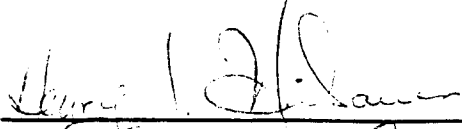
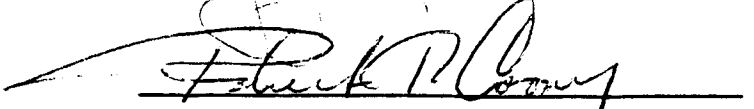
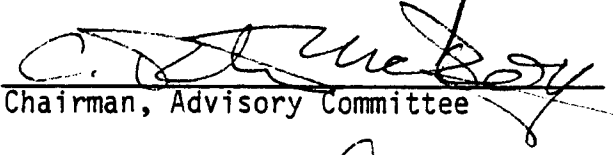


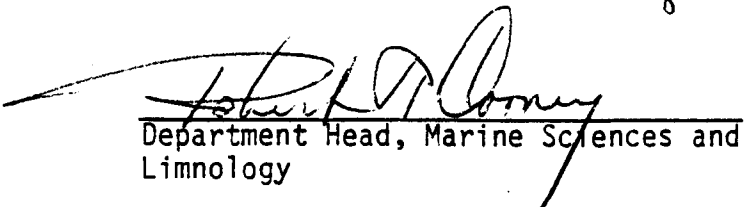
BREEDING PERFORMANCE OF KITTIWAKES AND MURRES
IN RELATION TO OCEANOGRAPHIC AND METEOROLOGIC CONDITIONS
ACROSS THE SHELF OF THE SOUTHEASTERN BERING SEA

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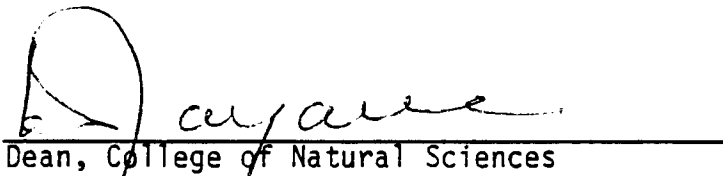




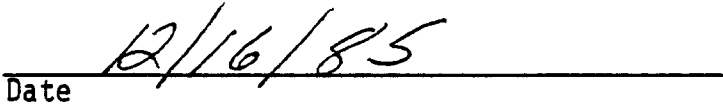

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BREEDING PERFORMANCE OF KITTIWAKES AND MURRES
IN RELATION TO OCEANOGRAPHIC AND METEOROLOGIC CONDITIONS
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A
THESIS

Presented to the Faculty of the University of Alaska
in Partial Fulfillment of the Requirements
for the Degree of

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By

Denby Sturgis Lloyd, B.S.

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ABSTRACT

Contrary to expected results, black-legged and red-legged kittiwakes on St. George Island exhibited more variability in annual breeding performance than black-legged kittiwakes at Cape Peirce. Thick-billed and common murres at St. George also showed more annual variability than common murres at Cape Peirce. Kittiwakes at St. George exhibited improved breeding performance during years with colder water temperatures and lower summer wind speeds. Correlations between breeding performance in kittiwakes and murres and environmental conditions at Cape Peirce were inconclusive. A general decline in the annual breeding success of kittiwakes and murres at St. George between 1976 and 1984 coincided with reduced abundance of juvenile walleye pollock. Consistently low breeding success of kittiwakes and murres at Cape Peirce varied little among six years observed between 1970 and 1984. These results challenge previous considerations of pelagic food webs on the outer shelf as being more stable than those in the coastal domain.

TABLE OF CONTENTS

	<u>Page</u>
Abstract	iii
List of Figures	vi
List of Tables	vii
Preface	ix
Introduction	1
Study Area	8
Methods	12
Field Methods	12
Field Data Reduction	15
Compilation of Oceanographic and Meteorologic Data	17
Statistical Analysis	19
Results	21
Kittiwakes and Murres, St. George Island and Cape Peirce	21
Black-legged Kittiwakes, St. George Island	24
Red-legged Kittiwakes, St. George Island	31
Common Murres, St. George Island	35
Thick-billed Murres, St. George Island	40
Black-legged Kittiwakes, Cape Peirce	41
Common Murres, Cape Peirce	46
Discussion	48
Hypothesis 1 - Constancy Between Colonies	48
Hypothesis 2 - Relation to Sea Surface Temperature	54
Hypothesis 3 - Relation to Weather	57
Hypothesis 4 - Relation to Intra-annual Timing	60

Hypothesis 5 - Temporal Trends	61
General	65
Summary	75
Appendices	78
Appendix A - Field Studies, St. George Island 1981	78
Appendix B - Field Studies, Cape Peirce 1981	83
Appendix C - Data Summary, St. George Island 1976-1984	86
Appendix D - Data Summary, Cape Peirce 1970-1984	91
Appendix E - Food Samples: St. George Island, Cape Peirce ..	94
Appendix F - Definition of Abbreviations	97
Literature Cited	99

LIST OF FIGURES

	<u>Page</u>
Figure 1. Location of the Pribilof Islands and Cape Peirce in relation to oceanographic domains in the southeastern Bering Sea	10
Figure 2. Location of subcolonies, or study plots, on St. George Island	13
Figure 3. Location of subcolonies, or study plots, at Cape Peirce/Shaiak Island	14
Figure 4. Comparison of breeding performance in kittiwakes, St. George Island and Cape Peirce	26
Figure 5. Comparison of breeding performance in murrelets, St. George Island and Cape Peirce	27
Figure 6. Comparison of productivity in black-legged kittiwakes to environmental conditions, St. George Island	30
Figure 7. Comparison of productivity in red-legged kittiwakes to environmental conditions, St. George Island	34
Figure 8. Comparison of reproductive success in common murrelets to environmental conditions, St. George Island	38
Figure 9. Comparison of reproductive success in thick-billed murrelets to environmental conditions, St. George Island ..	39
Figure 10. Comparison of productivity in black-legged kittiwakes to environmental conditions, Cape Peirce	44
Figure 11. Comparison of reproductive success in common murrelets to environmental conditions, Cape Peirce	45
Figure 12. Estimated abundance of age 1 pollock in the eastern Bering Sea	64

LIST OF TABLES

	<u>Page</u>
Table 1. Breeding performance of kittiwakes and murre, and oceanographic and meteorological conditions for St. George Island	22
Table 2. Breeding performance of kittiwakes and murre, and oceanographic and meteorological conditions for Cape Peirce	23
Table 3. Squared ranks test for variances of breeding performance in kittiwakes and murre, St. George Island and Cape Peirce	25
Table 4. Correlation of breeding performance in black-legged kittiwakes with oceanographic and meteorologic conditions, St. George Island	29
Table 5. Correlation of breeding performance in red-legged kittiwakes with oceanographic and meteorologic conditions, St. George Island	33
Table 6. Correlation of breeding performance in common murre and thick-billed murre with oceanographic and meteorologic conditions, St. George Island	37
Table 7. Correlation of breeding performance in black-legged kittiwakes and common murre with oceanographic and meteorologic conditions, Cape Peirce.....	43
Table 8. Summary of significant relations between breeding performance in kittiwakes and murre and oceanographic and meteorologic conditions across the shelf of the southeastern Bering Sea	49
Table A1. Results of field studies on black-legged kittiwakes on St. George Island, July 6 - September 13, 1981	79
Table A2. Results of field studies on red-legged kittiwakes on St. George Island, July 6 - September 13, 1981	80
Table A3. Results of field studies on common murre on St. George Island, July 6 - September 13, 1981	81
Table A4. Results of field studies on thick-billed murre on St. George Island, July 6 - September 13, 1981	82
Table B1. Results of field studies on black-legged kittiwakes at Cape Peirce, June 14 - August 16, 1981	84

Table B2. Results of field studies on common murrens at Cape Peirce, June 14 - August 16, 1981	85
Table C1. Summary of studies on black-legged kittiwakes on St. George Island, 1976-1984	87
Table C2. Summary of studies on red-legged kittiwakes on St. George Island, 1976-1984	88
Table C3. Summary of studies on common murrens on St. George Island, 1976-1984	89
Table C4. Summary of studies on thick-billed murrens on St. George Island, 1976-1984	90
Table D1. Summary of studies on black-legged kittiwakes at Cape Peirce, 1970-1984	92
Table D2. Summary of studies on common murrens at Cape Peirce, 1970-1984	93
Table E1. Analysis of food samples for kittiwakes and murrens, St. George Island 1980-1981	95
Table E2. Analysis of food samples for kittiwakes and murrens, Cape Peirce 1981	96
Table F. Definition of abbreviations used in figures and tables ..	98

PREFACE

The well-nigh inexorable control of certain special types of oceanic environments upon birds has not yet been generally realized by either zoologists or oceanographers... Oceanic birds seem, in the main, to have been regarded somewhat naively as aerial rather than aquatic animals, notwithstanding that their relationships to sea and land, as concerned with feeding and breeding, respectively, are precisely the same as those of the seals among mammals or the sea turtles among the reptiles... Seabirds, which are more easily observed than almost any other animals, offer a ready key to many characteristics of the ocean water and of its hidden life. The correlations are still very imperfectly worked out...[yet] as we shall see...birds are sensitively adjusted to, and quick to respond to, periodic changes in the character of surface waters.

Robert Cushman Murphy, 1936
Oceanic Birds of South America

Has a decade of oceanographic and biological research provided us with enough information to relate the breeding performance of seabirds to the structure, processes, and vagaries of surface waters in the southeastern Bering Sea?

I wish to personally acknowledge the guidance and conceptual support given by Dr. C. Peter McRoy, chairman of my graduate studies committee. Also I extend personal gratitude to Robert H. Day for his constant enthusiasm and good humor.

Assistance was given by Dr. R. Ted Cooney and Dr. H. Joe Niebauer as members of my graduate studies committee; Dr. George L. Hunt, Jr., Zoe Eppley, and Alan M. Springer through data and discussion on ecology of Bering Sea birds; Dale R. Herter, Brian E. Lawhead and again Robert H. Day in the field; as well as Kitty J. Farnham and Mike E. Frost for typing and drafting of figures.

I dedicate this thesis to my parents, Carl and Adele Lloyd. My mother instilled a primary love of nature and, at age 70, still entices birds as close to the house as possible. My father provided an example, sterling or otherwise, of professional conduct and ambition.

Finally, I thank my wife and daughter, Diana and Theresa. I appreciate and depended upon their support and indulgence.

Funding in support of this project was provided by grants from the National Science Foundation, Division of Polar Programs: DPP-7623340 to the study of Processes and Resources of the Bering Sea Shelf (PROBES) and DPP-8300916 to the study of Inner Shelf Transport and Recycling (ISHTAR). Logistic support was given by the National Marine Fisheries Service and the U.S. Fish and Wildlife Service during field work on the colonies.

INTRODUCTION

There has been a recent, but rapidly developing, trend to consider seabirds as marine organisms dependent upon physical oceanographic and marine biological factors, rather than simply as birds that feed in the ocean. Although R.C. Murphy (1936) made an excellent attempt to recognize these birds as much dependent upon oceanographic processes as fish and other marine life, it has only been within about the past decade that widespread research has investigated the overriding influence and importance of oceanography to seabirds (e.g., Ashmole 1971, Shuntov 1974, Pocklington 1979, Ainley 1980, Brown 1980).

As a result of studies funded predominantly under the Outer Continental Shelf Environmental Assessment Program (OCSEAP) by the U.S. Department of the Interior and under a program entitled Processes and Resources of the Bering Sea Shelf (PROBES) by the National Science Foundation, much information has been obtained on the oceanography and marine biology of the southeastern Bering Sea. These programs have concurrently funded studies on the breeding and feeding ecology of seabirds. The southeastern Bering Sea encompasses one of the broadest and most productive continental shelf areas in the world (Hood 1981) and supports one of the world's richest and most important breeding areas for seabirds (Hunt et al. 1981b).

Associated with both the recognition of seabirds as marine organisms and gains in knowledge of the oceanography and biology of the southeastern Bering Sea shelf, two complementary hypotheses have been advanced regarding the breeding ecology of seabirds. First, in a broad

ecological context, it is suggested that the stability or constancy of annual reproductive parameters in seabirds are controlled by or reflect the stability or constancy of oceanographic conditions either directly or through trophic interactions. Second, in a more proximal sense, it is suggested that annual variations in breeding performance of seabirds are related to annual variations in oceanographic conditions.

This study was initiated to complement work conducted under PROBES to test these two general hypotheses about breeding performance in seabirds. In addition, a third general hypothesis that annual breeding performance in seabirds is modified or even controlled by short-term meteorological events, a fourth hypothesis that annual breeding performance is related to within-year timing of breeding activity, and a fifth that there has been a consistent decline in production of kittiwakes and murrelets in the late 1970's and early 1980's are also evaluated.

PROBES investigators conducted several years (1976-1981) of cross-shelf transect studies and work at associated stations to define various oceanographic processes leading to the high biological productivity of the southeastern Bering Sea. The major study transect led from a point off the continental shelf break, approximately equidistant from the Pribilof Islands and the Alaska Peninsula, across the continental shelf toward Cape Newenham on the mainland coast at the northern boundary of Bristol Bay.

PROBES AND OCSEAP studies discovered low rates of cross-shelf transport (Coachman and Charnell 1979) allowing the development, at least during summer, of four distinct mixing regimes or domains across

the shelf separated by three thermohaline fronts (Kinder and Schumacher 1981). These domains exhibit distinct biological characteristics supported by distinct physical and biological processes (Iverson et al. 1979).

The oceanic domain is composed of oceanic water from the central Bering Sea and supports a typically oceanic biological community. An outer, or shelf-break, front is situated approximately over the 200-meter bathymetric contour (Kinder and Coachman 1978) and separates the oceanic and outer shelf domains. The outer shelf domain supports a predominantly pelagic community similar to that of comparable depths in the adjacent oceanic domain, with upper trophic levels characterized by an oceanic community of zooplankton capable of making ontogenetic migrations into the outer shelf domain (Cooney 1981). This pelagic community, including fishes, is thought to provide a reliable and high flux of energy to seabirds as apex consumers (Schneider and Hunt 1982).

A middle front, situated approximately over the 100-meter contour (Coachman and Charnell 1979), separates the outer shelf and middle shelf domains. This middle front acts as a barrier to horizontal shoreward transport of oceanic communities of zooplankton, therefore phytoplankton production in the middle shelf domain goes largely ungrazed and sinks to support a productive benthic, rather than pelagic, community (Iverson et al. 1979, Cooney 1981, Haflinger 1981, Cooney and Coyle 1982).

An inner front, situated approximately over the 50-meter contour (Schumacher et al. 1979), separates the stratified middle shelf domain from the vertically homogeneous coastal domain. The coastal domain, which hosts a nearshore zooplankton community (Cooney 1981) and forage

fishes, is subject to tidal and wind conditions that can mix the entire water column.

Definition of the domains has led to consideration of the oceanic and outer shelf domains as more stable or constant, subject to less annual variation in some physical processes and supporting a biological community evolved to rely and capitalize on this constancy. In contrast, the middle shelf and coastal domains have been characterized as driven by more highly variable physical processes and supporting biological communities forced to adapt to and controlled by fluctuating physical conditions (Iverson et al. 1979, Schumacher et al. 1979, Vidal and Smith 1982).

As part of earlier and concurrent OCSEAP studies, and also other investigations, the breeding and feeding ecology of seabirds nesting at large colonies in the southeastern Bering Sea have been studied. The Pribilof Islands, particularly St. George Island, constitute one of the largest seabird colonies in the North Pacific and are located near the edge of the continental shelf. Waters of the oceanic and outer shelf domains support a diverse community of seabirds on the Pribilof Islands including the predominant piscivorous species: black-legged kittiwakes (Rissa tridactyla), red-legged kittiwakes (R. brevirostris), common murre (Uria aalge), and thick-billed murre (U. lomvia). These piscivorous birds are largely dependent upon walleye pollock (Theragra chalcogramma), myctophids, and to some extent euphausiids as prey during the breeding season (Hunt et al. 1981c, Bradstreet 1985).

Cape Peirce, with Shaiak Island, in northern Bristol Bay reportedly constitutes the largest seabird colony along the mainland coast of

Alaska. Waters of the coastal domain support a less diverse community of seabirds at Cape Peirce including the predominant piscivorous species, black-legged kittiwakes and common murre; red-legged kittiwakes and thick-billed murre are not present. Piscivorous seabirds at Cape Peirce apparently rely primarily upon sand lance (Ammodytes hexapterus), capelin (Mallotus villosus), and perhaps herring (Clupea harengus) (M. Petersen, personal communication; Appendix E).

Using data obtained during field studies in 1980 and 1981, information reported by OCSEAP and other seabird investigations on the Pribilof Islands and at Cape Peirce, and available oceanographic and meteorological information, the five general hypotheses described earlier can be tested for the predominant piscivorous seabirds (kittiwakes and murre) in the southeastern Bering Sea. In order to make the project more manageable, and recognizing the limits of available information, five sets of specific working hypotheses were developed to address the five more general questions. This thesis attempts to reject the following sets of null hypotheses:

1. Annual reproductive performance of kittiwakes and murre at the Pribilof Islands is no less variable than annual reproductive performance of kittiwakes and murre at Cape Peirce; annual reproductive performance of red-legged kittiwakes and thick-billed murre at the Pribilof Islands is no less variable than annual reproductive performance of black-legged kittiwakes and common murre, respectively, also at the Pribilof Islands.

2. Annual reproductive performance of kittiwakes and murrelets at the Pribilof Islands or at Cape Peirce is not significantly correlated with annual differences in sea surface temperature.
3. Annual reproductive performance of kittiwakes and murrelets at the Pribilof Islands or at Cape Peirce is not significantly correlated with annual differences in wind speed, precipitation, or heating degree days.
4. Annual reproductive performance of kittiwakes and murrelets at the Pribilof Islands or at Cape Peirce is not significantly correlated with annual mean date of hatching for each species.
5. Annual reproductive performance of kittiwakes and murrelets at the Pribilof Islands or at Cape Peirce is not significantly correlated with year between 1970-1984.

Within the first set of hypotheses the Pribilof Islands, in particular St. George Island, represent an oceanic colony while Cape Peirce represents a coastal colony; red-legged kittiwakes and thick-billed murrelets at St. George represent more oceanic species while black-legged kittiwakes and common murrelets at St. George offer comparison to more cosmopolitan congeners.

Within the second set of hypotheses, sea surface temperature is used as the only readily available indicator of oceanographic conditions. Breeding performance is likely more directly related to food abundance and availability, however adequate information is sorely lacking for the principal prey species.

Within the third set of hypotheses wind speed, precipitation, and heating degree days are used as available indicators of meteorological conditions that may affect foraging efficiency of parental birds as well as growth and survival of eggs and chicks. Within the fourth set of hypotheses, mean date of hatching is used as the only readily available indicator of within-year timing of reproductive activity. Within the fifth set of hypotheses, correlation of breeding performance with year is used as a mechanism to define temporal trends.

STUDY AREA

Data considered in this thesis were collected on St. George Island of the Pribilof Island group and at Cape Peirce/Shaiak Island. The Pribilof Islands support an estimated 2.79 million seabirds during the summer including approximately 110,000 black-legged kittiwakes; 220,000 red-legged kittiwakes; 230,000 common murre; and 1,600,000 thick billed murre (Sowls et al. 1978). Cape Peirce and nearby Shaiak Island reportedly support an estimated 220,000 black-legged kittiwakes; no red-legged kittiwakes; 550,000 common murre; and no thick-billed murre (Sowls et al. 1978). These estimates for Cape Peirce are likely too high, but no more rigorous censuses have been reported (D. Lloyd, personal observation; D. Herter, personal communication).

