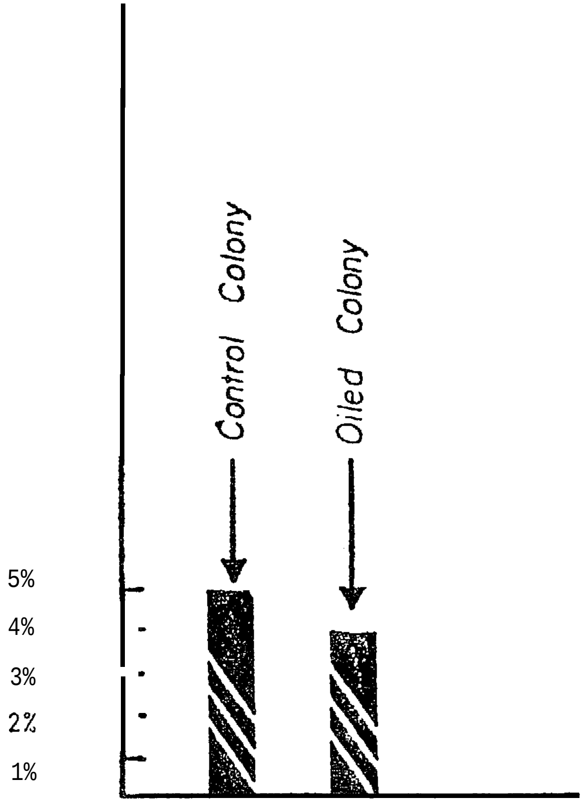


Figure 10

PERCENTAGE REPLACEMENT CLUTCHES,
EXPERIMENTAL AND CONTROL COLONIES



MIDDLETON ISLAND STUDY AREA

Middleton Island (58° 24′ N, 164° 19′ W) lies in the Gulf of Alaska, 130 km south of Cordova (Figure 42).* It is situated directly in the Valdez tanker lanes. Oil-laden tankers regularly pass within 20 km west of Middleton Island. Oil spill danger to Middleton Island is considered high (BLM, 1976). For this reason, RU 96, as part of its activities, conducted experiments at this site during the 1978 field season to determine effects of petroleum on marine bird reproduction.

The history of Middleton Island has been reviewed in an anonymous report in FAA and USF&WS (OBS-CE) files; the geology and geography of Middleton Island have been reviewed by Miller (1953); vascular plants by Thomas [1957); occurrence and distribution of birds by Rausch (1958); wintering birds by O'Farrell and Sheets (1962); introduced rabbits by O'Farrell (1965), and the breeding of seabirds by Frazer and Howe (1977).

The island bedrock is composed of Cenozoic glacial conglomerate mud and sandstone, dotted with occasional, large Pleistocene boulders known as "glacial erractics." The surface of the island 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 at irregular intervals, the last of which was in 1964 when the strong earthquake of that year raised the island level 4.5 m. The eroding cliffs below the terraces are now bordered by sandy and marshy areas above the intertidal , The terraces merge into sand dunes above a sanely spit 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

* in Part II.

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 is quite mild, but rainy, with strong winds. Prevailing gales are southeasterly.

The terraces are covered with wet, grass-forb meadows, dominated by Calamagrostris spp., Carex spp., and Heracleum lanatum. Willows (Salix barclayi) and salmonberry (Rubus spectabulus) form thickets on meadow margins and terrace slopes. A few Sitka spruce (Picea sitchensis) are scattered over the island.

The island extends approximately 8 km along a NE - SW axis, is 1.6 km wide, and covers about 890 hectares. The shoreline, nearly completely enclosed by driftwood, reefs, rocks and heavy kelp, offers shelter to small boats only at the north end of the island, immediately west of the FAA communications station. (The FAA station was manned by six persons during the Summer of 1978.) The central portion of the island consists of a gravel airstrip and inactivated U.S. Air Force base, now under private ownership.

Middleton Island was the site of commercial fox farming during the early years of this century (Parker, 1923), but no known foxes remain. Large numbers of feral rabbits (Oryctolagus cuniculus), descended from a few individuals released in 1954, now inhabit the island and cause localized damage to vegetation and soils. The damage is particularly evident in the vicinity of the FAA station, the site of the original introduction. The summer population of rabbits may reach 10,000 individuals.

Among the more numerous seabirds breeding on Middleton Island in 1978 were the Black-legged Kittiwake (Rissa tridactyla) and the Glaucous-winged Gull (Larus glaucescens). Kittiwakes numbered about 120,000 and gulls approximately 2,000 individuals of which FWS estimates approximately 750 breeding gull pairs. Rausch (1958) reported only a few thousand kittiwakes and gulls as non-breeders. Our observations indicate that populations of both species are expanding.

METHODS

We experimented with both kittiwakes and gulls to determine the effects of small amounts of petroleum on their reproductive success. Petroleum used on kittiwakes included both "raw" and weathered Prudhoe Bay (North Slope) Crude Oil. Petroleum used on gulls *was* weathered oil only. Effects of raw oil on gull reproduction were previously tested by RU 96 - 77. Mineral oil served as the control in both kittiwake and gull experiments. Microliter syringes were used to apply drops of oil in microliter doses to the surface of kittiwake and gull eggs. The doses were applied to the eggs within several days of clutch completion. This time has been demonstrated as being the most vulnerable period for oil conlamination (cf. RU 96 - 77).