Both the Pribilof Islands (centered upon 57° N, 170° W) and Cape Peirce (approximately 58°35' N, 161°45' W) are subarctic colonies that lie at nearly the same latitude and are subject to apparently similar climatic conditions common to the southeastern Bering Sea. Although seasonal sea ice regularly intrudes into the area during winter and spring, records show extremely low probabilities that ice remains at either location at the onset of seabird breeding in May and June (Webster 1981).

The most apparent physical difference between these colonies is their location in relation to the broad continental shelf. The Pribilof Islands lie adjacent to the oceanic/outer shelf domains near the continental shelf break, while Cape Peirce and Shaiak Island are located over 500 kilometers eastward on the mainland coast adjacent to the

coastal domain (Figure 1). These megacolonyes lie approximately at opposite ends of a cross-shelf transect occupied during oceanographic studies conducted by PROBES to define hydrographic structure and partitioning of biological processes across the continental shelf.

Use of only St. George Island to represent the Pribilof Islands as an oceanic/outer shelf colony, as opposed to both St. George and St Paul or St. Paul alone, was selected for simplicity but is further justified by the following:

1. St. George Island supports approximately 2.52 million of the combined Pribilof Island total of 2.79 million seabirds, including 220,000 of the combined total of 222,200 red-legged kittiwakes as well as a majority of the black-legged kittiwakes, common murrees, and thick-billed murrees (Sowls et al. 1978).
2. Most measures of breeding performance (except growth rate) in kittiwakes and murrees have shown no significant within year difference between populations at St. George and St. Paul (Hunt et al. 1981a, 1982; Johnson and Baker 1985).
3. St. George Island has substantially more cliff area available for nesting of kittiwakes and murrees, lies closer to the continental shelf break, and supports a more oceanic community of seabirds that apparently depends more upon oceanic/outer shelf food webs (Schneider and Hunt 1984).

Cape Peirce was the primary location representing a coastal colony. Shaiak Island was also monitored, however, mainly for measurement of

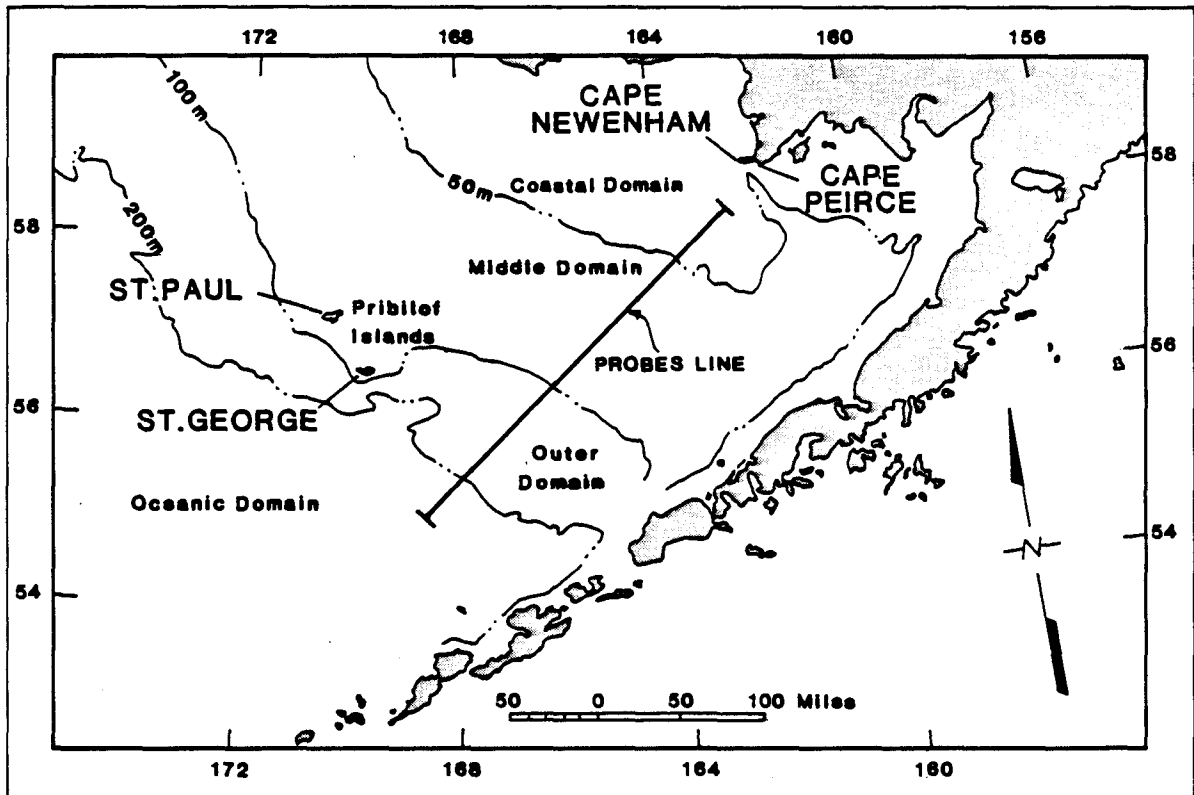


Figure 1. Location of the Pribilof Islands and Cape Peirce in relation to oceanographic domains in the southeastern Bering Sea.

growth rates, because of its immediate proximity to Cape Peirce and the accessibility of black-legged kittiwake nests.

METHODS

Field work specifically for this thesis was conducted at subcolonies, or plots, on St. George Island in 1980 and 1981 and at Cape Peirce/Shaiak Island in 1981. Locations of individual study plots used to monitor breeding performance are shown in Figures 2 and 3. Appendices A and B describe the species investigated, parameters measured, and dates of observation for study plots on St. George Island. Appendices C and D describe the species, parameters, and observation dates for study plots at Cape Peirce/Shaiak Island. Appendix E describes analyses of food samples taken at St. George and Cape Peirce.

Field Methods

Field methods for collection of information on breeding performance followed those of Hunt et al. (1981a). Study sites were selected for good visibility and relatively safe vantage point, and were visited at intervals ranging from one to five days. No sites were intentionally disturbed by observers except those chosen to provide growth information on chicks.

Dates of egg laying, hatching, and fledging were recorded for each identified nest-site within study plots, depending upon the seasonal timing of observations. The amount of time spent at each plot varied considerably depending upon vantage point of observers and behavior of the birds. Observations of murre plots generally took longer than did those at kittiwake plots because of the difficulty in distinguishing between separate murre "nest-sites" and the typical posture of murre which prevents easy detection of an egg or chick.

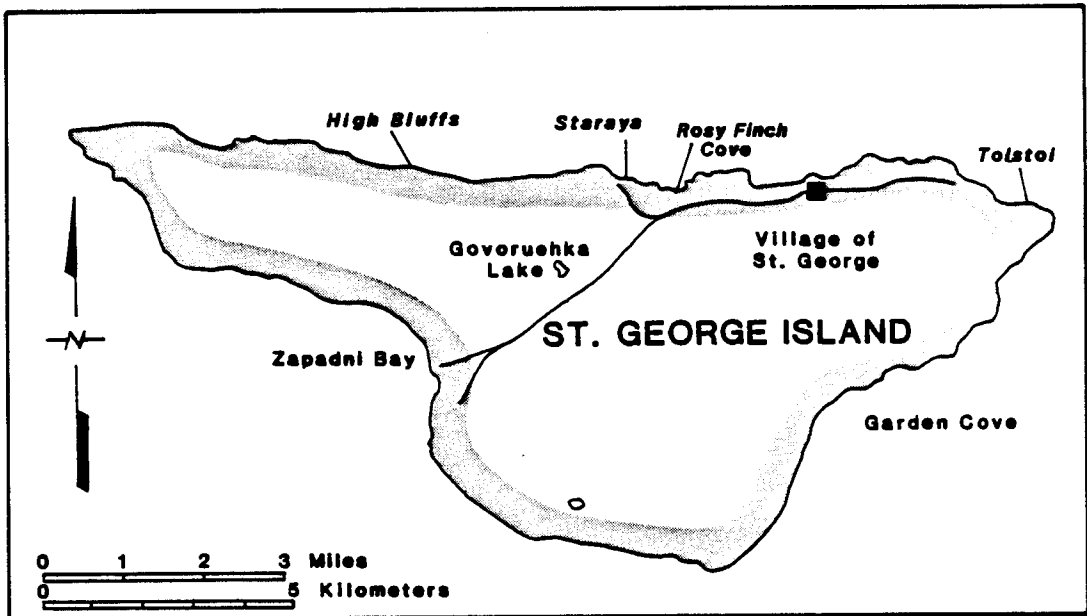


Figure 2. Location of subcolonies, or study plots, on St. George Island.

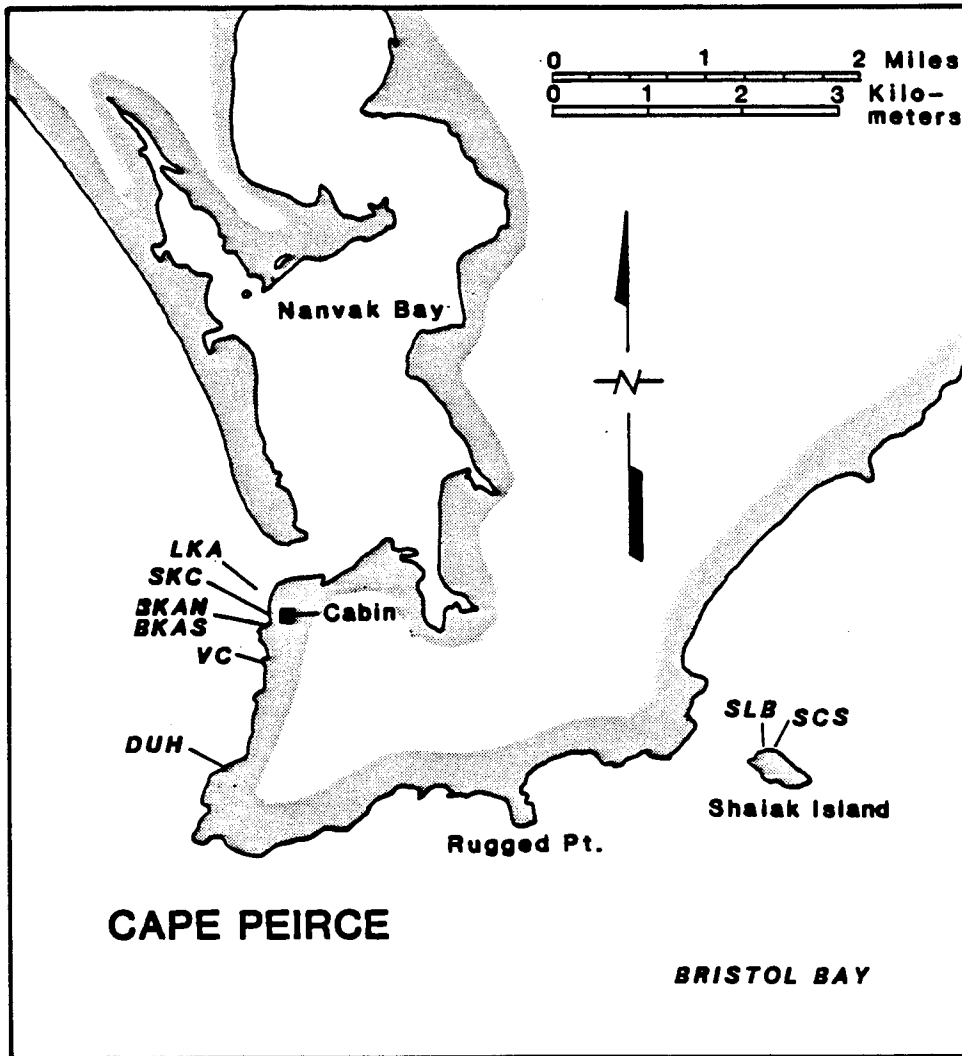


Figure 3. Location of subcolonies, or study plots, at Cape Peirce/Shaik Island.

Growth of chicks was measured at ladder-accessible nest-sites with Pesola spring scales at intervals of 3 to 5 days.

Food samples were taken mostly from adult birds shot on or near the colonies. Offshore samples could not be obtained because no boat was available at St. George and the boat available at Cape Peirce was not suitable for prolonged use (the Zodiac had a chronic, irreparable leak). Contents of adult bird stomachs and incidental regurgitations of chicks handled for growth measurements were preserved in ten-percent ethyl alcohol in water.

Field Data Reduction

Data acquired through field work conducted specifically in connection with this thesis were compiled according to procedures established by Hunt et al. (1981a) during previous work on the Pribilof Islands. Since plots were visited at intervals ranging to several days exact dates of egg laying, hatching, and chick fledging could not be determined. Therefore, we credited the mid-date between two consecutive visits on which we noted a transition from no egg to egg, egg to chick, or chick to fledgling for each individual nest-site. If a critical observation could not be made of a particular nest-site in consecutive visits, then that nest-site was not used for phenology estimates.

Mean clutch size was calculated only for black-legged kittiwake nests with eggs; nests with no eggs were not included in calculations. Red-legged kittiwakes were observed to lay a maximum of one egg, as were common and thick-billed murre.

Hatching success was calculated as the number of chicks hatched per number of eggs laid. Values for hatching success are reported as ranges

because of uncertainty whether the observation of an egg on one visit but not on the next visit indicated the loss of an egg or the loss of a recently hatched chick. The ranges are bound by lower values assuming that these observations indicated loss only of eggs and by upper values assuming that these eggs hatched and the chicks subsequently died and were lost before the next visit.

Fledging success was calculated as the number of chicks fledged per number of chicks hatched. Fledging in this and previous studies (Hunt et al. 1981a) is a relative term. For kittiwakes, it indicates actual fledging, where chicks equipped with flight feathers are capable or nearly capable of flight. For murre, "fledging" actually indicates the stage of chick growth when the chicks jump from nesting ledges and go to sea. Murre "jumpers" do not have plumage suitable for flight, but are no longer available for observation at study plots. Chicks were assumed to have fledged if, on the last visit seen, they exhibited plumage development as described by Hunt et al. (1981a) or had attained an age of at least 35 days for black-legged kittiwakes, 30 days for red-legged kittiwakes, or 15 days for either common or thick-billed murre (Hunt et al. 1981a). As for hatching success, values for fledging success are reported as ranges because of uncertainty regarding hatching of some eggs between observations.

Reproductive success was calculated as the number of chicks fledged per number of nests with eggs for kittiwakes and as the number of chicks fledged (jumped) per number of known eggs laid for murre. Murre chicks fledged for which no egg had been previously observed were not included in calculations of reproductive success.

Productivity for kittiwakes was calculated as the number of chicks fledged per number of nesting attempts, regardless of whether or not eggs were laid in each nest. Productivity for murre was calculated as the total number of chicks fledged (jumped) per mean number of adults on the study plots. The mean number of adults constitutes our best estimate of number of the breeding pairs and therefore of "nest attempts." Productivity for murre is likely underestimated because mean number of adults on the study plots probably includes non-breeding as well as breeding birds or both members of some breeding pairs; this effect may be compensated for to an unknown degree, however, by the disappearance of unsuccessful breeding birds from the study plots over the period of observation. Because of uncertainties surrounding the accuracy of productivity measures for murre, and more consistent reporting of reproductive success in previous publications, only reproductive success is used in this thesis as an indicator of breeding performance in murre.

Formal analysis of food habits was not performed; however, general species presence in collected food samples is reported to allow some comparison to previous work. Samples were identified by N.M. Harrison at the University of California - Irvine, under direction of G.L. Hunt, Jr.

Compilation of Oceanographic and Meteorological Information

Monthly mean sea surface temperatures (SST), in degrees Celsius, were obtained from the Naval Fleet Numerical Oceanographic Center in Monterey, California via D.R. McLain of the National Marine Fisheries

Service. The data represent analysis of surface water temperature as reported from ships passing through 300-km² areas centered at the Pribilof Islands (57° N, 170° W) and Bristol Bay (57° N, 163° W). These are the same data used by Niebauer (1980, 1983) to relate variability of sea ice and SST in the southeastern Bering Sea to large scale atmospheric fluctuations. Additional sets of monthly mean SST data were obtained for coordinates over the shelf break immediately south of St. George Island (56° N, 170° W) and in coastal waters immediately south of Cape Peirce (58° N, 162° W), but these latter data exhibited trends similar to those used by Niebauer, therefore the former sets are used in this thesis.

Information on wind speed near the Pribilof Islands was obtained from monthly summaries of local climatological data for St. Paul Island published by the U.S. Department of Commerce, National Weather Service; no comprehensive weather information was available for St. George Island. Wind speed information for Cape Peirce is not published in monthly summaries of local climatological data; however, daily observations are recorded at the neighboring Cape Newenham Air Force Station and microfiche reports are distributed by the U.S. Department of Commerce, Environmental Data and Information Service. These microfiche reports of daily weather observations were inspected at the University of Alaska, Arctic Environmental Information and Data Center (AEIDC) in Anchorage. Uncompiled observations for 1984 were obtained from the National Weather Service, National Climatic Data Center, Asheville, North Carolina.

Information on average daily wind speed was not consistently

available from published records, but daily maximum speeds were available for each day. Therefore an index for maximum wind speed was developed to represent the proportion of days during the breeding season that daily maximum wind speed equaled or exceeded specific values in miles per hour. The breeding season was delimited as the 112 day period (16 weeks) between May 23 and September 11 each year for St. George Island and between May 9 and August 28 each year for Cape Peirce, encompassing the period of early nesting activity through the fledging of chicks. The two week shift in summer periods between St. George Island and Cape Peirce reflects differences in mean hatching dates for both black-legged kittiwakes and common murrelets between St. George and Cape Peirce.

Precipitation data were obtained from the same sources as those for wind speed. Similar indices were developed based upon the 112 day summer periods, indicating the proportion of days that equaled or exceeded specific levels of precipitation. In addition, total precipitation for the 112 day summer period was calculated.

Data on heating degree days were available for the Pribilof Islands from the same source as that for wind speed and precipitation. Comparable information was not available for Cape Peirce or neighboring Cape Newenham.

Statistical Analysis

Given the typically non-normal distribution of data presented in proportional format (productivity, hatching success, fledging success, etc.) and the sensitivity of most parametric statistical tests to distributions other than normal, non-parametric tests for equality of

variance and for correlation were used to test hypotheses. Specifically, the squared ranks test for variances (Conover 1980) was used to test hypotheses regarding constancy of breeding performance. Spearman rank correlation (Conover 1980, Minitab 1982) was used to test correspondence of breeding performance to annual changes in SST, wind speed, precipitation, heating degree days, and to trends over time. More typical parametric correlation using the Pearson product moment was also used for hypothesis testing, however, because small sample sizes are not analyzed as well by Spearman rank correlation and also to provide comparison to results of the nonparametric test.

The asymptotic relative efficiency of the squared ranks test for variances to the typical parametric F-test for variances is 0.76 for normally distributed populations, and is equal to or greater than 1.00 for several nonnormal distributions. Conover (1980) argues that the sensitivity of the F-test to deviations from normality, coupled with its lack of power in reasonable nonnormal situations, points to the need for the nonparametric test. Spearman rank correlation is a commonly accepted nonparametric statistic for testing correlation of populations with nonnormal or unknown bivariate distributions (Conover 1980, Zar 1984). Both nonparametric tests rely on rank transformation of sample data.

Hypothesis testing was performed on entire sets of available data as well as on selected data considered more reliable. Selected data sets exclude short-term or more qualitative observations of breeding performance but are limited to a smaller number of years.

RESULTS

Summary information on the breeding performance of kittiwakes and murrelets and concurrent environmental data are presented in Table 1 for St. George Island and in Table 2 for Cape Peirce. Definitions for abbreviations used in tables and figures are given in Appendix F. Results of hypothesis testing are explained under subheadings by species and location. Significance levels of correlation analysis cited in the text are those for the parametric Pearson product moment, because the nonparametric Spearman rank test was not applicable in many instances due to small sample sizes and because trends of significance for the parametric and nonparametric correlations were similar when both were applied.

Kittiwakes and Murrelets, St. George Island and Cape Peirce

The squared ranks tests for variances (Table 3) provide unanticipated results for the first set of hypotheses regarding constancy of breeding performance of birds on St. George Island versus Cape Peirce. Although null hypotheses concerning breeding performance of black-legged kittiwakes at both colonies were rejected, results were opposite to what was expected. Annual reproductive success and productivity of black-legged kittiwakes were apparently more constant at coastal Cape Peirce rather than at oceanic St. George Island ($p < 0.02$, $p < 0.01$ respectively); the null hypothesis concerning mean date of hatching could not be tested. A plot of the data from Tables 1 and 2 (Figure 4) reveals that breeding performance of both black-legged and red-legged kittiwakes at St. George ranges widely between years compared

Table 1. Breeding performance of kittiwakes and murre, and oceanographic and meteorologic conditions for St. George Island (see Appendix F for definition of abbreviations).

Year	Reproductive success ^a				Productivity ^b		Mean date of hatching				Sea surface temperature (°C)				Mean May-Aug	Mean ^c Sept-Aug
	BLKI	RLKI	COMU	TBMU	BLKI	RLKI	BLKI	RLKI	COMU	TBMU	May	June	July	Aug		
1976	0.79	0.67	-	-	0.62	0.38	7-28	8-05	8-03	8-03	-0.03	2.80	7.00	8.64	4.60	3.14
1977	0.56	0.68	-	0.43	0.45	0.54	7-27	7-31	8-04	8-05	3.03	5.95	5.64	10.69	6.33	4.51
1978	0.48	0.43	0.70	0.51	0.22	0.13	8-01	8-10	8-02	7-29	4.20	6.05	7.83	9.32	6.85	5.18
1979	-	-	-	-	0.40 ^g	0.18 ^g	-	-	-	-	4.66	7.29	8.66	10.22	7.71	5.75
1980	-	-	-	-	0.38 ^g	0.27 ^g	-	7-30 ^g	-	-	2.89	5.85	7.49	8.45	6.17	4.66
1981	0.12	0.29	0.30	0.15	0.07	0.11	7-22	7-24	7-30	7-26	4.13	7.18	8.73	9.73	7.44	5.15
1982	0.01 ^g	0.01 ^g	0.01 ^g	0.01 ^g	0.01 ^g	0.01 ^g	-	-	-	-	2.88	4.45	6.21	8.06	5.40	4.51
1983	0.01 ^g	0.01 ^g	-	-	0.01 ^g	0.01 ^g	-	-	-	-	2.86	4.50	9.06	10.20	6.66	4.01
1984	0.13 ^g	0.07 ^g	-	0.73 ^g	0.14 ^g	0.13 ^g	-	-	-	-	0.50	3.41	7.42	7.47	4.70	2.73

Year	Index for daily maximum wind speed ^d								Index for daily precipitation ^e							Heating degree days (base 65°F)					Total May-Sept
	10	15	20	25	30	35	40	0.01	0.05	0.1	0.2	0.3	0.4	0.5	Accum. ^f total	May	June	July	Aug	Sept	
1976	0.98	0.87	0.54	0.13	0.05	0.01	0.01	0.42	0.19	0.14	0.07	0.04	0.03	0.02	5.01	1055	745	610	532	649	3591
1977	0.95	0.62	0.33	0.15	0.04	0.00	0.00	0.29	0.13	0.04	0.00	0.00	0.00	0.00	1.61	889	642	499	420	508	2958
1978	0.97	0.88	0.63	0.31	0.12	0.01	0.01	0.60	0.32	0.24	0.11	0.04	0.02	0.01	7.17	803	616	564	496	518	2997
1979	0.97	0.90	0.63	0.21	0.06	0.00	0.00	0.70	0.33	0.20	0.13	0.08	0.05	0.04	8.05	747	548	497	444	501	2737
1980	1.00	0.98	0.79	0.47	0.24	0.13	0.04	0.62	0.32	0.21	0.12	0.07	0.06	0.04	8.72	823	608	532	568	617	3148
1981	1.00	0.96	0.85	0.51	0.23	0.11	0.02	0.52	0.24	0.14	0.07	0.04	0.03	0.02	5.65	757	651	527	541	613	3089
1982	0.99	0.96	0.79	0.54	0.35	0.21	0.07	0.46	0.28	0.19	0.10	0.07	0.03	0.00	6.24	915	702	638	507	661	3423
1983	1.00	0.97	0.79	0.42	0.22	0.09	0.02	0.49	0.32	0.21	0.12	0.07	0.05	0.01	7.37	868	632	541	519	620	3180
1984	1.00	0.93	0.77	0.43	0.22	0.11	0.04	0.46	0.29	0.19	0.11	0.06	0.04	0.03	8.13	968	646	579	492	561	3246

^a Reproductive success = number of chicks fledged per nest with egg.

^b Productivity = number of chicks fledged per nest attempt.

^c Mean SST for Sept-Aug refers to September of previous year through August of current year.

^d Index for daily maximum wind speed presents proportion of days within arbitrary 112 day (16 week) summer, May 23 - September 11, that maximum wind speed in miles per hour equaled or exceeded value of table subheading.

^e Index for daily precipitation presents proportion of days within arbitrary 112 day (16 week) summer, May 23 - September 11, that precipitation in inches equaled or exceeded value of table subheading.

^f Accumulated total precipitation presents total precipitation in inches for entire 112 day (16 week) summer, May 23-September 11.

^g Values represent short-term or qualitative observations.

Table 2. Breeding performance of kittiwakes and murre, and oceanographic and meteorologic conditions for Cape Peirce (see Appendix F for definition of abbreviations).

Year	Reproductive success ^a		Productivity ^b		Mean date of hatching		Sea surface temperature (°C)					Mean ^c May- Aug	Mean ^c Sept- Aug
	BLK1	COMU	BLK1	BLK1	COMU	May	June	July	Aug				
1970	-	-	0.15	-	-	2.05	4.76	7.61	8.35	5.69	5.03		
1973	-	-	0.09 ^g	-	-	0.63	3.53	7.09	9.07	5.08	3.68		
1976	-	0.20 ^g	0.25	7-15	7-21	-0.60	3.56	7.72	9.96	5.16	3.12		
1977	0.00 ^g	0.01 ^g	0.00 ^g	-	-	2.19	6.37	6.58	11.52	6.67	4.78		
1981	0.23	0.17	0.16	6-26	7-12	4.95	8.00	9.26	10.43	8.16	5.25		
1984	0.01 ^g	0.13 ^g	0.01 ^g	-	-	1.43	3.68	8.09	8.73	5.48	3.21		

Year	Index for daily maximum wind speed ^d							Index for daily precipitation ^e							Accum. ^f total
	10	15	20	25	30	35	40	0.01	0.05	0.1	0.2	0.3	0.4	0.5	
1970	0.96	0.85	0.71	0.54	0.38	0.33	0.21	0.47	0.36	0.29	0.15	0.14	0.10	0.06	13.10
1973	0.94	0.78	0.57	0.35	0.21	0.19	0.14	0.38	0.23	0.16	0.10	0.05	0.03	0.02	8.12
1976	0.96	0.81	0.63	0.47	0.29	0.19	0.11	0.41	0.24	0.21	0.13	0.09	0.05	0.04	7.95
1977	0.88	0.74	0.52	0.33	0.28	0.18	0.10	0.42	0.32	0.25	0.14	0.13	0.08	0.06	10.56
1981	0.94	0.83	0.69	0.47	0.39	0.27	0.16	0.54	0.35	0.28	0.17	0.14	0.09	0.06	12.70
1984	0.94	0.76	0.55	0.35	0.27	0.17	0.11	0.49	0.30	0.25	0.16	0.08	0.06	0.05	11.71

^a Reproductive success = number of chicks fledged per nest with egg.

^b Productivity = number of chicks fledged per nest attempt.

^c Mean SST for Sept-Aug refers to September of previous year through August of current year.

^d Index for daily maximum wind speed presents proportion of days within arbitrary 112 day (16 week) summer, May 9 - August 28, that maximum wind speed in miles per hour equaled or exceeded value of table subheading.

^e Index for daily precipitation presents proportion of days within arbitrary 112 day (16 week) summer, May 9 - September 11, that precipitation in inches equaled or exceeded value of table subheading.

^f Accumulated total precipitation presents total precipitation in inches for entire 112 day (16 week) summer, May 9 - September 11.

^g Values represent short-term or qualitative observations.

with that of black-legged kittiwakes at Cape Peirce, and that breeding performance of both kittiwake species at St. George has declined steadily from 1976 to 1984. Breeding performance of black-legged kittiwakes at Cape Peirce has been relatively consistent, but low, for all years investigated between 1970 and 1984.

Given that red-legged kittiwakes are considered more strictly oceanic than the more ubiquitous black-legged kittiwakes, variance tests were also performed on breeding performance of these congeners on St. George Island. Null hypotheses comparing reproductive success and productivity between the two kittiwake species at St. George were not rejected, although the mean date of hatching for red-legged kittiwakes was more variable than that for black-legged kittiwakes ($p < 0.025$, Table 3, Figure 4), another unexpected result.

More equivocal results were derived from comparison of common and thick-billed murres between and within the colonies (Table 3, Figure 5). There was a nonsignificant ($p < 0.10$) suggestion by the squared ranks variance tests that reproductive success of common murres on St. George Island was more variable than that at Cape Peirce and that the mean date of hatching for thick-billed murres at St. George was more variable than that for common murres also at St. George ($p < 0.10$). Again, these results run counter to a priori assumptions of more stable reproduction on oceanic St. George Island and consideration of thick-billed murres as perhaps more oceanic, thus more stable, than common murres.

Black-legged Kittiwakes, St. George Island

Productivity and reproductive success in black-legged kittiwakes on St. George Island correlated with several measures of oceanographic and

Table 3. Squared ranks test for variances of breeding performance in kittiwakes and murre, St. George Island and Cape Peirce (see Appendix F for definition of abbreviations).

Parameter	Alternate hypothesis ^a		Data set ^b	Sample size n,m	Test statistic	Significance ^c
Reproductive success	VAR(BLKI/StG)	<	VAR(BLKI/CP)	All 7,3 Selected 4,1	T ₁ = 2.070 -	ns ^d na
	VAR(BLKI/StG)	>	VAR(BLKI/CP)	All 7,3 Selected 4,1	T ₁ = 2.070 -	p < 0.020 na
	VAR(BLKI/StG)	≠	VAR(RLKI/StG)	All 7,7 Selected 4,4	T ₁ = -0.563 T ₁ = 118	ns ns
	VAR(COMU/StG)	<	VAR(COMU/CP)	All 3,4 Selected 2,1	T = 89 -	ns na ^e
	VAR(COMU/StG)	>	VAR(COMU/CP)	All 3,4 Selected 2,1	T = 89 -	ns ^e na
	VAR(COMU/StG)	≠	VAR(TBMU/StG)	All 3,5 Selected 2,4	T = 75 -	ns na
Productivity	VAR(BLKI/StG)	<	VAR(BLKI/CP)	All 9,6 Selected 4,3	T ₁ = 2.355 T ₁ = 22	ns ns
	VAR(BLKI/StG)	>	VAR(BLKI/CP)	All 9,6 Selected 4,3	T ₁ = 2.355 T ₁ = 22	p < 0.01 p < 0.005
	VAR(BLKI/StG)	≠	VAR(RLKI/StG)	All 9,9 Selected 4,4	T ₁ = 0.019 T ₁ = 126	ns ns
	Mean date hatching	<	VAR(BLKI/CP)	All 4,2 Selected 4,2	- -	na na
	>	VAR(RLKI/StG)	All 4,5 Selected 4,4	T = 46 T = 46	ns ns	
	<	VAR(RLKI/StG)	All 4,5 Selected 4,4	T = 46 T = 46	p < 0.025 p < 0.05	
	<	VAR(COMU/CP)	All 4,2 Selected 4,2	- -	na na	
	>	VAR(TBMU/StG)	All 4,4 Selected 4,4	T = 50 T = 50	ns ns ^f	
	<	VAR(TBMU/StG)	All 4,4 Selected 4,4	T = 50 T = 50	ns ^f ns	

^a All null hypotheses assume equality of variances.

^b "Selected" data sets exclude short-term or qualitative observations listed with superscript letter "g" in Tables 1 and 2.

^c Significance is defined at p < 0.05.

^d na indicates test not applicable, will not test for n or m ≤ 2.

^e p for this test was relatively close to 0.05; p < 0.10.

^f p for these tests were very close to 0.05; p < 0.10. Both data sets were equivalent.

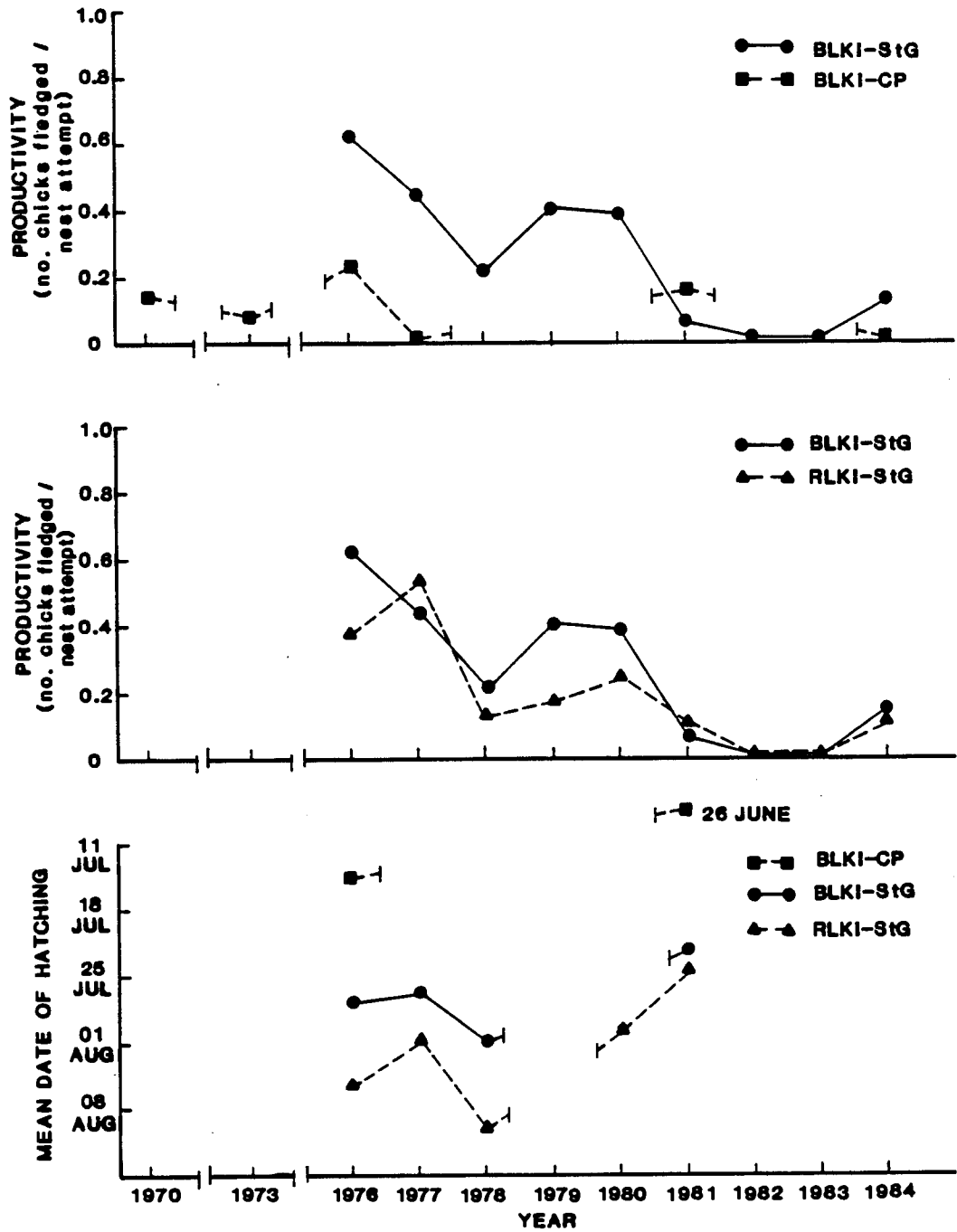


Figure 4. Comparison of breeding performance in kittiwakes, St. George Island and Cape Peirce (see Appendix F for definition of abbreviations).

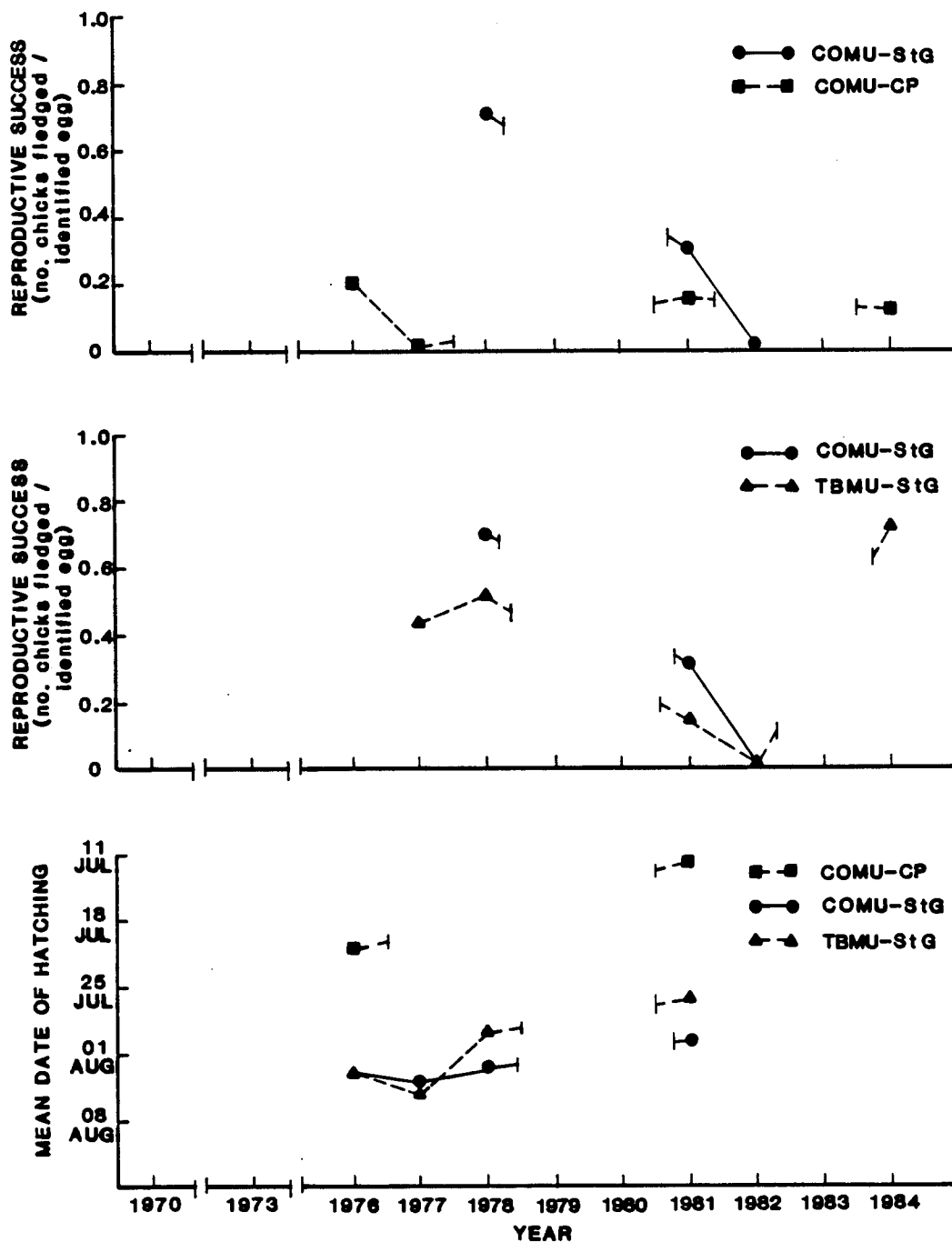


Figure 5. Comparison of breeding performance in murre, St. George Island and Cape Peirce (see Appendix F for definition of abbreviations).

meteorologic conditions (Table 4). Selected data sets, representing four years of the more rigorous investigations on breeding performance, correlated both productivity and reproductive success of black-legged kittiwakes with summer-time average sea surface temperature ($p < 0.05$). Entire data sets for nine and seven years, respectively, correlated productivity and reproductive success not with sea surface temperature of contemporaneous years, but instead with sea surface temperature of years immediately prior or two years earlier. All correlations with sea surface temperature were negative, indicating that better breeding performance may be related to colder water temperatures.