The kittiwake experiment was thus divided into four treatment groups: "raw" Prudhoe Bay Crude Oil; weathered Prudhoe Bay Crude Oil; Mineral Oil, and Control (no treatment). The weathered oil, provided by Battelle Northwest Marine Research Laboratory (RU 454), was weathered by a combination Of lightand **water parameters.** We express our gratitude to RU 454 for the donation of this oil. We selected weathered oil known as "Tank #2" as our experimental substance, since oil from "Tank #1" was too thick to pass through a microliter syringe, and oil from "Tank #3" was not exposed to sunlight in order to reduce photooxidation of hydrocarbons (cf. Anderson. Augenfeld, Crecelius and Riley, 1978: RU 454

Quarterly Report, October). Thus the weathered oil from "Tank #2" appeared most suitable for our experiments. The kittiwake eggs were dosed with uniform amounts (2o ul) of the three treatment oils at the beginning of incubation. Our previous results from experiments involving the effect of raw oil on gulls led us to expect an LD_{50} with a 20 ul dose applied to eggs at the beginning of the incubation period.

The Glaucous-winged Gull experiment used similar but not identical methods, involving the use of weathered oil and mineral oil treatments. Each treatment was applied in three different doses: 20 ul; 50 ul; and 100 ul. The results of these oil doses were compared to an unexposed control group.

RESULTS AND DISCUSSION

The results of both kittiwake and gull experiments were divied into three categories: hatching success, loss to predation, and failure to hatch. Loss to predation, while an uncontrolled variable, was an unavoidable part of these field experiments. Table 6 and Figure 11 contain the results of the kittiwake oiling experiment. The results are quite unexpected. All four groups cannot effectively be distinguished from each other in hatching success, loss to predation, or failure to hatch. While there is variation between the treatment groups, the three oil treatment groups do not differ significantly from the control (p .05). The phenomena which occurred in the 1978 kittiwake oiling experiment were thus independent of treatment effect. Stated otherwise, we could determine no effect of oil treatment on kittiwake hatchability at the 20 ul dose, whether with raw, weathered, or mineral oil, a distinct contrast to the markedly depressed hatching success of gull eggs exposed to 20 ul doses of raw oil (RU 96 - 77).

The results of the 1978 Glaucous-winged Gull experiment, involving the exposure of eggs to weathered and mineral oil doses, are contained in Table 7 and Figures 12, 13, and 14. Note that hatching success at each dose of weathered oil is " ess than that of equivalent amounts of mineral oil. similarly, hatching failure is greater at each dose of weathered oil when compared to equivalent amounts of mineral oil. Hatching success of either oil treatment is less than the unexposed control (Table 7), suggesting both physical and chemical effects. The comparison between equivalent 20 ul doses of weathered oil on gulls and kittiwakes indicates that gulls had lower hatching success [44% vs. 62%), higher hatching failure (33% vs. 8%) and similar loss to predation (33% vs. 29%) (Tables 6 & 7).

When the results of the kittiwake and gull oiling experiments are compared, there is a strong suggestion of species-specific response to petroleum exposure on egg surfaces. The kittiwakes are apparently more resistant than the gulls to the toxic and respiratory-inhibitive effects of oil exposure to egg surfaces. Based upon our knowledge of the size, adaptability, and niche breath of these two species, we would have expected the robust, intrusive, "weedy" gulls to be more tolerant of oil exposure than the kittiwakes. We emphasize that these results are indicative of further research. The species-specific response to minute amounts of petroleum on egg surfaces reveals an unexplored realm of marine bird conservation, at the interface of physiology, organic chemistry, and field biology.

Table 6

Kittiwake Oiling Experiment - Middleton Island, 1978
Oil dose: 20 ul

Oil Treatment	Hatching success (%)	Loss to Predation (%)	Failure to Hatch (%)	n eggs
"raw" Prudhoe Bay Crude Oil	57.7	26.9	15.4	29
weathered Prudhoe Bay Crude Oil	62.5	29.2	8.3	24
mineral oil (non-toxic)	70.8	20.8	8.4	24
control (no treatment,)	54.2	29.2	16.6	24

Table 7

Glaucous-winged Gull Oiling Experiment
Middleton Island, 1978

Weathered Oil/ Mineral Oil Dose	Hatching Success (%)	Loss to Predation (%)	Failure to Hatch (%)	n eggs
100 ul weathered	41.6	16.6	41.6	24
100 ul mineral	55.0	11.1	33.3	18
50 ul w	58.3	8.3	33.3	24
50 u-l m	100.0	0.0	0.0	18
20 ul w	44.4	22.2	33.3	18
20 ul m	66.0	16.6	16.6	12
unexposed control	82.0	12.0	6.0	150

Table 8

Productivity of Black- legged Kittiwakes
Middleton Island, 1978
'C' Area*

Colony I. D. Number	Nests with Eggs/ Nests Built (%)	Clutch Size	% 3-egg Clutches	Chicks Fledged/ Nests with Eggs (%)
1	33/40 (82)	1.96	2/33 (6)	1/33 (3)
2	63.75 (84)	1.81	1/63 (1.5)	0/63 (0)
3	48/55 (87)	1.93	0/48 (0)	4/48 (8.3)
4	168/175 (96)	1.79	1/168 (0.6)	19/168 (11.3)
USFWS Study Areas**	145/180 (81)	1.94	--	-- (17.2)

* This study area is closest to the FAA station and is disturbed daily. Compare to the USFWS study areas, which were relatively undisturbed by human intrusion.