Breeding performance of black-legged kittiwakes on St. George Island correlated most strongly, and negatively, with indices of maximum daily wind speed. In particular, the proportion of days during summer with maximum daily wind speed equal to or exceeding 25 miles per hour may have adversely affected both productivity ($p < 0.005$) and reproductive success ($p < 0.001$).

Only a single significant correlation was detected for precipitation, between reproductive success in seven years and the proportion of days during summer equal to or exceeding 0.3 inches of rain ($p < 0.05$). This indicates that the influence of rain on breeding performance of black-legged kittiwakes at St. George is not great.

The selected data sets for both productivity and reproductive success in black-legged kittiwakes on St. George Island exhibited positive correlations ($p < 0.025$, $p < 0.05$) with heating degree days in May, the beginning of the breeding season. These results indicate again

Table 4. Correlation of breeding performance in black-legged kittiwakes with oceanographic and meteorologic conditions, St. George Island (see Appendix F for definition of abbreviations).

Species	Reproductive parameter	Data set, sample size	Correlated parameter ^a	Correlation analysis						
				Pearson product moment		Spearman rank				
				r	p <	r _s	p <			
BLKI	Productivity	All n = 9	RLKI-P	.853	.0025	.962	.0005			
			SST-SG	-.511	ns	-.605	.05			
			WIND-20 ⁿ⁻²	-.718	.025	-.804	.01			
			WIND-25	-.829	.005	-.803	.01			
			WIND-30	-.795	.01	-.716	.025			
			WIND-35	-.681	.025	-.661	.05			
			WIND-40	-.557	ns	-.685	.05			
			YEAR	-.839	.0025	-.845	.005			
			Selected n = 4	SST-MG	-.947	.05	-1.000	ns		
		SST-SG		-.913	.05	-.800	ns			
		WIND-25		-.948	.05	-1.000	ns			
		WIND-30		-.909	.05	-.800	ns			
		HDD-MY		.964	.025	1.000	ns			
		YEAR		-.938	.05	-1.000	ns			
		BLKI		Reproductive success	All n = 7	RLKI-R	.943	.001	.927	.01
						BLKI-P	.965	.0005	1.000	.001
			SST-MY ⁿ⁻¹			-.863	.0025	-.703	ns	
SST-MG ⁿ⁻¹	-.691		.025			-.577	ns			
SST-SG ⁿ⁻¹	-.811		.005			-.845	.025			
SST-MY ⁿ⁻¹	-.793		.025			-.775	.05			
SST-SG ⁿ⁻²	-.754		.05			-.775	.05			
WIND-10 ⁿ⁻²	-.719		.05			-.673	ns			
WIND-15	-.636		ns			-.936	.005			
WIND-20	-.814		.025			-.855	.025			
WIND-25	-.935		.001			-.847	.025			
WIND-30	-.910		.0025			-.864	.025			
WIND-35	-.842		.01			-.771	.05			
WIND-40	-.680		.05			-.780	.05			
PREC-.3	-.692		.05			-.812	.025			
YEAR	-.934		.0025			-.775	.05			
Selected n = 4	SST-MG		-.916			.05	-1.000	ns		
	WIND-25	-.950	.025	-1.000	ns					
	WIND-30	-.923	.05	-.800	ns					
	HDD-MY	.908	.05	1.000	ns					
	YEAR	-.988	.01	-1.000	ns					
BLKI	Mean date of hatching	All n = 4	none							

^a Subscripts (n-1, n-2) refer to SST of year immediately prior and SST of year two years prior.

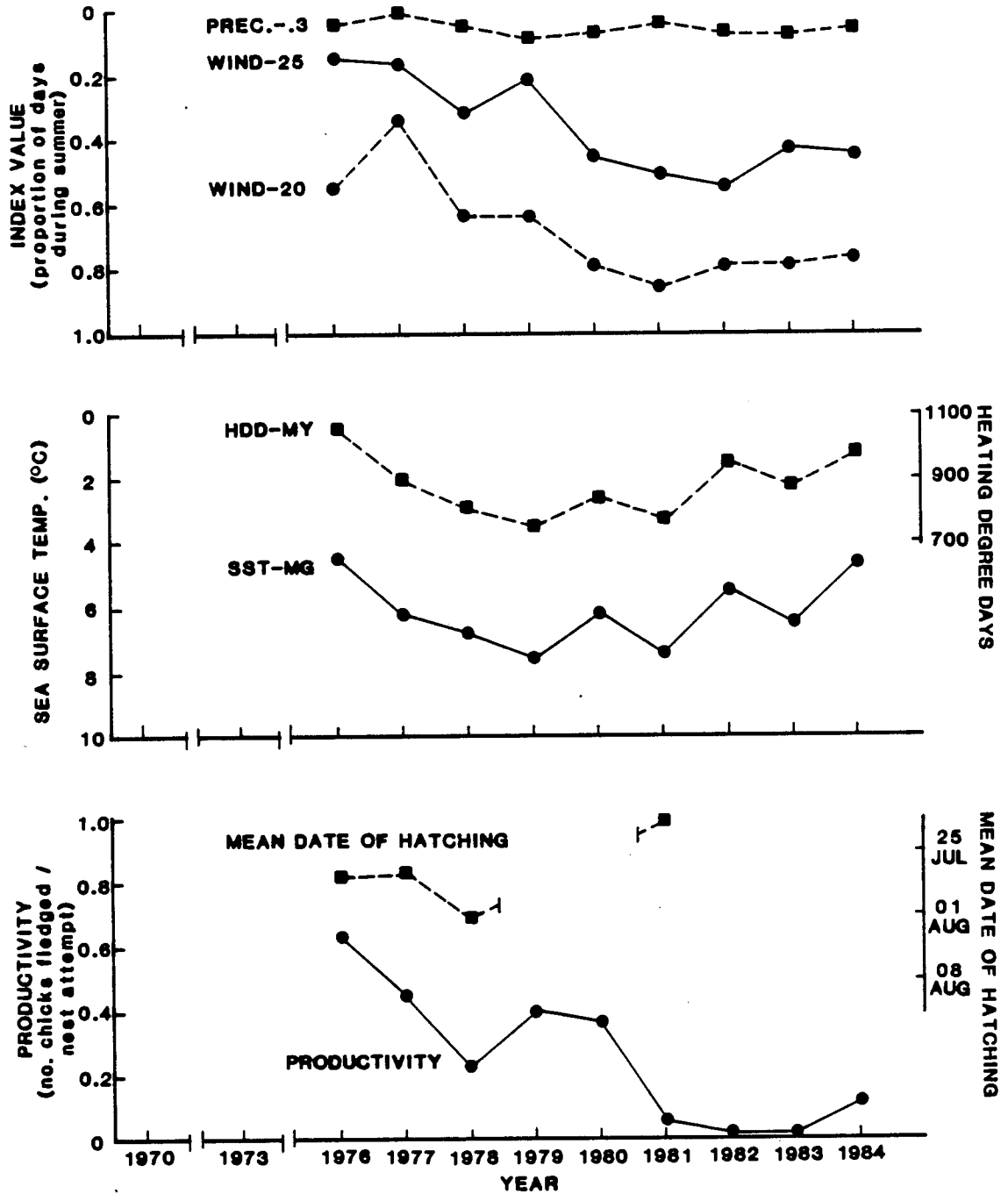


Figure 6. Comparison of productivity in black-legged kittiwakes to environmental conditions, St. George Island (see Appendix F for definition of abbreviations).

a possible relationship between greater breeding success and colder years, particularly since colder winter air temperatures are associated with colder summer sea surface temperatures (Niebauer 1980). These correlations do not, however, suggest a compelling effect of air temperature directly on egg and chick survival.

No significant correlation was found between mean date of hatching and any of the environmental parameters. Moreover, mean date of hatching did not correlate with breeding performance, particularly due to the early date of hatching observed in 1981.

Both productivity and reproductive success for black-legged kittiwakes at St. George also showed strong negative correlations with year ($p < 0.0025$), indicating a definite declining trend in breeding performance between 1976 and 1984. In addition, productivity and reproductive success in black-legged kittiwakes correlated with productivity ($p < 0.0025$) and reproductive success ($p < 0.001$), respectively, in red-legged kittiwakes.

Plots of productivity along with several of the more significantly correlated environmental parameters (Figure 6) show that annual differences in wind speed over 20 and 25 miles per hour, and to a lesser extent heating degree days in May and summer-time mean sea surface temperature, correspond with breeding performance over time in the past decade.

Red-legged Kittiwakes, St. George Island

Productivity and reproductive success of red-legged kittiwakes on St. George Island exhibited similar, and generally stronger, correlations with oceanographic and environmental conditions as did

black-legged kittiwakes (Table 5), except that there was not even a single significant correlation with heating degree days.

Selected data sets correlated both productivity and reproductive success of red-legged kittiwakes with sea surface temperature in July ($p < 0.025$, $p < 0.05$). As in black-legged kittiwakes, however, the entire data sets did not correlate breeding performance of red-legged kittiwakes with contemporaneous sea surface temperatures, but rather to temperatures of prior years. Again, all correlations with sea surface temperature were negative, indicating better breeding performance during or subsequent to years with colder water temperatures.

Breeding performance in red-legged kittiwakes correlated most strongly, and negatively, with indices of daily maximum wind speed. Productivity correlated most strongly ($p < 0.0025$) with the proportion of days during summer with maximum wind speeds equal to or exceeding 20 miles per hour, while reproductive success correlated most strongly with days of wind speeds equal to or exceeding 30 miles per hour ($p < 0.0025$).

For precipitation, several significant and negative correlations were found with breeding performance of red-legged kittiwakes, in contrast to the single correlation detected for black-legged kittiwakes at St. George. Indices of low to high daily precipitation and total precipitation during the breeding season both exhibit significant correlations, perhaps suggesting that production of red-legged kittiwakes is more sensitive to precipitation than is production of black-legged kittiwakes, and that annual fluctuations in even relatively

Table 5. Correlation of breeding performance in red-legged kittiwakes with oceanographic and meteorologic conditions, St. George Island (see Appendix F for definition of abbreviations).

Species	Reproductive parameter	Data set, sample size	Correlated parameter ^a	Correlation analysis					
				Pearson product moment		Spearman rank			
				r	p <	r _s	p <		
RLKI	Productivity	All n = 9	BLKI-P	.853	.0025	.962	.0005		
			SST-MY _{n-2}	-.627	.05	-.471	ns		
			WIND-10	-.658	.05	-.533	ns		
			WIND-15	-.812	.005	-.603	.05		
			WIND-20	-.844	.0025	-.751	.025		
			WIND-25	-.744	.025	-.706	.025		
			WIND-30	-.721	.025	-.684	.05		
			WIND-35	-.596	.05	-.562	ns		
			PREC-.05	-.758	.01	-.299	ns		
			PREC-.1	-.749	.025	-.362	ns		
			PREC-.2	-.732	.025	-.260	ns		
			PREC-.3	-.709	.025	-.400	ns		
			PREC-T	-.660	.05	-.210	ns		
			YEAR	-.759	.01	-.765	.025		
			Selected n = 4	SST-JL	-.962	.025	-1.000	ns	
			WIND-20	-.917	.05	-1.000	ns		
			PREC-.01	-.954	.025	-.800	ns		
		RLKI	Reproductive success	All n = 7	BLKI-R	.943	.001	.927	.01
					RLKI-P	.897	.005	.936	.005
					SST-MY _{n-1}	-.863	.0025	-.595	ns
SST-JN _{n-1}	-.590				.05	-.577	ns		
SST-MG _{n-1}	-.739				.025	-.685	ns		
SST-SG _{n-1}	-.792				.01	-.700	ns		
SST-MY _{n-2}	-.757				.025	-.739	.05		
SST-SG _{n-2}	-.674				.05	-.739	.05		
WIND-10	-.788				.025	-.748	.05		
WIND-15	-.756				.025	-.918	.01		
WIND-20	-.849				.01	-.782	.05		
WIND-25	-.889				.005	-.775	.05		
WIND-30	-.912				.0025	-.845	.025		
WIND-35	-.839				.01	-.826	.025		
WIND-40	-.764				.025	-.890	.025		
PREC-.05	-.773				.025	-.645	ns		
PREC-.2	-.745				.05	-.716	.05		
PREC-.3	-.872			.01	-.963	.005			
PREC-.4	-.746			.05	-.767	.05			
PREC-T	-.741			.05	-.721	.05			
YEAR	-.953	.0005	-.847	.025					
Selected n = 4	SST-JL	-.915	.05	-1.000	ns				
WIND-20	-.913	.05	-1.000	ns					
WIND-25	-.982	.01	-.800	ns					
WIND-30	-.972	.025	-1.000	ns					
YEAR	-.931	.05	-.800	ns					
RLKI	Mean date of hatching	All n = 5	none						
		Selected n = 4	none						

^a Subscripts (n-1, n-2) refer to SST of year immediately prior and SST of year two years prior.

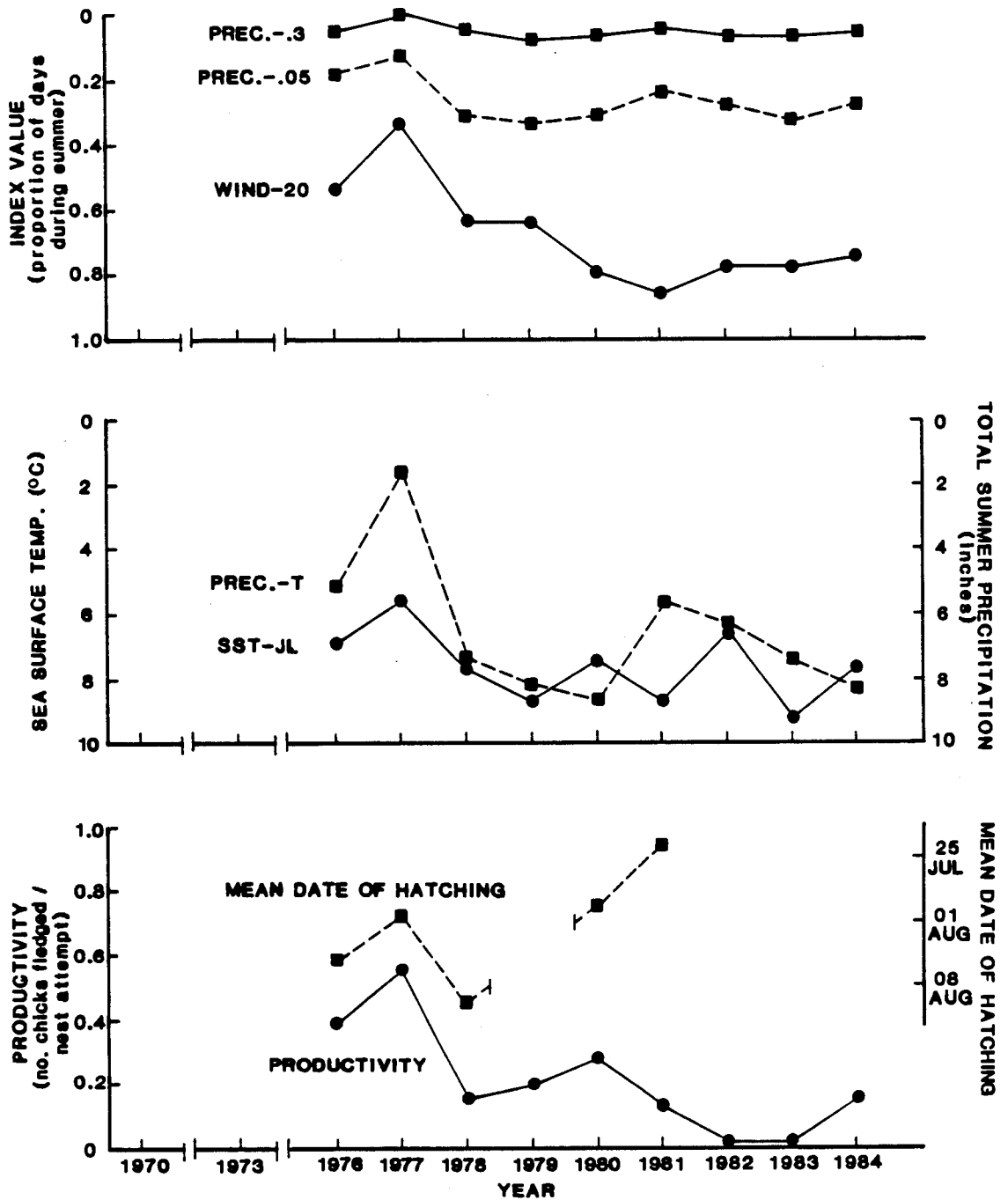


Figure 7. Comparison of productivity in red-legged kittiwakes to environmental conditions, St. George Island (see Appendix F for definition of abbreviations).

low as well as high levels of precipitation can affect red-legged kittiwake breeding performance.

As mentioned earlier, no significant correlations were found between breeding performance of red-legged kittiwakes and heating degree days. No significant correlation was found between mean date of hatching and breeding performance, or between mean date of hatching and environmental conditions.

Both productivity and reproductive success correlated strongly and negatively with year ($p < 0.01$, $p < 0.05$). Red-legged kittiwakes on St. George Island, like black-legged kittiwakes there, exhibited a declining trend in breeding performance between 1976 and 1984. As mentioned earlier, productivity and reproductive success in red-legged kittiwakes correlated with the same parameters in black-legged kittiwakes.

Plots of productivity along with several of the more significantly correlated environmental parameters (Figure 7) show that annual differences in wind speeds of 20 miles per hour, and to a lesser extent indices of precipitation and other indices of wind speed, correspond with breeding performance of red-legged kittiwakes over time in the past decade. In earlier years, July sea surface temperatures and mean date of hatching also correspond with productivity, but these relations do not continue after 1980-1981.

Common Murres, St. George Island

Reproductive success in common murres on St. George Island exhibited far fewer significant correlations with oceanographic and meteorologic conditions than did breeding performance of either kittiwake species (Table 6). Reproductive success, based upon three

years of data, correlated strongly and negatively with sea surface temperature for July of the previous year ($p < 0.025$), but not with any other measure of sea surface temperature. Common murres may be somewhat affected by high wind speeds, as indicated by negative correlations with the proportion of days during summer with maximum wind speeds equal to or exceeding 30 ($p < 0.05$) and 35 ($p < 0.05$) miles per hour.