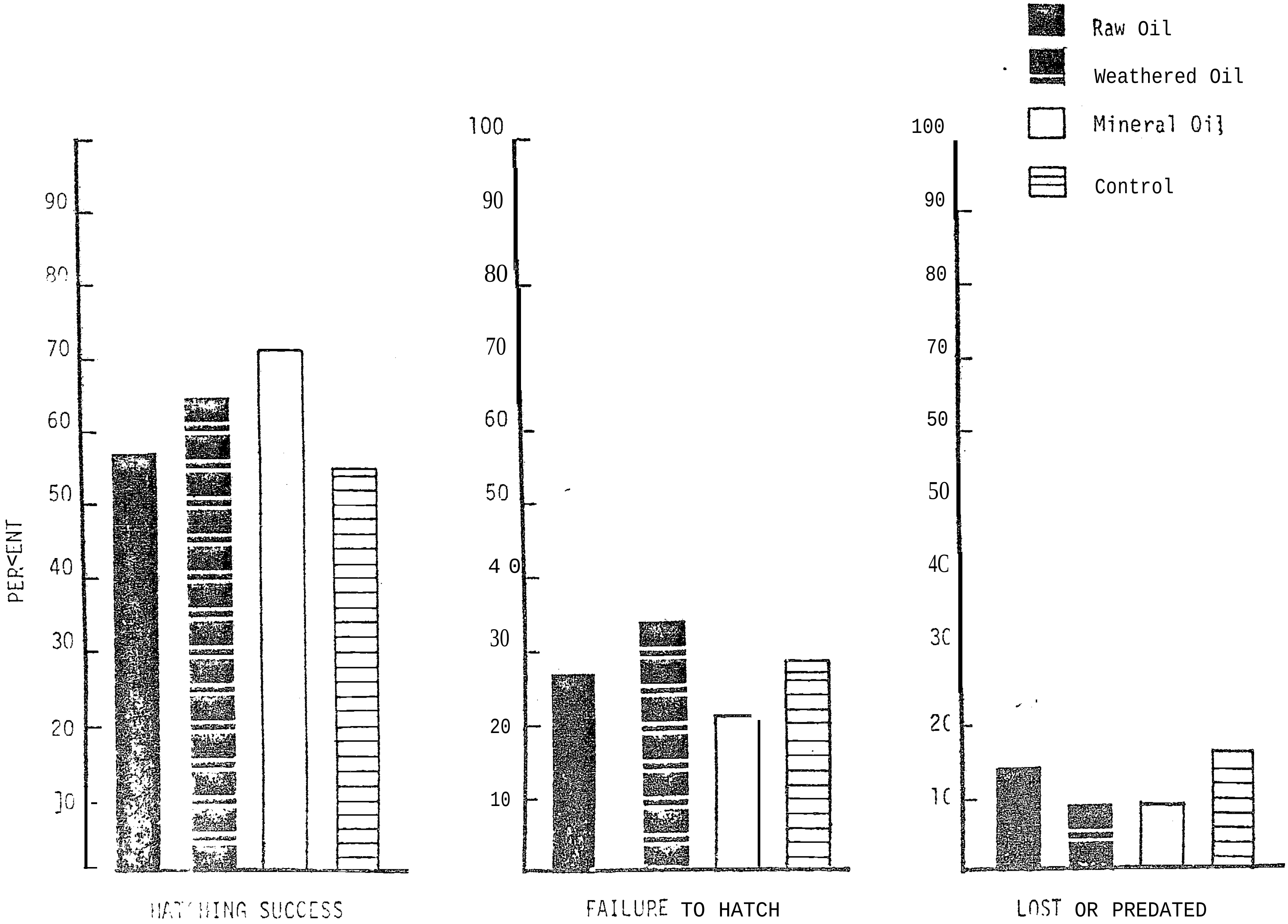
** cf. Hatch, Pearson, & Gould. (1979) RU 341.

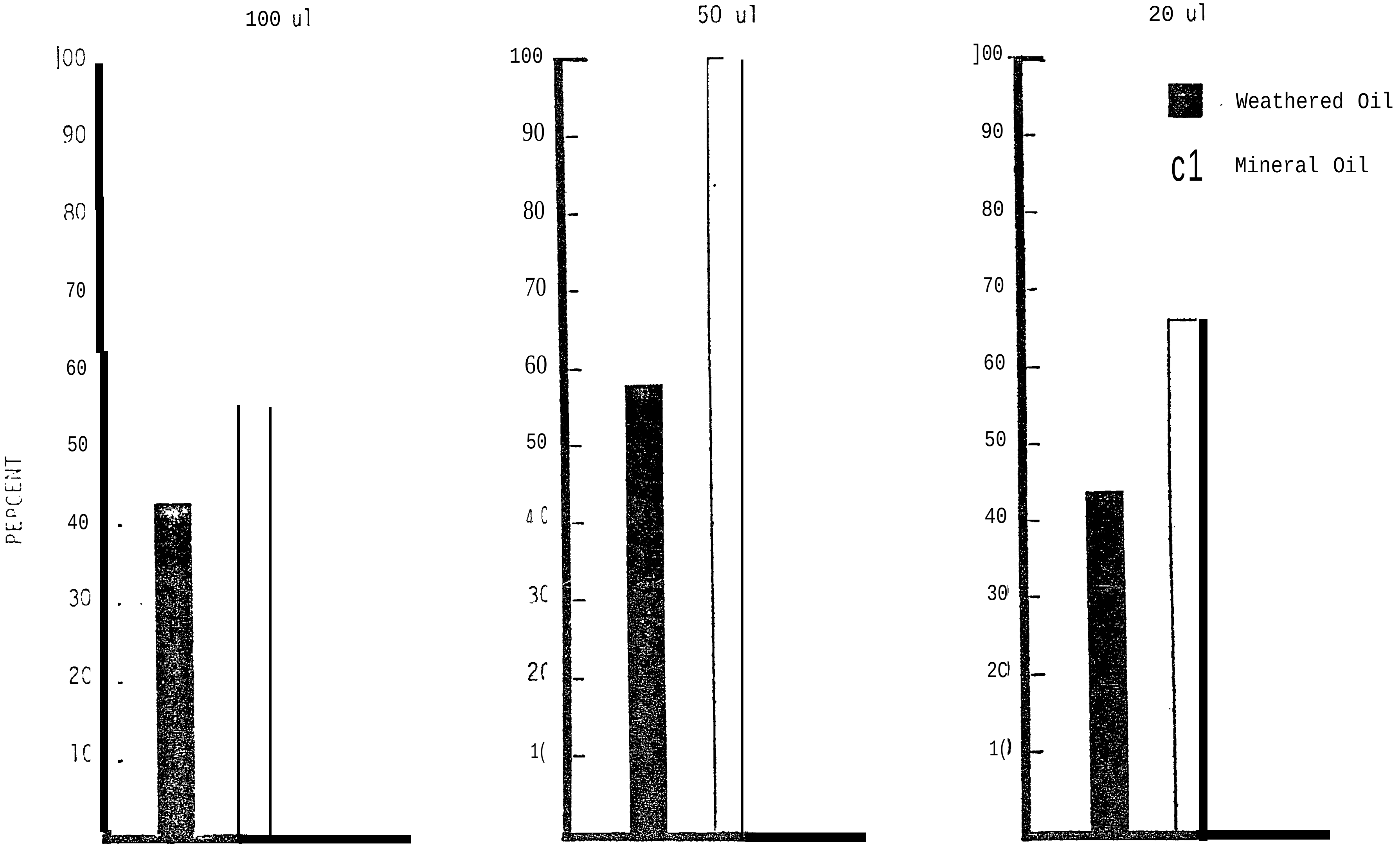
Kittiwake Breeding Biology in Disturbed Colonies

In addition to our petroleum experiments we monitored four colonies of kittiwakes in "C" area, directly east of the FAA station and immediately south of the dirt road which bisects the north end of the island. These four colonies, numbered sequentially from North to South, are disturbed daily by recreational activities and the movement of people, including biologists in transit to other areas. The colonies provide an example of the potentially disruptive nature of human development in proximity to seabird colonies. The four colonies are located on shallow 10 - 15 m dirt cliffs. These four kittiwake colonies experienced essentially marginal to complete reproductive failure in 1978 (Table 8; Figures 15, 16, 17, 18). The proximate cause of reproductive failure was human disturbance and subsequent gull predation on eggs, and to a greater degree, on chicks. However, when compared to the relatively undisturbed USFWS study areas at the south end of Middleton Island, these four disturbed sites do not differ greatly from the general trend, which in 1978 was a poor year for kittiwake productivity (cf. RU 341).

Figure 11.

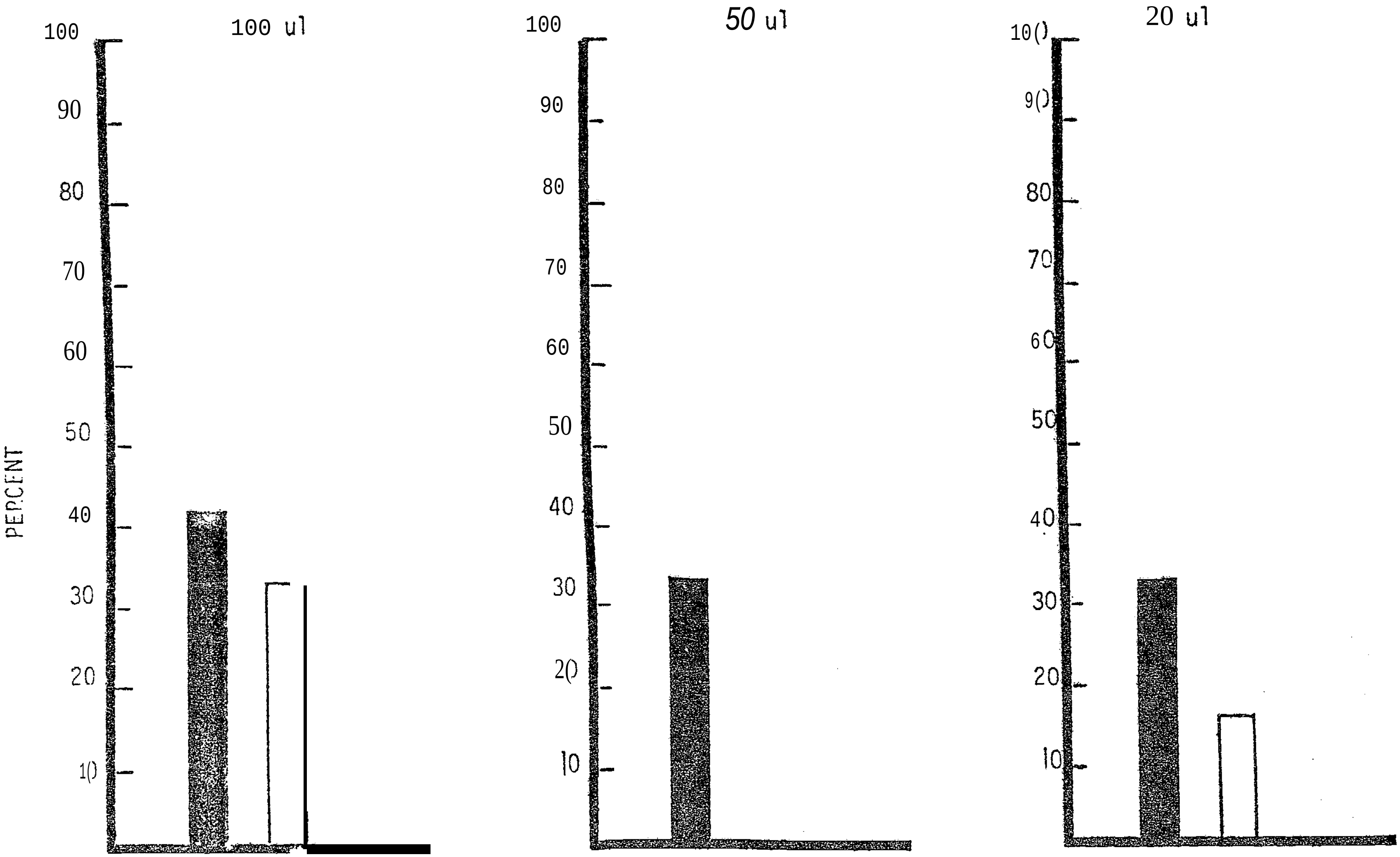
KITTIWAKE OILING EXPERIMENT, MIDDLETON ISLAND, 1978