Reproductive success also showed positive correlation with an index of relatively low precipitation, as shown by correlation with the proportion of days during summer with precipitation equal to or exceeding 0.01 inches ($p < 0.01$). Reproductive success in common murres did not significantly correlate, however, with other indices of daily precipitation, nor with total precipitation.

Reproductive success of common murres on St. George Island also correlated significantly and negatively, for the three years measured, with heating degree days in September ($p < 0.05$) indicating a possible relation to warmer air temperatures; however, air temperature in September would seem to have little impact on breeding of adults or survival of chicks since breeding activity is completed by September and the mean date of fledging as reported by Hunt et al. (1981a) for common murres 1976-1978 is in late August.

Insufficient data were available to test correlations between mean date of hatching and reproductive success. However, there was a significant negative correlation ($p < 0.05$) between mean date of hatching and July sea surface temperature, suggesting that common murres on St. George Island bred later during years of colder water temperatures. Data for 1981, however, argue against such a

Table 6. Correlation of breeding performance in common murre and thick-billed murre with oceanographic and meteorologic conditions, St. George Island (see Appendix F for definition of abbreviations).

Species	Reproductive parameter	Data set, sample size	Correlated parameter ^a	Correlation analysis			
				Pearson product moment		Spearman rank	
				r	p <	r _s	p <
COMU	Reproductive success	All ^b n = 3	TBMU-R	.988	.05	na ^c	na
			SST-JL _{n-1}	-1.000	.025	na	na
			WIND-30	-.993	.05	na	na
			WIND-35	-.996	.05	na	na
			PREC-.01	1.000	.01	na	na
			HDD-ST	-.995	.05	na	na
			YEAR	-.982	ns ^d	na	na
	Mean date of hatching	All n = 4	SST-JL	-.930	.05	-1.000	ns
			YEAR	-.929	.05	-.800	ns
TBMU	Reproductive success	All n = 5	COMU-R	.988	.05	na	na
	Mean date of hatching	All n = 4	SST-JL	-.966	.025	-1.000	ns
			YEAR	-.877	ns ^d	-.800	ns

^a Subscript (n-1) refers to SST of previous year.

^b Only the entire data set was analyzed because more reliable data were compiled for only two years.

^c na indicates test not applicable; will not test for $n \leq 3$.

^d Correlation was not significant at $p < 0.05$, but $p < 0.10$.

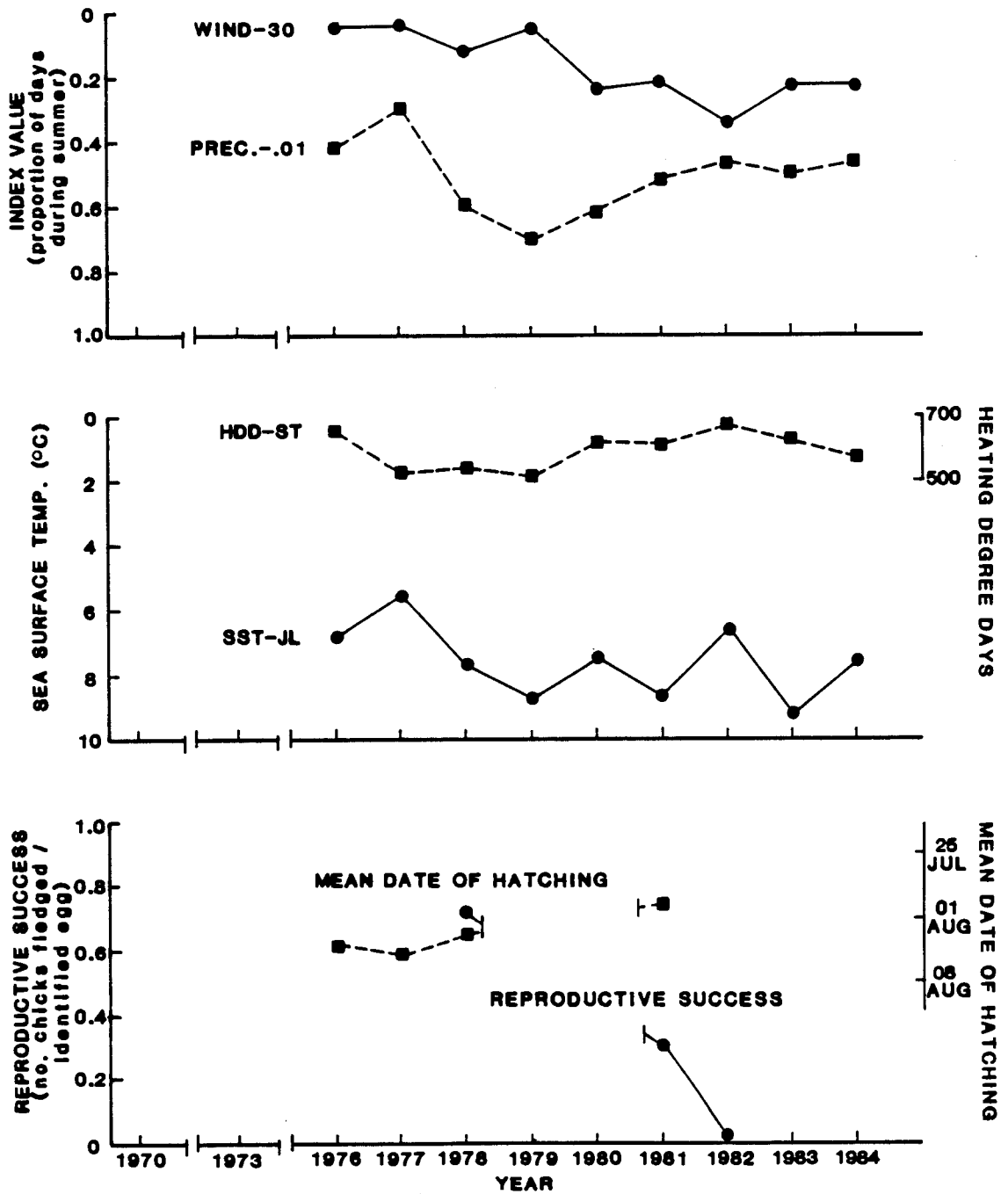


Figure 8. Comparison of reproductive success in common murrelets to environmental conditions, St. George Island (see Appendix F for definition of abbreviations).

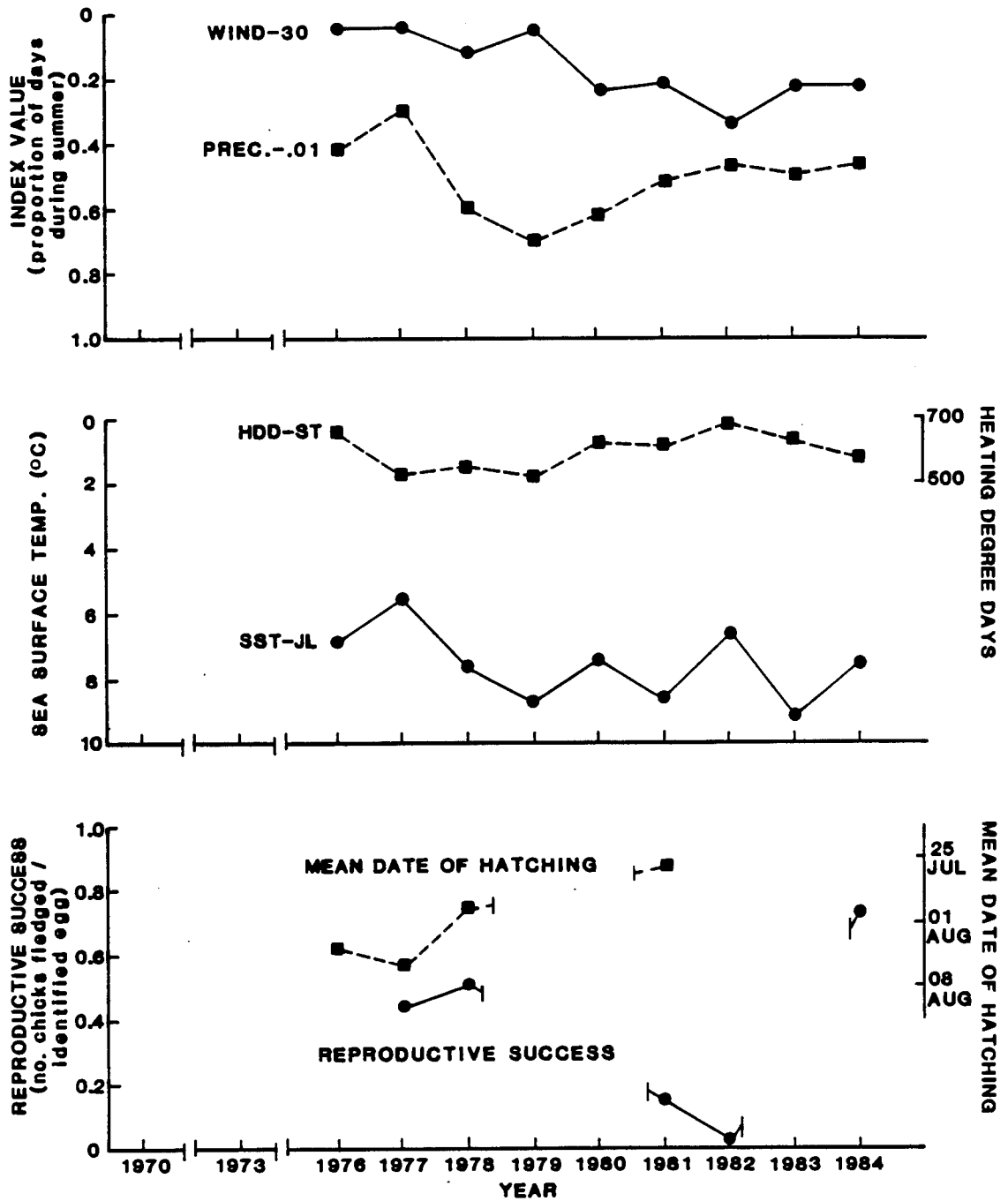


Figure 9. Comparison of reproductive success in thick-billed murrelets to environmental conditions, St. George Island (see Appendix F for definition of abbreviations).

straightforward relation. Mean date of hatching also correlated negatively with year ($p < 0.05$) for the four years of observation.

Although not considered significant, there is a suggestion from the three years of available data that reproductive success of common murrelets at St. George declined during the past decade ($p < 0.10$), similar to trends noted for black-legged and red-legged kittiwakes.

Plots of reproductive success in common murrelets on St. George Island along with several significantly correlated environmental parameters, as well as sea surface temperature for July, are shown in Figure 8. It is difficult to decipher any obvious trends, particularly with only three years of data on breeding performance; however, reproductive success appears to have declined and mean date of hatching appears to have become progressively earlier.

Thick-billed Murrelets, St. George Island

Neither the entire data set nor selected data for reproductive success in thick-billed murrelets on St. George Island correlated significantly with oceanographic or meteorological conditions, mean date of hatching, or time (Table 6). Although mean date of hatching showed no significant correlation with reproductive success, as with common murrelets, hatching date did correlate negatively ($p < 0.025$) with July sea surface temperature and suggested a trend with year ($p < 0.10$).

Plots of thick-billed murrelet reproductive success along with indices of environmental conditions (Figure 9) show that, excluding data for 1984, a decline in breeding performance is apparent between the early 1980's and the late 1970's. Data for 1984 reproductive success are particularly high and subject to doubt because investigators left St.

George Island on August 13, before fledging (Johnson and Baker 1985). Correspondence of environmental parameters and reproductive success, and likely correlations as well, might be better if data for 1984 were excluded or if reproductive success in 1984 was actually lower, as suspected. The mean date of hatching appears to have become progressively earlier since the mid 1970's, based on four years of observation.

Black-legged Kittiwakes, Cape Peirce

Breeding performance of black-legged kittiwakes at Cape Peirce correlated with fewer measures of oceanographic and meteorologic conditions, and less strongly, than did breeding performance of kittiwakes at St. George (Table 7). Neither productivity nor reproductive success correlated significantly with contemporaneous measures of sea surface temperature. Reproductive success, for the three years measured, did exhibit significant correlations with sea surface temperatures in June and July two years prior ($p < 0.05$) but, contrary to correlations at St. George, black-legged kittiwakes at Cape Peirce correlated positively with sea surface temperature. It is difficult to ascribe particular importance to these correlations since they apply to two-year lag times, and only to reproductive success but not to productivity.

Entire data sets for productivity and reproductive success in black-legged kittiwakes at Cape Peirce exhibited, surprisingly, significant positive correlations with indices for daily maximum wind speed ($p < 0.05$). Reproductive success even exhibited positive correlation ($p < 0.05$) with the proportion of days during summer with

maximum wind speeds equal to or exceeding 40 miles per hour, the highest wind speed index calculated. Paradoxically, selected data for those three years of more complete studies on breeding performance at Cape Peirce exhibited a significant negative correlation ($p < 0.05$) with the proportion of days during summer with maximum wind speeds equal to or exceeding 20 miles per hour. It is difficult to define a mechanism whereby higher winds would benefit breeding performance of black-legged kittiwakes, except perhaps through the possibility that wind mixing might aid the production of or increase the availability of forage fishes; usable data on nearshore fishes are not available to test this idea, however. The contradictory trends exhibited by the entire versus the selected sets of productivity data further confound any interpretation of correlation between wind speed and breeding performance of black-legged kittiwakes at Cape Peirce.

For precipitation, the entire data set for productivity showed no significant correlation, while three years of data selected from more complete studies exhibited significant negative correlations between productivity and nearly all of the indices for precipitation ($p < 0.05$ and $p < 0.01$). Reproductive success in black-legged kittiwakes at Cape Peirce, observed in three different years than the selected data for productivity, showed a significant positive correlation ($p < 0.025$) with the proportion of days during summer with precipitation equal to or exceeding 0.1 inches, but not with any of the other indices of precipitation. Similar to correlations with wind speed, there was no consistent indication of the effect that precipitation may have on breeding performance of black-legged kittiwakes at Cape Peirce.

Table 7. Correlation of breeding performance in black-legged kittiwakes and common murrelets with oceanographic and meteorologic conditions, Cape Peirce (see Appendix F for definition of abbreviations).

Species	Reproductive parameter ^a	Data set, sample size	Correlated parameter ^b	Correlation analysis			
				Pearson product moment		Spearman rank	
				r	p <	r _s	p <
BLKI	Productivity	All n = 6	SST-JL	.686	ns ^d	.600	ns
			WIND-15 ^{b-2}	.782	.05	.771	ns
			WIND-20	.738	.05	.771	ns
			WIND-25	.785	.05	.794	ns
		Selected n = 3	WIND-20	-.989	.05	na ^c	na
			WIND-30	-.984	ns ^d	na	na
			PREC-.05	-1.000	.01	na	na
			PREC-.1	-1.000	.01	na	na
			PREC-.3	-.996	.05	na	na
			PREC-.4	-.995	.05	na	na
	Reproductive success	All ^e n = 3	BLKI-P	1.000	.01	na	na
			SST-JN	.991	.05	na	na
			SST-JL ⁿ⁻²	.990	.05	na	na
			WIND-20 ^{b-2}	.992	.05	na	na
			WIND-25	.996	.05	na	na
			WIND-30	.994	.05	na	na
			WIND-35	.992	.05	na	na
WIND-40	.993	.05	na	na			
PREC-.1	.999	.025	na	na			
Mean date of hatching	All n = 2		na	na	na	na	
COMU	Reproductive success	All ^e n = 4	SST-JL	.725	ns ^f	.400	ns
			WIND-10	.981	.01	.949	ns
	Mean date of hatching	All n = 2		na	na	na	na

^a Insufficient data available to test mean date of hatching.

^b Subscript (n-2) refers to SST of two years prior.

^c na indicates test not applicable; will not test for $n \leq 3$.

^d Correlation was not significant at $p < 0.05$, but $p < 0.10$.

^e Only the entire data set was analyzed because more reliable data were compiled for only one year.

^f Although correlation is not significant, SST-JL trends with COMU reproductive success in Figure 11.

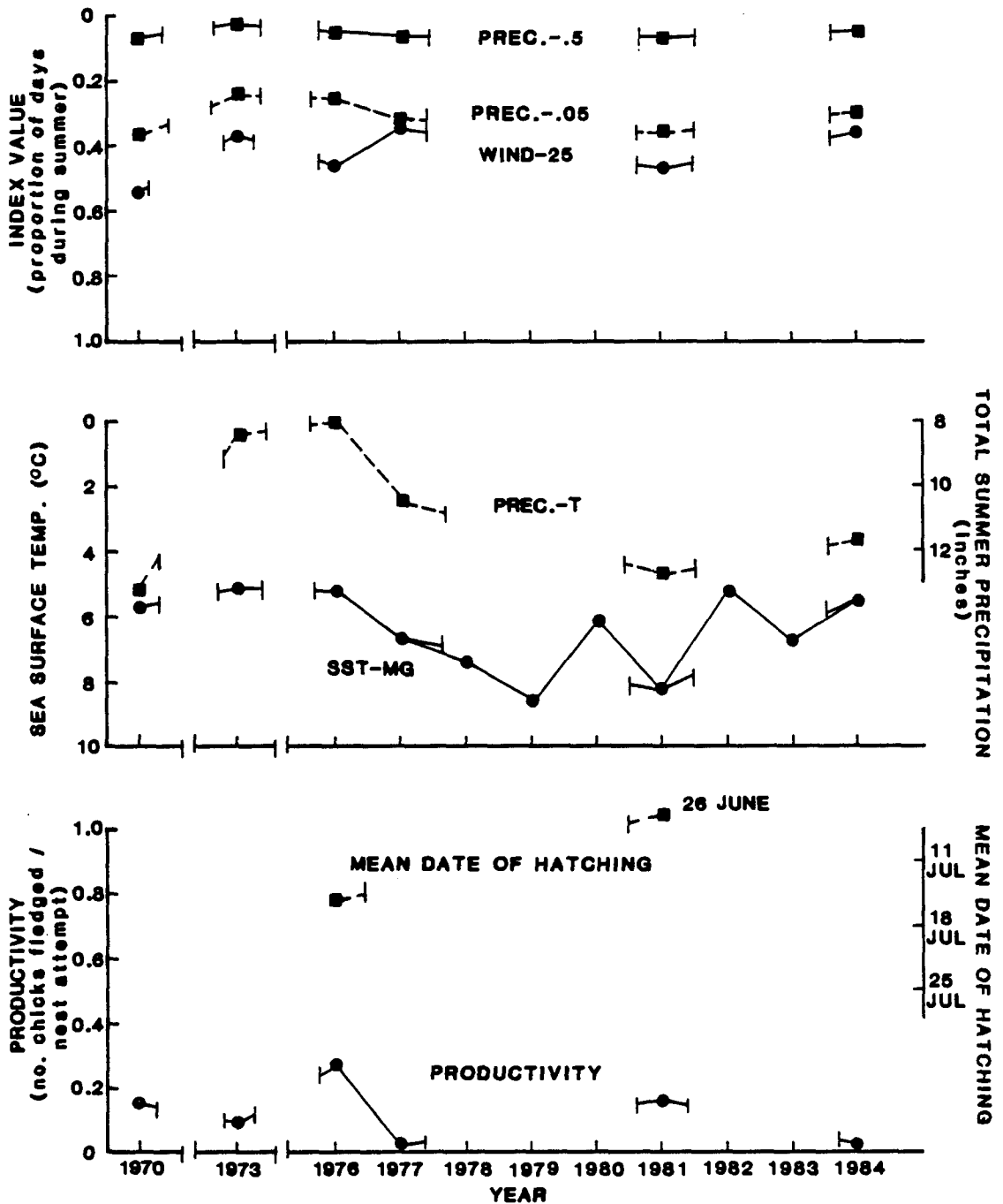


Figure 10. Comparison of productivity in black-legged kittiwakes to environmental conditions, Cape Peirce (see Appendix F for definition of abbreviations).