GLAUCOUS-WINGED GULL HATCHING SUCCESS, 1978, MIDDLETON ISLAND, ALASKA

Figure 12.

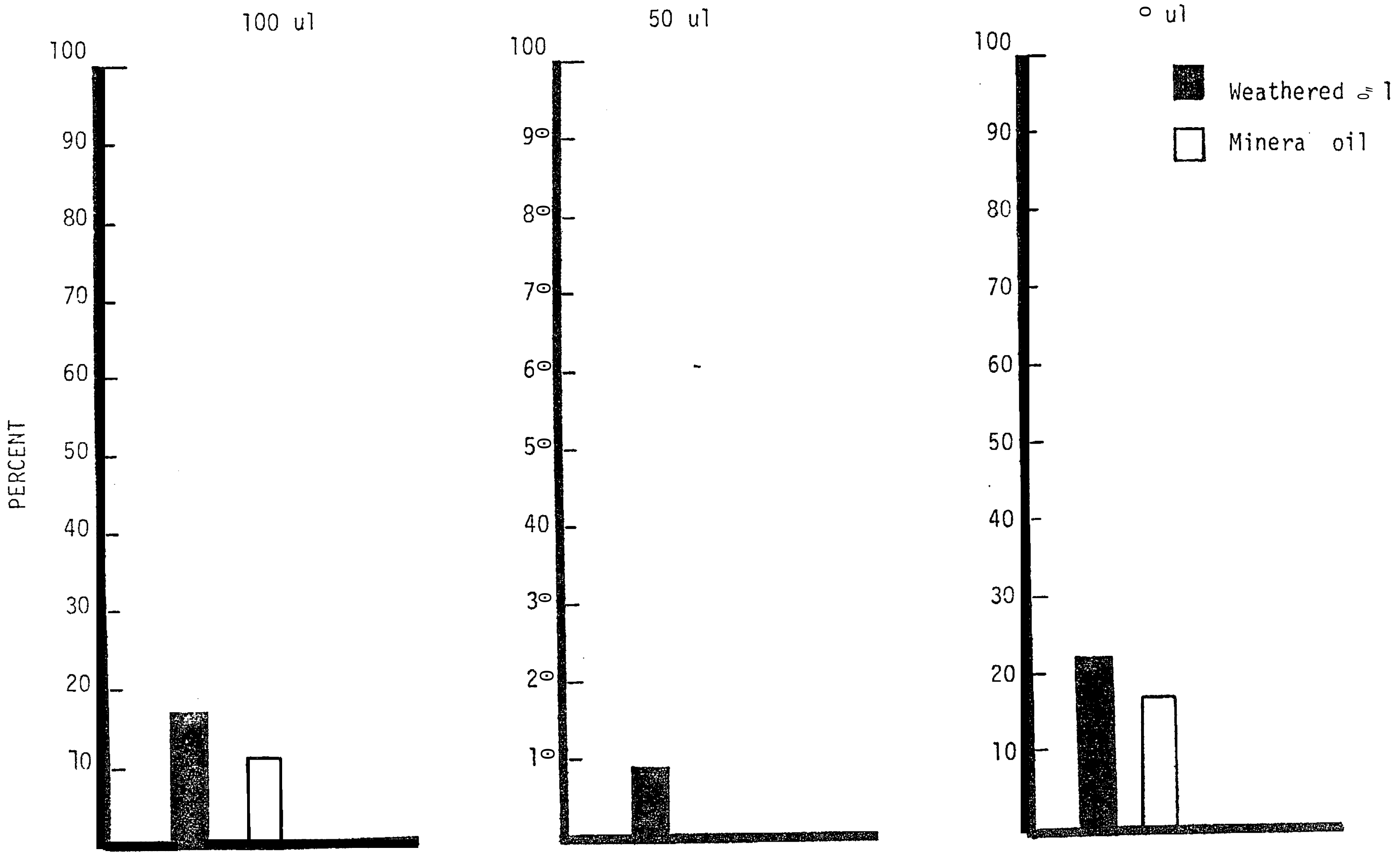


GLAUCOUS-WINGED GULL HATCHING FAILURE, MIDDLETON ISLAND, 1978,

▨ Weathered oil

☐ Mineral oil

Figure 13.