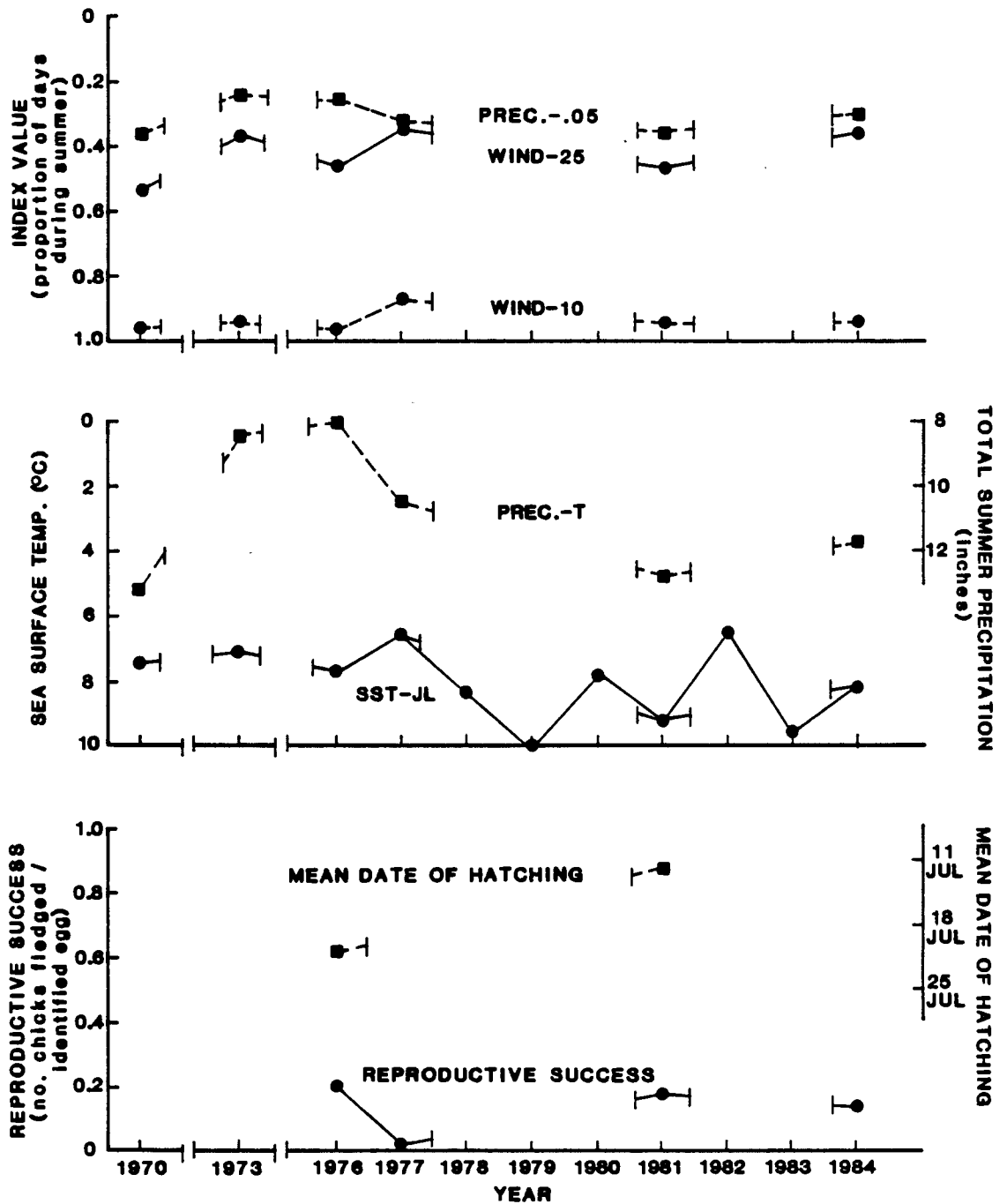


Figure 11. Comparison of reproductive success in common murrelets to environmental conditions, Cape Peirce (see Appendix F for definition of abbreviations).

Information on heating degree days was not available for Cape Peirce; therefore, no analyses were conducted to test the effects of air temperature. Breeding performance of black-legged kittiwakes showed no significant correlation with year, indicating that there are no identified signs of decline in breeding performance at Cape Peirce.

Plots of productivity with several environmental parameters (Figure 10) indicate vaguely discernible trends with mean summer sea surface temperature, wind speed, and precipitation opposite to those found for black-legged kittiwakes on St. George Island. Productivity at Cape Peirce also appears to be oscillating about a low mean value rather than steadily declining as in black-legged kittiwakes on St. George Island.

Common Murres, Cape Peirce

Reproductive success in common murres at Cape Peirce exhibited only a single significant correlation with oceanographic or meteorologic conditions (Table 7). For all four years observed, reproductive success correlated positively ($p < 0.01$) with the proportion of days during summer with daily maximum wind speeds equal to or exceeding 10 miles per hour. Given that 10 miles per hour represents the slowest wind speed index analyzed, the correlation may represent a positive relationship with low winds, but as for black-legged kittiwakes it is difficult to explain increased breeding performance in common murres at Cape Peirce with increased days of wind speed equal to or exceeding specific values.

Plots of reproductive success along with several environmental parameters (Figure 11) indicate slightly opposing trends with the index for wind speeds equal to or exceeding 10 miles per hour, but corresponding trends between reproductive success and sea surface

temperature in July. Low wind speeds and warm sea surface temperatures may benefit breeding performance in common murrelets at Cape Peirce.

DISCUSSION

The testing of hypotheses comparing the breeding performance of kittiwakes and murre and relating it to oceanographic and meteorologic conditions across the southeastern Bering shelf has, of necessity, relied on a wide variety of data from many separate investigations. Additionally, most of the consistently available information is of a general nature, such as estimates of overall productivity or mean sea surface temperature, and cannot be used to penetrate fine spatial or temporal scales. A particularly important gap in available information is a paucity of data on the annual abundance, distribution, or availability of forage fishes that constitute the bulk of the diets of breeding kittiwakes and murre. Therefore, the results of this current investigation must be viewed as a general reconnaissance of possible relationships and mechanisms affecting the breeding ecology of these birds. Comparison of available data over the past decade does, however, expose possible relationships between breeding performance of kittiwakes and, to a lesser extent, murre and environmental parameters (Table 8). These comparisons should be helpful in confirming or refuting earlier conclusions and in developing further studies.

Hypothesis 1 - Constancy Between Colonies

Seabirds generally exhibit low reproductive rates, high age at maturity, and low adult mortality characteristic of K-selected species in MacArthur and Wilson's (1967) arguably overused terminology. Lack (1967, 1968) described offshore colonial seabirds as exemplifying these characteristics over more fecund nearshore birds, particularly within

Table 8. Summary of significant relations between breeding performance in kittiwakes and murrees and oceanographic and meteorologic conditions across the shelf of the southeastern Bering Sea, 1970-1984 (see Appendix F for definition of abbreviations).^a

Hypothesis	Parameter	Kittiwakes	Murrees
Constancy	Reproductive success	VAR(BLKI/StG) > VAR(BLKI/CP)	VAR(COMU/StG) > VAR(COMU/CP) ^b
		VAR(BLKI/StG) = VAR(RLKI/StG)	VAR(COMU/StG) = VAR(TBMU/StG)
	Productivity	Same as reproductive success	na
	Mean date of hatching	VAR(BLKI/StG) < VAR(RLKI/StG)	VAR(COMU/StG) < VAR(TBMU/StG) ^b
Sea surface temperature	Reproductive success	BLKI/StG ↑ : SST-MG ↓ ^c	-
		RLKI/StG ↑ : SST-JL ↓ ^c	-
		-	COMU/CP ↑ : SST-JL ↑
	Productivity	BLKI/StG ↑ : SST-MG ↓ ^c	na
		BLKI/StG ↑ : SST-SG ↓ ^c	na
		RLKI/StG ↑ : SST-JL ↓ ^c	na
	Mean date of hatching	-	COMU/StG ↑ : SST-JL ↓
-		TBMU/StG ↑ : SST-JL ↓	
Weather	Reproductive success	BLKI/StG ↑ : WIND-25 ↓	COMU/StG ↑ : WIND-30 ↓
		BLKI/StG ↑ : PREC-.3 ↓	COMU/StG ↑ : PREC-.01 ↑
		BLKI/StG ↑ : HDD-MY ↑ ^c	-
		RLKI/StG ↑ : WIND-20 ↓	-
		RLKI/StG ↑ : PREC-.3 ↓	-
		RLKI/StG ↑ : PREC-T ↓	-
		BLKI/CP ↑ : WIND-25 ↑ ^c	COMU/CP ↑ : WIND-10 ↑
	Productivity	BLKI/StG ↑ : WIND-25 ↓	na
		BLKI/StG ↑ : HDD-MY ↑	na
		RLKI/StG ↑ : WIND-20 ↓	na
		RLKI/StG ↑ : PREC-.05 ↓	na
		RLKI/StG ↑ : PREC-.3 ↓	na
		RLKI/StG ↑ : PREC-T ↓	na
Mean date of hatching	BLKI/CP ↑ : WIND-25 ↑	na	
	BLKI/CP ↑ : WIND-20 ↓ ^c	na	
	Mean date of hatching	-	-

(Table 8 continued next page)

Table 8. (continued).

Hypothesis	Parameter	Kittiwakes	Murres
Intra-annual timing	-	-	-
Temporal trends	Reproductive success	BLKI/StG ↓ : YEAR ↑	COMU/StG ↓ : YEAR ↑ ^b
		RLKI/StG ↓ : YEAR ↑	TBMU/StG ↓ : YEAR ↑ ^d
	Productivity	Same as reproductive success	na
	Mean date of hatching	-	COMU/StG ↓ : YEAR ↑
		-	TBMU/StG ↓ : YEAR ↑

^a Arrow symbols indicate correlations: $x \downarrow : y \downarrow$ means negative correlation; $x \uparrow : y \uparrow$ means positive correlation.

^b $p < 0.10$.

^c Significant correlations found for selected, but not entire, data sets.

^d Trend suggested if suspected overestimate for 1984 is excluded.

family groups. Following Pianka (1974), K-selected species are expected to inhabit areas with less environmental variability and more predictable ecosystem functions. An intuitive extension of these distinctions is the application to congeneric species or even to populations within the same species that inhabit both offshore and nearshore colonies. Recent work on kittiwakes and murre in the southeastern Bering Sea supplies a test for these ideas within genera and species.

Hunt et al. (1981b) compared kittiwakes at the Pribilof Islands with those at coastal colonies at Bluff in Norton Sound and Cape Thompson in the Chukchi Sea. They concluded that the annual productivity of Pribilof Island kittiwakes, observed between 1975 and 1978, was less variable than was that of black-legged kittiwakes at the coastal colonies during a similar time period. The reasonable explanation was that Pribilof Island kittiwakes had access to a more consistent offshore pelagic food web (Iverson et al. 1979; Hunt et al. 1981b,c) while oceanographic processes near coastal colonies exhibited higher variability, causing fluctuations in the abundance or availability of prey species, and therefore caused more dramatic fluctuations in annual breeding performance (Springer et al. 1984, 1985).

Although promoted primarily as a comparison of oceanic versus coastal colonies, these conclusions more reasonably result from comparison of subarctic versus arctic colonies. Breeding seabirds and prey species at the Pribilof Islands and Cape Peirce are rarely, if ever, directly constrained by seasonal sea ice (Webster 1981) while the

feeding and breeding ecology of marine birds at Bluff and Cape Thompson, as well as Cape Lisburne, appear dominated by the timing of sea ice retreat and consequent effects on the movement, availability, and abundance of forage fishes, particularly sandlance (Springer et al. 1984, 1985).

Analysis of a larger number of years of breeding performance in kittiwakes and murrelets at St. George Island between 1976 and 1984 reveals much greater variability than described in previous accounts (Hunt et al. 1981a,b). Furthermore, comparison to a coastal colony, Cape Peirce, at the same latitude and subject to presumably more similar environmental conditions reveals that greater stability of breeding performance cannot be presumed simply because a colony is more oceanic. In fact, data presented here suggest that Cape Peirce actually exhibits greater constancy, albeit at lower levels, in the breeding performance of kittiwakes, as well as murrelets, than does St. George Island.

The congeneric kittiwake species exhibit a basic difference in clutch size, one of the particular characteristics used by Lack (1967, 1968) to distinguish between offshore and nearshore species and by Pianka (1974) to distinguish between K-selected and r-selected species. Red-legged kittiwakes, endemic to a small number of oceanic islands in the North Pacific Ocean, have been reported to periodically lay two-egg clutches on the Pribilof Islands (Kenyon and Phillips 1965) but have been observed to lay only single-egg clutches in the Commander Islands (Firsova 1978) and on the Pribilof Islands since 1975 (Hunt et al. 1981b). On the other hand, the more ubiquitous black-legged kittiwakes lay two-egg, and sometimes three-egg, clutches on the Pribilof and

Commander Islands (Kenyon and Phillips 1965, Firsova 1978, Hunt et al. 1981b) and even four-egg clutches in northern Europe (Belopolskii 1957). Although Firsova (1978) reported higher reproductive success of black-legged kittiwakes than red-legged kittiwakes in the Commander Islands, differences in clutch size have not apparently worked to the advantage of either black-legged or red-legged kittiwakes on the Pribilof Islands. Both species at the Pribilof Islands exhibited similar annual productivity during 1975-1978 (Hunt et al. 1981b) as well as similar variability and overall decline in production at St. George between 1976 and 1984. One cannot presume greater stability of breeding performance in the more oceanic red-legged kittiwake than in its cosmopolitan congener, at least on St. George Island.

Similar conclusions are derived for the congeneric species of murre, although both have a uniform clutch size of one, in the southeastern Bering Sea. Thick-billed murre proved no less variable than common murre on St. George Island, and common murre at coastal Cape Peirce proved perhaps even more stable, albeit lower overall, in annual reproductive success than common murre at St. George.

It appears that the proximity of St. George Island to oceanic and outer shelf pelagic food webs has not conferred greater stability, nor consistently greater performance, to the annual reproduction of kittiwakes and murre over that exhibited at Cape Peirce within the coastal domain. Either the birds at St. George, as apex consumers, are not capable of uniformly exploiting predictable supplies of food, or some mechanism is operating to vary the annual availability of food, or the pelagic food webs of the outer Bering Sea shelf are not as

consistently productive as expected. Coastal food webs, however, appear to support piscivorous seabirds at consistent but low levels of annual reproduction, implying that availability of forage fishes may be low but also fairly consistent.

Hypothesis 2 - Relation to Sea Surface Temperature

Work at Bluff, Cape Thompson and other northern colonies in Alaska (Drury et al. 1981; Springer et al. 1984, 1985) has illustrated the extreme importance of timing of the retreat of seasonal sea ice and resulting summer-time sea surface temperatures on the feeding and breeding success of kittiwakes and murre. Springer et al. (1985) concluded that annual variation in the breeding performance of kittiwakes and murre is a function of prey availability and is predictable from conditions in the physical environment, particularly sea surface temperature and heating degree days. Progressively earlier retreat of seasonal sea ice between 1976 and 1980 resulted in progressively higher July sea surface temperature, was reflected in lower heating degree days measured at Nome, allowed earlier mean dates of hatching, and likely facilitated higher levels of successful reproduction in both black-legged kittiwakes and murre. The higher reproductive performance in these birds was attributed to better foraging conditions due to increased abundance or availability of forage fishes, especially sandlance, with warmer sea surface temperatures earlier in the breeding season. Belopolskii (1957) reported similar trends between earlier, warmer water temperatures, increased prey availability, earlier kittiwake breeding phenology, and higher kittiwake production over several years in the Barents Sea. Although sea surface

temperatures were not reported, Nettleship et al. (1979) and Birkhead and Nettleship (1981) attributed delays in breeding phenology and lower reproductive success in thick-billed murre and black-legged kittiwakes to severe seasonal ice conditions in Lancaster Sound, Northwest Territories, in 1978 and 1979.

At less physically (sea ice) dominated colonies on St. George Island and Cape Peirce, however, such trends have not been observed. The data indicate, rather, that higher reproduction in kittiwakes and murre at St. George is more closely associated with colder sea surface temperatures, either within the same year or in one to two years prior. Without contemporaneous observations of feeding and the abundance or availability of prey it is difficult to analyze these apparent relationships, but there is information to suggest that colder temperatures may increase the availability of prey to kittiwakes and murre on the outer shelf.

Juvenile walleye pollock, ages 0 to 2, constitute a major and apparently crucial portion of the diets of both kittiwake species and both murre species breeding on St. George Island (Hunt et al. 1981 a,c; Schneider and Hunt 1984). The seasonal distribution of juvenile and adult pollock is not constant from year to year, but appears to be constrained by cold bottom water and sea surface temperatures (Francis and Bailey 1983, Bakkala and Alton 1984). Since June bottom water temperatures and annual sea surface temperatures are correlated and are both related to air temperatures of the previous winter and spring (Coachman and Charnell 1979, Niebauer 1980) general annual variations in

water temperature and their effects on pollock in the southeastern Bering Sea can be discussed.

Spawning adult pollock from the continental slope apparently do not penetrate continental shelf waters colder than approximately 1 to 2° C, therefore spawning is more limited in colder years to outer shelf waters rather than more dispersed farther inward across the shelf as in warmer years (Nishiyama 1982, Chen 1983, Bakkala and Alton 1984). Aggregation of spawning pollock would likely limit the dispersal of eggs, and therefore of age 0 fish, to waters more immediately adjacent to the shelf break during colder years. Juvenile pollock of ages 1 and 2 are also constrained, but to a lesser degree, by cold water temperatures (Chen 1983) and tend to be concentrated in outer shelf waters during colder years (Bakkala and Alton 1984). Concentrations of age 0 to 2 year old pollock closer to the shelf break may arguably act to increase the availability of these important prey to piscivorous seabirds foraging from colonies on the Pribilof Islands, thereby accounting for higher reproductive performance in colder years (see also Schneider et al., in press). Unfortunately, this scenario does not agree with characterization of 1979 as a warm year with relatively wide dispersal of pollock (Nishiyama 1982, Bakkala and Alton 1984), since productivity of black-legged kittiwakes at St. George was relatively high (see Figure 6). This anomaly might be explained, however, by the extremely high abundance of age 1 pollock in 1979 relative to earlier and later years (Bakkala et al. 1984; also see Figure 12). Whether or not temperature constraints affect the dispersal or availability of other important seabird prey, such as myctophids, is unknown.

Explanation of correlations between higher reproduction in seabirds and colder sea surface temperatures of prior years requires even more imaginative speculation, but may suggest benefits of greater year class strength of pollock or other fish spawned in those previous years. Unfortunately, the dynamics of juvenile pollock, particularly before recruitment to the commercial fishery, are poorly known (Francis and Bailey 1983) and the dynamics of myctophids and other seabird prey in the outer southeastern Bering Sea are virtually unknown.

Observed relationships between breeding performance in black-legged kittiwakes and common murres and sea surface temperature at Cape Peirce are not strong or particularly informative. Reproductive success, but not productivity, of black-legged kittiwakes correlated positively with sea surface temperatures two years prior. Reproductive success of common murres showed no significant correlations, but may have shown positive trends, with contemporaneous sea surface temperatures. Data on the abundance or availability of sandlance and capelin are not available, and factors affecting the relative abundance of herring are not known (Wespestad and Barton 1981, Wespestad and Fried 1983). Although temperature probably plays a role in the migration, reproduction and survival of these nearshore fishes, it is difficult to speculate on mechanisms acting through sea surface temperature to affect the breeding performance of kittiwakes and murres at Cape Peirce.