GLAUCOUS-WINGED GULL, EGGS LOST OR PREDATED, 19 8 MIDDLETON ISLAND, ALASKA

Figure 14

Figure 15

NESTING ACTIVITY AND FLEDGING SUCCESS PER NEST,
KITTIWAKE "C" AREA, MIDDLETON ISLAND, 1978

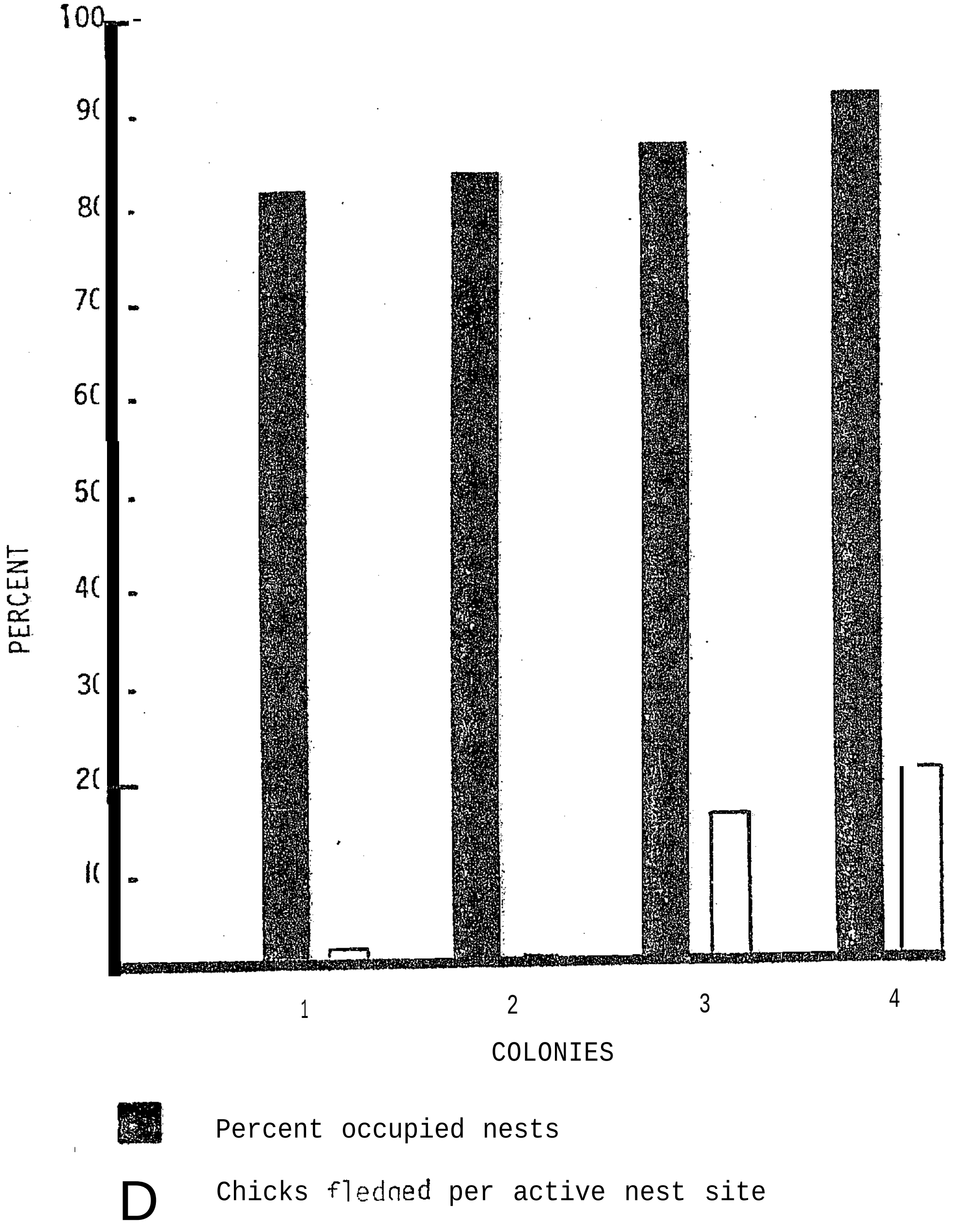


Figure 16.