Hypothesis 3 - Relation to Weather

Severe weather conditions have been implicated in high mortality and reproductive failure for both kittiwakes and murres (Tuck 1961, Bailey and Davenport 1972, Threlfall et al. 1974, Byrd and Tobish 1978,

Bourne 1984). Particularly high winds and sea state apparently affect attendance of common murrelets during incubation and the rate at which common murrelets feed their chicks in Britain (Birkhead 1976, 1978).

Hunt et al. (1981b) suggested that weather directly affects the foraging efficiency of kittiwakes. Hunt et al. (1981a) described a decrease in black-legged and red-legged kittiwake productivity, particularly in hatching success, between 1976-77 and 1978 associated with an increase in the proportion of days during parts of the breeding season with high winds, however no effect was detected for increased precipitation.

Analysis of a longer series of data (1976-1984) from St. George Island reveals very strong negative correlations between indices of wind speed and the productivity and reproductive success of black-legged and red-legged kittiwakes and, to a lesser extent, the reproductive success of common murrelets. Average wind speeds recorded at St. Paul for May to September over an 18 year period range between 13 and 16 miles per hour (Brower et al. 1977). Indices for daily maximum wind speeds equal to or exceeding 20 and 25 miles per hour correlated most closely with lower productivity in red-legged and black-legged kittiwakes, respectively. Indices for 30 and 35 miles per hour correlated with lower reproductive success in common murrelets, but no significant correlation was found for thick-billed murrelets.

Given that red-legged kittiwakes are somewhat smaller than black-legged kittiwakes and generally forage at greater distances from the breeding colonies (Hunt et al. 1981a) wind speed reasonably has a greater effect on their foraging efficiency and ability to raise chicks.

Since murrelets are considered stronger fliers than kittiwakes and their diving for food is likely less affected by wind and sea state than is the surface feeding habit of kittiwakes, it is reasonable to expect a smaller impact of wind speed on the breeding performance of murrelets. Wind speed, via wind mixing of the water column, could also have direct trophic implications through prey abundance and availability (Sambrotto and Goering 1983) but adequate time series of data are not available to define detailed mechanisms leading to variation in feeding and breeding of seabirds. In contrast to St. George Island, correlations between wind speed indices and breeding performance of black-legged kittiwakes and common murrelets at Cape Peirce are inconsistent and inconclusive.

Indices for precipitation correlated strongly with reduced productivity in red-legged kittiwakes, but not in black-legged kittiwakes, on St. George Island. Interestingly, a single significant correlation between precipitation and reproductive success in common murrelets was positive, but none was found for thick-billed murrelets. Conclusions are difficult to draw, but intuitively it seems reasonable to expect high levels of precipitation to affect thermoregulatory control in chicks (e.g., Johnson and West 1975, Barrett 1978) and perhaps in severe cases induce hypothermia. The data from St. George suggest, however, that only red-legged kittiwakes may have been affected by precipitation. Again, in contrast to St. George, correlations with precipitation at Cape Peirce were inconsistent and inconclusive.

Correlations between breeding performance in kittiwakes and murrelets at St. George and heating degree days were also weak. However, selected data sets for productivity and reproductive success in black-legged

kittiwakes suggest that breeding performance may be improved in years of higher heating degree days (i.e., lower air temperatures) in May. This corresponds to suggestions, discussed earlier, that breeding performance may be better during years with colder sea surface temperatures, which are related to cooling of the water column during the previous winter and spring.

Hypothesis 4 - Relation to Intra-Annual Timing

Although it is presumed that the breeding season of birds coincides with the time of year that food is likely to be most available for the successful rearing of young, Perrins (1970) argued that in environments with limited dates of high food availability birds that breed earlier will produce more young. Constraint on the initiation of breeding in birds in such environments would be food availability sufficient to allow egg development by females. Temperate and arctic seabirds live in such environments, where oceanographic and atmospheric conditions limit the production, abundance, or availability of suitable prey.

Earlier dates of egg laying and hatching, by even just a few days, have resulted in larger clutch size and reproductive success in black-legged kittiwakes and thick-billed murre, respectively, in Britain and Canada (Coulson and White 1961, Birkhead and Nettleship 1981). Earlier mean date of hatching has also been related to increased growth rate of common murre chicks in the Baltic Sea (Hedgren and Linnman 1979).

Studies in northern Alaska (Springer et al. 1985) have illustrated similar relationships between earlier mean dates of hatching and greater reproductive performance of black-legged kittiwakes and murre

associated with earlier and greater availability of prey. Data collected by Hunt et al. (1981a) on St. George Island between 1976 and 1978 (see Figures 6-9) also suggest that, at least for red-legged kittiwakes and thick-billed murre, earlier mean date of hatching coincided with better breeding performance.

Analysis of longer-term trends on St. George Island between 1976 and 1981, however, shows a lack of consistent correspondence between earlier mean dates of hatching and breeding performance for either of the kittiwakes or murre. Analysis of the two years of data available from Cape Peirce also indicates no apparent advantage of earlier mean date of hatching; in fact, breeding performance of both black-legged kittiwakes and common murre at Cape Peirce was poorer in 1981, with earlier dates of hatching, than in 1976.

Hypothesis 5 - Temporal Trends

Many studies have been published on the breeding success of kittiwakes and murre; however, few have defined trends at specific colonies over a series of years. One such study in Norway (Barrett and Schei 1977) attributed poor breeding success and high variability in colonies of black-legged kittiwakes to an inherently greater instability of small colonies over large ones. This explanation cannot account for low production and the variability observed on St. George Island, however, because it is one of the largest colonies of kittiwakes and murre in the world.

Barrett and Runde (1980) concluded that food shortage accounted for low reproduction in black-legged kittiwakes at a large colony in Norway. Belopol'skii (1957) noted reduced breeding success in black-legged

kittiwakes during years when numbers of murres at the same colony increased and, presumably, competed effectively with kittiwakes for available food. Hunt et al. (1981a, 1982) suggested that competition among kittiwakes and murres resulted in reduced chick growth rates on St. George Island compared with the smaller colonies on St. Paul Island. Hunt et al. (1982) also identified relationships of lower reproductive performance with increased colony size and attributed the cause to competition for prey and, perhaps more specifically, to prey depletion.

At colonies in northern Alaska, Springer et al. (1985) attributed an increasing trend in reproductive performance of black-legged kittiwakes and at least common murres between 1976 and 1979-81 to a general warming trend and increased availability of food. A similar, or the same, generalized warming trend between 1976 and 1979, with temperatures remaining relatively warm through 1982, was described by Niebauer (1980, 1983) for the eastern Bering Sea and influenced waters near the Pribilof Islands. As discussed under Hypothesis 2, however, kittiwakes and murres on St. George Island appear to exhibit reduced, rather than improved, breeding success with warmer temperatures. This is supported by the general decline in productivity in both species of kittiwakes and both species of murres at St. George from 1976 to at least 1982 coincident with general warming of surface waters.

It appears that specific year-to-year fluctuations in availability of prey constrained by cold water temperatures on the shelf may partially contribute to reduced breeding success of piscivorous seabirds in warm years, as noted under Hypothesis 2, but it does not account for the relatively high productivity in kittiwakes during the warm year of

1979. There is apparently some other factor, such as overall prey abundance, acting to consistently depress reproductive performance in recent years.

Bakkala et al. (1984) described a rapid decline in pollock abundance between the early and mid 1970's, relative stability at low levels through 1980, then again further reduced abundance in 1981 and particularly in 1982. Estimated abundance of age 1 pollock, a predominant size class used by piscivorous seabirds at the Pribilof Islands, shows a general decline between 1975 and 1984. The only exception was a dramatic peak in abundance during 1979 (Figure 12), as a result of an especially strong year class spawned in 1978 (Bakkala et al. 1984). The particularly strong recruitment of age 1 pollock in 1979 may partially explain the relative peak of productivity estimated for black-legged kittiwakes in 1979 during a warm year, amid a general decline in productivity between 1976 and 1984.

The dynamics of pollock abundance, particularly in younger age classes, likely have a controlling influence on breeding performance in piscivorous seabirds on the Pribilof Islands. In addition, breeding performance may be accentuated by constraints of temperature on the annual dispersal of these prey as well as by competition among the different bird species.

A breakdown in relationships characterizing breeding performance of kittiwakes and murrelets as stable at St. George occurred after the conclusion of studies by Hunt et al. (1981a). This breakdown may be related to the reduced abundance of juvenile pollock observed in recent years. Limited food habits studies conducted on birds at St. George in

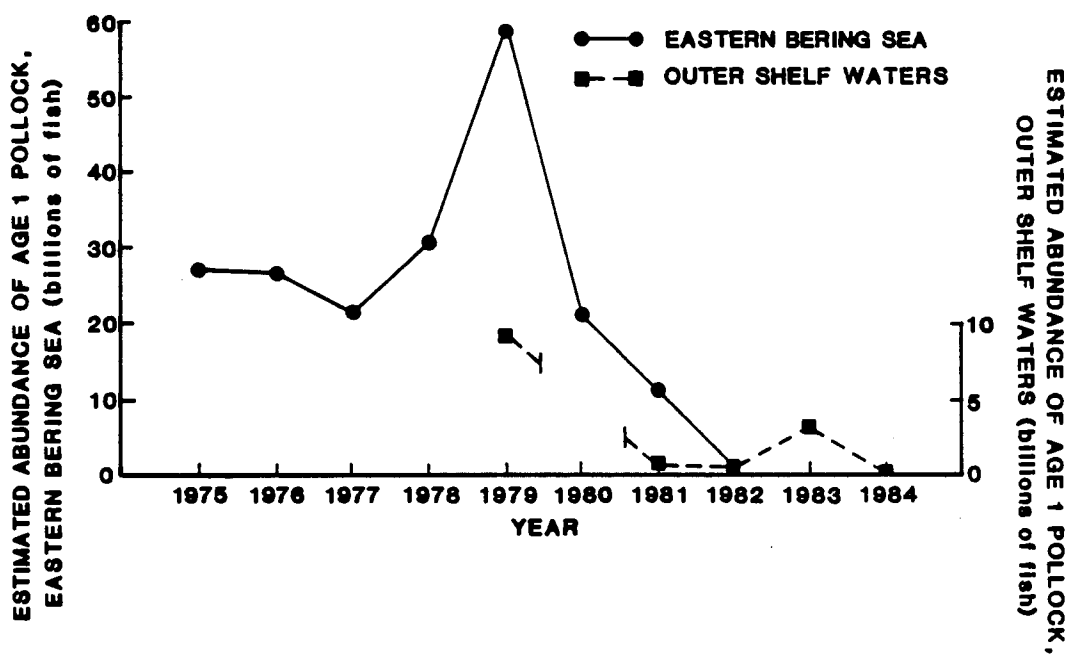


Figure 12. Estimated abundance of age 1 walleye pollock in the eastern Bering Sea (data from Bakkala et al. 1984).

1980 and 1981 (Table E1) support this contention, by the noticeable lack of pollock in many of the samples. Pollock reappeared in kittiwake and murre food samples obtained on St. George Island in 1984 (Bradstreet 1985), but no distinction was reported between pollock and other gadid fishes in discussion of diet composition. Lower chick growth rates measured in 1980 and 1981 (Appendix C) also suggest that prey abundance has decreased since 1976. It would be difficult to attribute consistent breeding failures during the early 1980's to normal short-term variation in oceanographic, meteorologic, or trophic processes. Variability and decline of breeding performance at this oceanic colony may illustrate the intrusion of commercial fishing into the trophodynamics of the Bering Sea, rather than more natural variability. A general decline of, and annual fluctuations in, the abundance of pollock has been implicated in the reduction in numbers of murrees that breed at more northern colonies but presumably overwinter in the southern Bering Sea (Springer et al. 1985) and also in multispecies interactions throughout pelagic food webs in the eastern Bering Sea (see Springer et al., in preparation).

Black-legged kittiwakes and common murrees at Cape Peirce exhibited relatively consistent but low breeding success during years studied between 1970 and 1984. Almost no information is available on the nearshore prey species in the area, and no upward or downward trend in seabird production was noted.

General

The declining trends, and associated variability, in breeding performance of kittiwakes and murrees on St. George Island indicate that

pelagic food webs along and adjacent to the continental shelf break of the southeastern Bering Sea cannot be ascribed general stability or constancy. Even within the years of preliminary investigation (1976-1978) kittiwakes and murre exhibited variability and their breeding success could be considered stable only in comparison to even more variable colonies such as those at Bluff and Cape Thompson. Although breeding success was inversely related to indices of wind speed at St. George, recent abysmal production of kittiwakes and lower production of murre suggests a cause other than the direct influence of meteorological events on the birds. I submit that, along the continental shelf break and surrounding the Pribilof Islands, oceanographic processes that influence the oceanic and outer shelf domains near the seabird colonies there cause more variability in transfer within pelagic food webs than has been previously considered (see also Walsh and McRoy, in press). Also, commercial exploitation of walleye pollock may have contributed to an overall decline in kittiwake and murre breeding success during the past decade.

Large scale meteorologic processes related to the North Pacific Oscillation, the relative position of the Aleutian Low, and the frequency and path of storm tracks through the Bering Sea act not only to determine the annual extent of seasonal sea ice cover (Niebauer 1980, 1983; Overland and Pease 1982) but also the intrusion of water from the Gulf of Alaska through several passes in the Aleutian Islands and movement of this water along the Bering Slope Current (Kinder et al. 1975, Schumacher et al. 1982, Schumacher and Reed 1983, Paluszkiwicz and Niebauer 1984). Lateral extension of the Bering Slope Current onto

the continental shelf and creation of eddies along the shelf break, dependent upon long and short-term variations in atmospheric forcing functions and transport of Alaskan Stream or Kenai Current water, impart physical variability to the oceanic and outer shelf domains in the southeastern Bering Sea (Schumacher and Reed 1983). This variability has been detected through changes in sea surface temperature, specifically that warmer temperatures reflect increased transport of southern Gulf of Alaska water along and perhaps onto the Bering Sea shelf (Paluszkiwicz and Niebauer 1984). The influence of variability in this transport has already been discussed in relation to migratory movements of sockeye salmon (Oncorhynchus nerka) by Fujii (1975) and to annual changes in a measure of biomass diversity for demersal fishes (Kihara 1977), and likely affects the distribution and perhaps abundance of walleye pollock (Francis and Bailey 1983). It is possible that this variability may also affect other trophic relationships and the annual or seasonal distribution and availability of vertically-migrating myctophids.

Annual differences in short-term wind mixing events also add to the physical variability of the oceanic and outer shelf domains. Production of both phytoplankton and zooplankton has been shown to differ between years in the outer shelf, and Sambrotto and Goering (1983) attribute much of this variation to frequency of storms and wind mixing, although specific effects on different portions of the food web are not well elucidated. They noted, however, that frequent storms, as in May and June of 1980, likely promote relatively high primary production and energy transfer to large water-column grazers, while the absence of such

storms, as in 1981, promotes the development of subsurface chlorophyll a maxima and production of small grazing copepods (e.g., Pseudocalanus spp.) which likely affects survival of larval walleye pollock. Possible effects of wind mixing on the survival of juvenile pollock have also been described by Nishiyama et al. (1982) in their identification of a pollock "nursery layer" and by Francis and Bailey (1983) in speculation that persistent stratification of the water column may provide refuge for juvenile pollock from cannibalistic adults.

In addition to temporal variability on the outer shelf caused by wind and current patterns, there is also some identifiable spatial variability in hydrographic structure not accounted for in the general scenario presented in earlier publications (e.g., Iverson et al. 1979, Cooney and Coyle 1982). Besides possible lateral extension of the Bering Slope Current onto the outer shelf and creation of eddies discussed earlier, there are also persistent "inner" fronts immediately surrounding the Pribilof Islands along the local 50 meter isobath (Schumacher et al. 1979). These local fronts separate well-mixed waters adjacent to the islands from deeper, typically stratified waters offshore. The Pribilof Islands and associated inner fronts are spatially heterogeneous compared to the broad domain structure evident across the remainder of the continental shelf, and this heterogeneity influences the distribution of feeding seabirds, particularly murre, presumably through trophic interactions (Kinder et al. 1983).

Seemingly predictable and consistent events in the oceanic and outer shelf domains, such as the regular ontogenetic migrations of large copepods and the on-shelf migrations of spawning pollock, are apparently

subject to a fair amount of spatial and temporal variability along the shelf edge near the Pribilof Islands. Variability in physical processes apparently translates to variable production and energy transfer within the pelagic food web. Therefore, kittiwakes and murrelets on St. George Island may well be subject to quite variable, rather than the presumed stable or constant, food availability which may affect their breeding performance. Contributory effects of the observed decline in juvenile pollock abundance may have overshadowed more regular oscillations in annual energy transfer to breeding kittiwakes and murrelets, resulting in the general decline of breeding success since 1976.

Possible spatial and temporal variability in the coastal domain near Cape Peirce has not been nearly so well identified. Net advection of water in the coastal domain is very low, but the interaction of tidal and wind mixing tends to keep the water column homogeneous, at least during ice-free periods (Schumacher et al. 1979). Persistent mixing of the water column was thought to constitute physical variability in the coastal domain, but may, rather, provide a consistently homogeneous and therefore more predictable environment than the outer shelf.

In contrast to coastal waters farther north near the seabird colonies at Bluff and Cape Thompson, seasonal sea ice generally leaves Bristol Bay prior to the breeding season of seabirds at Cape Peirce and therefore may not have such a direct influence on trophic relations and breeding success. Other distinctions between coastal waters farther north and the coastal domain near Cape Peirce include the origin of the Alaskan Coastal Current near Norton Sound (Ahlnas and Garrison 1984), the presence of a coastal jet in the Chukchi Sea (Wiseman and Rouse

1980), and the existence of apparent fronts offshore of the seabird colonies at Cape Thompson and Cape Lisburne (Springer et al. 1984). Annual variability in the strengths of these northern coastal currents and location of local fronts apparently affect annual feeding and breeding success of seabirds at the northern coastal colonies (Springer et al. 1984), whereas no similar advection regime seems to affect the seabird colony at Cape Peirce.

There are some likely effects of annual variations in sea ice retreat, sea surface temperature, and wind mixing on nearshore fish populations near Cape Peirce but no data are available to describe them. It is possible that kittiwakes and murrelets at Cape Peirce experience infrequent years of exceptionally high breeding success to sustain population levels, thereby more closely resembling the more northern coastal colonies, but the six years of available data have not illustrated such a boom year. On the contrary, available information on the breeding performance of kittiwakes and murrelets corresponds to a general description of relatively low biological productivity in the coastal domain (Cooney 1981) and to the idea presented here that persistent mixing of the water column may create a predictable environment compared to the physical variability of the outer shelf.

The reversal of original ideas regarding stability of biological processes across the continental shelf, as exemplified by the breeding performance of kittiwakes and murrelets, suggests that additional work should be accomplished to identify spatial and temporal variability along the shelf break and to investigate physical and biological processes in the coastal domain. Although work conducted under OCSEAP

and PROBES provides excellent models of hydrographic structure, biological studies have emphasized the distinction between the outer shelf and middle shelf domains. Extensions of multidisciplinary studies to consider interactions between the oceanic and outer shelf domains along the continental slope and shelf break, and to describe physical and biological processes in the coastal domain, are required to complete a characterization of the cross-shelf environment of the southeastern Bering Sea.