1978

KITTIWAKE CLUTCH SIZE, "c" AREA, MIDDLETON ISLAND

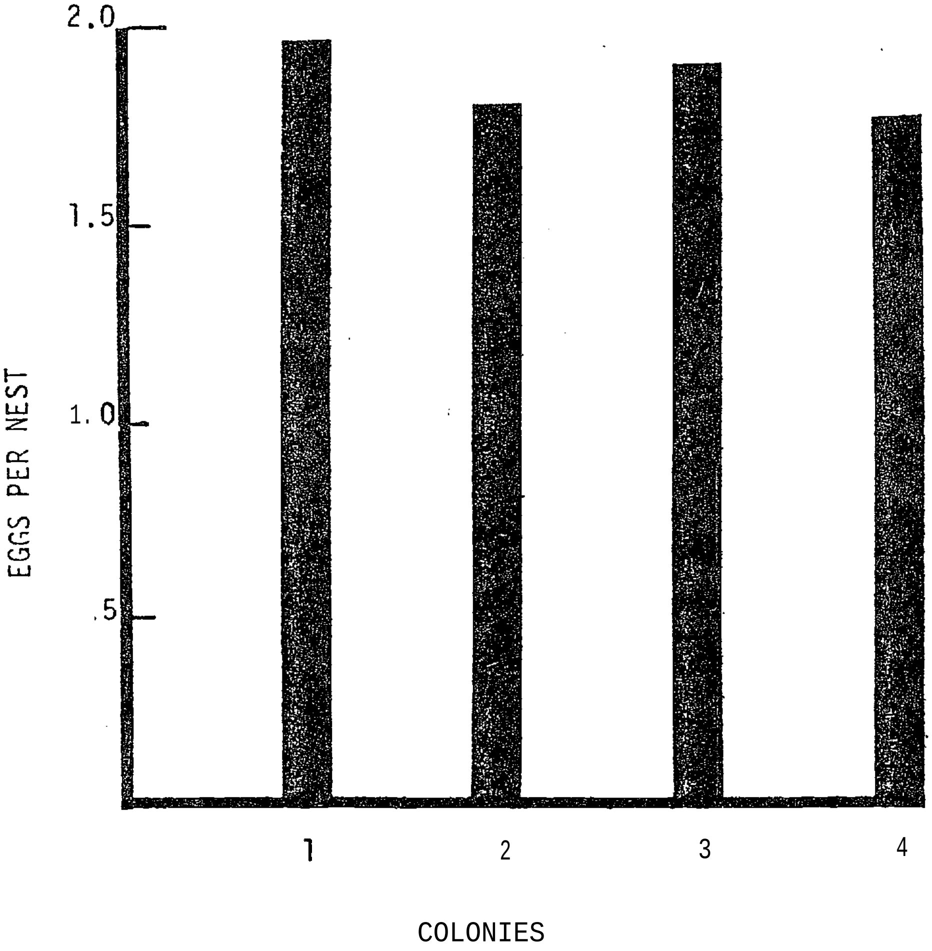


Figure 17

PERCENT THREE EGG CLUTCHES IN KITTIWAKE "C" AREA

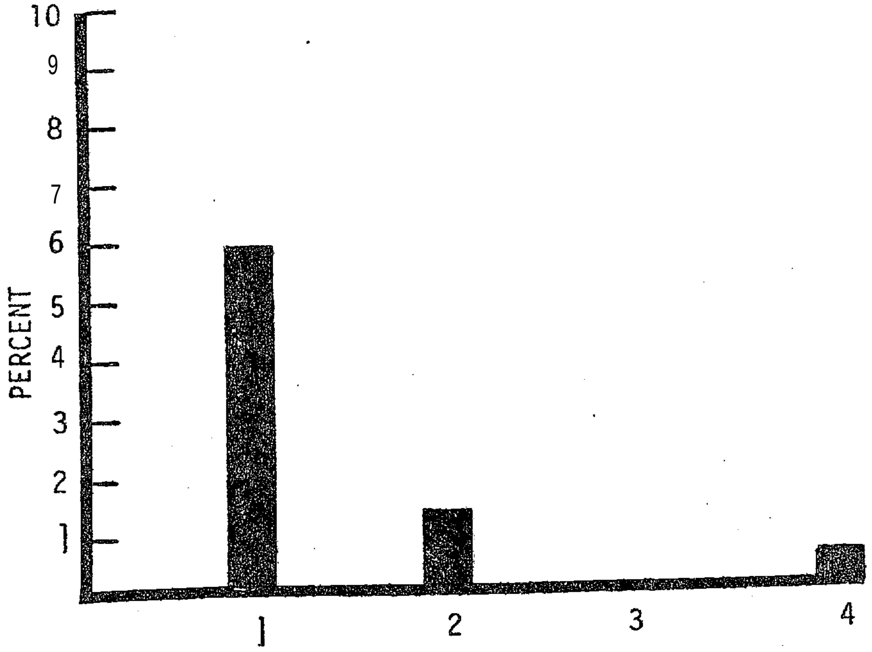
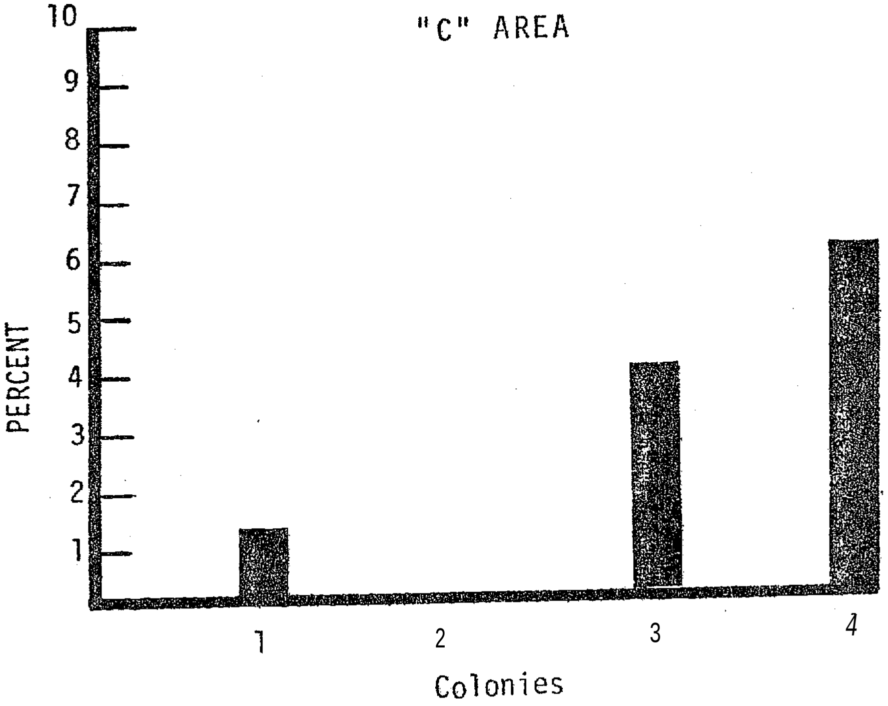


Figure 18

PERCENT EGGS LAID TO CHICKS FLEDGED

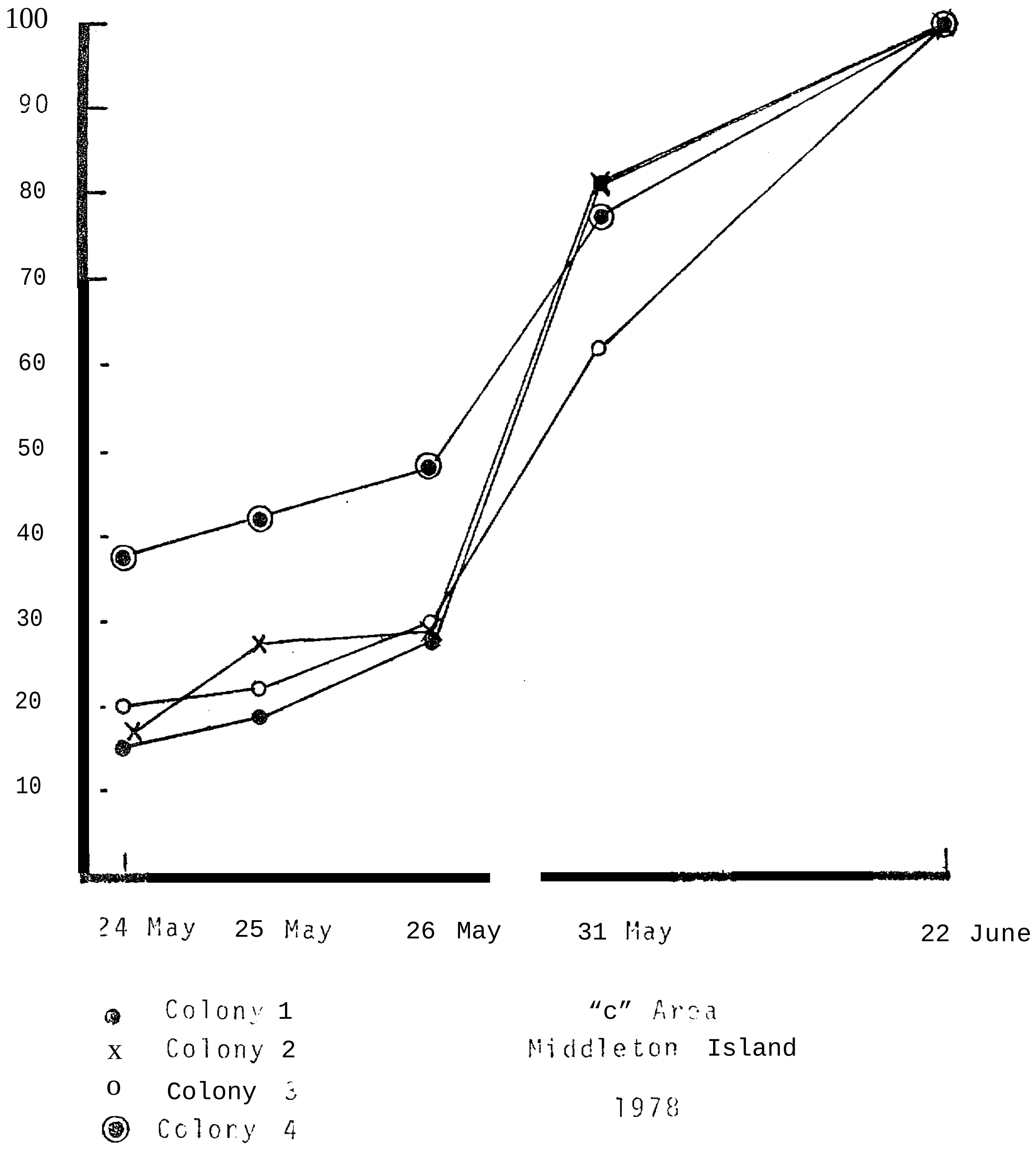
"C" AREA



MIDDLETON ISLAND, 1978

Figure 19.

Percentages of Clutch Initiation Per Active Nest Site



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PACIFIC SEABIRD GROUP

RESOLUTION

ON THE

STATUS OF LARGE GULL POPULATIONS IN ALASKA

Whereas the populations of Atlantic Coast Herring Gulls (*Larus argentatus*) have increased exponentially within the last seven decades,

Whereas studies from Juneau to the Prince William Sound region of the Northeast Gulf of Alaska indicate that the populations of Glaucous-winged Gulls (*Larus glaucescens*) are increasing,

Whereas recent observations along the Northwest Coast of Alaska indicate that the age structure of Glaucous Gulls (*Larus hyperboreus*) is close to -that of the Atlantic Coast Herring Gull population,

Whereas experience in other areas such as the British Isles, "Western Europe, Australia and New Zealand indicates that increase in gull populations is a secondary effect associated with economic development,

Whereas observations in other areas also indicate that increasing populations of large gulls are a public health risk and have both positive and negative effects on other seabirds, shorebirds and waterfowl,

We conclude that these are reasons to predict that a secondary effect of industrial development associated with Outer Continental Shelf Gas and Oil Exploration and Production and the rapidly developing coastal and marine fisheries will be increasing populations of large gulls in Alaska,

We therefore recommend that studies should be made now to:

a) establish the distribution and numbers of large gulls (*Larus*) in Alaska both during the breeding season and during the winter, a critical period of survival,

b) establish the age structure of these large gulls,

c) establish the relationship of successful breeding and subsequent survival to sources of food resulting from human waste, garbage and fish offal,

d) observe the effects of dense large gull populations on other wildlife species in order to assess the potential magnitude of ecological disruption through increased predation and competitive interactions.