In particular reference to studies of breeding seabirds, analysis of data available for nine years at St. George and for six years at Cape Peirce point to several deficiencies and needs for further study. First, almost all of the work conducted on the breeding performance of seabirds in the southeastern Bering Sea has produced relative measures of success (i.e., number of chicks fledged per nest attempt) but no absolute estimates of success (i.e., total number of chicks fledged); there is no way using the available data to assess whether or how total number of breeding attempts varied between years. Although no comparative censuses have been conducted for seabirds breeding at Cape Peirce, there is some indication from three censuses conducted on the Pribilof Islands (Hickey and Craighead 1977, Craighead and Oppenheim 1985, Troy 1985) that numbers of breeding kittiwakes and at least thick-billed murrelets have declined on St. George Island between 1976 and 1984. Combining estimates of reduced relative breeding success with a decline in total number of adults even attempting to breed indicates an even more drastic decrease in the production of seabirds at St. George than is described by breeding performance alone. To more accurately

describe such variations, however, would require the establishment of consistent study plots on the breeding colonies, which would be monitored for total number of adults or nesting attempts as well as for relative breeding success.

Second, in order to have confidence in measures of inter-annual variability in breeding performance, investigators should have concurrent information on intra-annual, between-plot variability. Although both Hunt et al. (1981a) and Johnson and Baker (1985) report little or no significant intra-annual, between-plot variability, their analyses may have been constrained by small sample sizes within individual study plots. Future investigators should consider larger sample sizes and estimates of intra-annual variability in breeding success, as well as total number of nest attempts, so that inter-annual variations can be analyzed more rigorously.

Third, in order to relate the breeding performance and population status of seabirds to environmental conditions, studies should be conducted over most of the breeding season to determine within-season effects, and over series of consecutive years to determine between-season effects. Although six separate years of available data indicate that the breeding performance of kittiwakes and murrelets at Cape Peirce is uniformly low, it is not reasonable to exclude the possibility that an occasional "boom year" in breeding success occurs, which would alter the preceding comparison of constancy between oceanic and coastal colonies. Given that the observed consistently low breeding success of kittiwakes and murrelets at Cape Peirce may not be sufficient to maintain population levels, it seems likely that there are years, as yet

undetected, of higher breeding success. Only by monitoring seabird colonies in consecutive years over a suitably long period of time will such questions be answered. Similarly, without monitoring the breeding performance of these birds over most of each individual breeding season, there is no way to determine if failure occurs due to few nesting attempts, few eggs laid, poor hatching success, high mortality of chicks, or some combination thereof.

Finally, studies on the feeding and growth of chicks should accompany monitoring of breeding performance if any connections are to be made between the success of breeding birds and the environmental conditions likely responsible for any variations. Although general information available for kittiwakes and murrelets at St. George suggests that reductions in chick growth rates and reductions in the use of walleye pollock have accompanied observed declines in breeding success, such connections to environmental conditions remain tenuous without consistently detailed information. Lack of any data on chick growth and feeding comparable to that obtained at Cape Peirce in 1981 has precluded even informed speculation on possible environmental forcing functions in the coastal domain.

Consideration of analyses conducted in this study and the arguments just described suggests that schedules recently proposed (Minerals Management Service 1985) for monitoring of seabird colonies in the Alaska outer continental shelf region are insufficient. Disregarding funding constraints, it appears that too little information will be obtained from periodic (every 3-4 years) intensive studies, even if supplemented by alternate (every 3-4 years) reconnaissance level

studies, to rigorously describe linkages between environmental conditions and the status of breeding seabird populations. It will be even more difficult to distinguish between natural fluctuations and those potentially induced by human activity such as oil and gas exploration and development or commercial fishing. Furthermore, without contemporaneous multidisciplinary studies, focusing particularly on trophic interactions, results of such monitoring studies may simply become descriptions of breeding performance in seabirds with little heuristic value.

SUMMARY

Five general hypotheses concerning breeding performance of piscivorous seabirds in the southeastern Bering Sea were tested using information available for the years 1970 to 1984. Null hypotheses regarding constancy of breeding performance between oceanic and coastal colonies were generally rejected, but to the opposite conclusion of what was expected. Breeding performance of kittiwakes and murrelets on St. George Island appears to be more variable than that for kittiwakes and murrelets at Cape Peirce. Null hypotheses distinguishing constancy of breeding performance between "more oceanic" and "more coastal" species at St. George were not rejected. Red-legged kittiwakes and thick-billed murrelets appear to be no more stable than black-legged kittiwakes and common murrelets, respectively, on the same island.

Null hypotheses regarding relation of breeding performance to sea surface temperature were partially rejected for kittiwakes on St. George Island. The data suggest that kittiwakes may experience improved productivity during or after colder, rather than warmer, years. This observation may be partially explained by the apparent concentration of juvenile pollock near the shelf break, thus increasing availability of prey, during colder years. Data for birds at Cape Peirce generally failed to reject null hypotheses, indicating no correlation between reproduction of kittiwakes and murrelets and sea surface temperature.

Null hypotheses concerning the relationships between breeding performance and wind speed were strongly rejected for both species of kittiwakes, and less strongly for common murrelets, on St. George Island.

High winds apparently can disrupt the foraging efficiency of the kittiwakes, particularly red-legged kittiwakes, and may similarly affect at least the common murre. Data for kittiwakes and murre at Cape Peirce also rejected null hypotheses concerning wind speed but, paradoxically, breeding performance appears generally greater during years of higher winds. Information has not been found to explain a direct benefit of high winds to the breeding performance of kittiwakes and murre at Cape Peirce.

Null hypotheses concerning the relationships between breeding success and precipitation were generally rejected for red-legged kittiwakes but not for black-legged kittiwakes or murre on St. George Island. Increased precipitation may have a selective effect on foraging efficiency or chick survival of red-legged kittiwakes but no mechanism has been defined that would apply exclusively to this species. Data for black-legged kittiwakes at Cape Peirce also suggest a negative effect of precipitation on breeding performance, but no significant correlation was found for common murre.

Null hypotheses concerning the relationships between heating degree days and breeding performance of kittiwakes and murre at St. George generally were not rejected, except that colder air temperatures in May correlated significantly with selected data for improved productivity in black-legged kittiwakes. This latter relation supports earlier findings of relations between colder sea surface temperatures and improved breeding performance. No data were available to test hypotheses regarding the effects of heating degree days specifically at Cape Peirce.

Null hypotheses concerning the relationship between mean date of hatching breeding performance of kittiwakes and murrelets at St. George were not rejected. Although data for earlier years (1976-1978) suggest improved breeding performance coincident with earlier dates of hatching, these apparent relations were not continued in 1980 and 1981. Only two years of information on date of hatching were available for kittiwakes and murrelets at Cape Peirce, but earlier hatching did not occur during the year of better reproductive performance for either species.

Null hypotheses testing for temporal trends in the breeding performance of kittiwakes and murrelets on St. George Island were generally rejected. Both species of kittiwakes and both species of murrelets have exhibited reduced breeding success since 1976, except for a suspected overestimate of success in thick-billed murrelets in 1984. These trends are supported by reported general declines in pollock abundance, specifically in juvenile age classes. The presumed competition associated with large seabird colonies, combined with a general decline in a principal prey species, likely have caused the dramatic and relatively long-term (4-5 year) breeding failure of kittiwakes and murrelets at St. George.

No temporal trend was observed for breeding success in either black-legged kittiwakes or common murrelets at Cape Peirce. Rather, both species have exhibited relatively constant, although consistently low, breeding success during the six years observed between 1970 and 1984.

APPENDIX A

Field Studies, St. George Island 1981

Table A1. Results of field studies on black-legged kittiwakes at St. George Island, July 6 - September 13, 1981.

Parameter	Subcolony									St. George Island Overall
	High Bluffs	Rosy Finch Cove A	Rosy Finch Cove B	Tolstoi 1	Tolstoi 2	Tolstoi 3	Tolstoi 4	Tolstoi Growth Plot	Staraya Growth Plot	
Nest attempts (sample size)	3	23	11	20	11	22	12			102
Nests w/eggs ^a	2	12	7	14	9	7	8			59
Eggs laid ^a	2	18	8	23	11	10	9			81
Eggs hatched ^b	2	9-15	0-3	10-18	4-10	6-10	0-4			31-62
Mean date hatching (n, ± S.D.)	7-26 (1,±0)	7-23 (8,±2.6)	-	7-22 (9,±3.8)	7-29 (3,±0)	7-21 (5,±3.0)	-	7-22 (11,±3.9)	7-18 (6,±3.1)	7-22 (43,±4.0)
Chick growth rate ^c (n, ± S.D.)	-	-	-	-	-	-	-	13.62 (1,±0)	7.04 (1,±0)	10.33 (2,±4.6)
Chicks fledged	0	1	0	6	0	0	0			7
Clutch size ^d	1.00	1.50	1.14	1.64	1.22	1.43	1.13			1.37
Hatching success ^e	1.00	0.50-0.83	0-0.38	0.43-0.78	0.36-0.91	0.60-1.00	0-0.44			0.38-0.77
Fledging success ^f	0	0.07-0.11	0	0.33-0.60	0	0	0			0.11-0.23
Reproductive success ^g	0	0.08	0	0.43	0	0	0			0.12
Productivity ^h	0	0.04	0	0.30	0	0	0			0.07

^a Observations began well after initiation of egg laying, therefore nests w/eggs and eggs laid may be underestimated.

^b Eggs hatched stated as a range due to uncertainty that observation of an egg on one visit but not on the next visit indicated loss of an unhatched egg or hatched chick.

^c Growth rate = grams per day.

^d Clutch size = number eggs per nests w/eggs.

^e Hatching success = eggs hatched per eggs laid, reported as range due to range of eggs hatched.

^f Fledging success = chicks fledged per eggs hatched, reported as range due to range of eggs hatched.

^g Reproductive success = chicks fledged per nests w/eggs.

^h Productivity = chicks fledged per nest attempt.

Table A2. Results of field studies on red-legged kittiwakes at St. George Island, July 6 - September 13, 1981.

Parameter	Subcolony					St. George Island Overall
	High Bluffs 1	High Bluffs 2	High Bluffs 3	Rosy Finch Cove A&B	Tolstoi 4	
Nest attempts (sample size)	15	45	13	4	2	79
Nests w/eggs ^a	7	19	4	1	0	31
Eggs laid ^a	7	19	4	1	0	31
Eggs hatched ^b	1-6	10-17	3-4	0	0	14-27
Mean date hatching (n, ± S.D.)	8-07 (1,±0)	7-20 (10,±3.0)	8-01 (3,±0)	-	-	7-24 (14,±6.8)
Chick growth rate ^c	-	-	-	-	-	-
Chicks fledged	0	7	2	0	0	9
Clutch size ^d	1	1	1	1	1	1
Hatching success ^e	0.14-0.86	0.53-0.89	0.75-1.00	0	0	0.45-0.87
Fledging success ^f	0	0.41-0.70	0.50-0.67	0	0	0.33-0.64
Reproductive success ^g	0	0.37	0.50	0	0	0.29
Productivity ^h	0	0.16	0.15	0	0	0.11

^a Observations began well after initiation of egg laying, therefore nests w/eggs and eggs laid may be underestimated.

^b Eggs hatched stated as a range due to uncertainty that observation of an egg on one visit but not on the next visit indicated loss of an unhatched egg or hatched chick.

^c No chicks survived on growth plots.

^d Clutch size assumed to be equal to one.

^e Hatching success = eggs hatched per eggs laid, reported as range due to range of eggs hatched.

^f Fledging success = chicks fledged per eggs hatched, reported as range due to range of eggs hatched.

^g Reproductive success = chicks fledged per nests w/eggs.

^h Productivity = chicks fledged per nest attempt.

Table A3. Results of field studies on common murres at St. George Island, July 6 - September 13, 1981.

Parameter	Subcolony					St. George Island Overall
	High Bluffs 4	Tolstoi 5A	Tolstoi 5B	Tolstoi 5C	Staraya Growth Plot	
Mean number adults ^a	33 ^l	24 ^l	90 ^l	15 ^l	-	162 ^{k,1}
Eggs identified ^b	13	7	22	1	21	64
Eggs hatched ^c	11-13	2-6	9-22	0-1	12-19	44-61
Mean date hatching (n, ± S.D.)	7-29 (7,±3.2)	-	7-29 (2,±0)	-	8-01 (10,±8.6)	7-30 (19,±6.5)
Chick growth rate ^d (n, ± S.D.)	-	-	-	-	4.89 (5,±2.1)	4.89 (5,±2.1)
Chicks fledged from identified eggs	7	1	5	0	6	19
Total chicks fledged ^e	10	4	10	2	6	26 ^{k,1}
Clutch size ^f	1	1	1	1	1	1
Hatching success ^g	0.85-1.00	0.29-0.86	0.41-1.00	0-1.00	0.57-0.90	0.69-0.95
Fledging success ^h	0.54-0.64	0.17-0.50	0.23-0.56	0	0.32-0.50	0.31-0.43
Reproductive success ⁱ	0.54	0.14	0.23	0	0.29	0.30
Productivity ^j	0.30 ^l	0.17 ^l	0.11 ^l	0.13 ^l	-	0.16 ^{k,1}

^a Mean number of adults observed each visit on breeding ledges surveyed for eggs and chicks, used as proxy for nest attempts.

^b Eggs observed at least once on surveyed ledges, used as proxy for nest w/eggs as well as eggs laid.

^c Eggs hatched out of eggs identified.

^d Growth rate = grams per day.

^e Total chicks fledged = those from identified eggs as well as others for which eggs had not been identified.

^f Clutch assumed to be equal to one.

^g Hatching success = eggs hatched per eggs identified.

^h Fledging success = chicks fledged (jumped) from identified eggs per eggs hatched.

ⁱ Reproductive success = chicks fledged (jumped) from identified eggs per eggs identified.

^j Productivity = total chicks fledged (jumped) per mean number adults.

^k Calculated as 26/162, excludes Staraya growth plot.

^l Values represent short-term or qualitative observations.

Table A4. Results of field studies on thick-billed murres at St. George Island, July 6 - September 13, 1981.

Parameter	Subcolony					St. George Island Overall
	High Bluffs 1	High Bluffs 2	High Bluffs 3	Rosy Finch Cove A&B	Staraya Growth Plot	
Mean number adults ^a	5 ^l	45 ^l	16 ^l	8 ^l	-	74 ^{k, l}
Eggs identified ^b	1	21	9	5	52	88
Eggs hatched ^c	0	16-19	7-8	2-4	32-46	57-77
Mean date hatching (n, ± S.D.)	-	7-21 (8, ±3.6)	7-21 (5, ±3.8)	7-24 (1, ±0)	7-29 (30, ±6.0)	7-26 (44, ±6.3)
Chick growth rate ^d (n, ± S.D.)	-	-	-	-	4.50 (8, ±2.6)	4.50 (8, ±2.6)
Chicks fledged from identified eggs	0	3	2	1	7	13
Total chicks fledged ^e	0	3	4	1	7	8 ^{k, l}
Clutch size ^f	1	1	1	1	1	1
Hatching success ^g	0	0.76-0.90	0.78-0.89	0.40-0.80	0.62-0.88	0.65-0.88
Fledging success ^h	0	0.16-0.19	0.25-0.29	0.25-0.50	0.15-0.22	0.17-0.23
Reproductive success ⁱ	0	0.14	0.22	0.20	0.13	0.15
Productivity ^j	0 ^l	0.07 ^l	0.25 ^l	0.13 ^l	-	0.11 ^{k, l}

^a Mean number of adults observed each visit on breeding ledges surveyed for eggs and chicks, used as proxy for nest attempts.

^b Eggs observed at least once on surveyed ledges, used as proxy for nest w/eggs as well as eggs laid.

^c Eggs hatched out of eggs identified.

^d Growth rate = grams per day.

^e Total chicks fledged = those from identified eggs as well as others for which eggs had not been identified.

^f Clutch assumed to be equal to one.

^g Hatching success = eggs hatched per eggs identified.

^h Fledging success = chicks fledged (jumped) from identified eggs per eggs hatched.

ⁱ Reproductive success = chicks fledged (jumped) from identified eggs per eggs identified.

^j Productivity = total chicks fledged (jumped) per mean number adults.

^k Calculated as 8/74, excludes Staraya growth plot.

^l Values represent short-term or qualitative observations.

APPENDIX B

Field Studies, Cape Peirce 1981

Table B1. Results of field studies on black-legged kittiwakes at Cape Peirce, June 14 - August 16, 1981.

Parameter	Subcolony									Cape Peirce Overall
	Little Kittiwake Arch	Small Kittiwake Colony	Big Kittiwake Arch-North	Big Kittiwake Arch-South	Shaiak Landing Beach 1	Shaiak Landing Beach 2	Shaiak Landing Beach 3	Shaiak Landing Beach 4	Shaiak Caliper Slide	
Nest attempts (sample size)	76	12	38	30	48	17	38	39	10	308
Nests w/eggs ^a	66	6	35	9	24	12	25	22	10	209
Eggs laid ^a	118	10	62	14	40	18	36	27	18	343
Eggs hatched ^b	85-110	3-8	41-57	6-10	22-39	7-10	16-25	12-27	12-18	204-304
Mean date hatching (n, ± S.D.)	6-27 (53,±4.9)	6-22 (1,±0)	6-22 (19,±2.2)	6-27 (4,±7.4)	6-26 (18,±5.4)	7-03 (6,±4.9)	6-27 (16,±3.6)	6-29 (11,±3.5)	6-25 (12,±3.5)	6-26 (139,±4.9)
Chick growth rate ^c (n, ± S.D.)	-	-	-	-	13.30 (1,±0)	10.70 (1,±0)	-	10.84 (5,±1.2)	10.10 (2,±1.0)	10.93 (9,±1.3)
Chicks fledged	32	0	6	0	2	1	0	5	2	48
Clutch size ^d	1.79	1.67	1.77	1.56	1.67	1.50	1.44	1.23	1.80	1.64
Hatching success ^e	0.72-0.93	0.30-0.80	0.66-0.92	0.43-0.71	0.55-0.98	0.39-0.56	0.44-0.69	0.44-1.00	0.67-1.00	0.59-0.89
Fledging success ^f	0.20-0.38	0	0.11-0.15	0	0.05-0.09	0.10-0.14	0	0.19-0.42	0.11-0.17	0.16-0.24
Reproductive success ^g	0.48	0	0.17	0	0.08	0.08	0	0.23	0.20	0.23
Productivity ^h	0.42	0	0.16	0	0.04	0.06	0	0.13	0.20	0.16

^a Observations began after beginning of laying, therefore nests w/eggs and eggs laid may be underestimated.

^b Eggs hatched stated as range due to uncertainty that observation of an egg on one visit but not on the next indicated loss of an unhatched egg or hatched chick.

^c Growth rate = grams per day.

^d Clutch size = number of eggs per nests w/eggs.

^e Hatching success = eggs hatched per eggs laid, reported as range due to range of eggs hatched.

^f Fledging success = chicks fledged per eggs hatched, reported as range due to range of eggs hatched.

^g Reproductive success = chicks fledged per nests w/eggs.

^h Productivity = chicks fledged per nest attempt.

Table B2. Results of field studies on common murres at Cape Peirce, June 14 - August 16, 1981.

Parameter	Subcolony		Cape Peirce Overall
	Vertebral Colony	Distant Uria Heap	
Mean number adults ^a	129	161	290
Eggs identified ^b	34	54	88
Eggs hatched ^c	13-32	26-50	39-82
Mean date hatching (n, ± S.D.)	7-13 (7, ±9.8)	7-12 (12, ±3.4)	7-12 (19, ±6.4)
Chick growth rate ^d	-	-	-
Chicks fledged from identified eggs	3	12	15
Total chicks fledged ^e	16	30	46
Clutch size ^f	1	1	1
Hatching success ^g	0.41-0.94	0.48-0.93	0.44-0.93
Fledging success ^h	0.09-0.23	0.24-0.46	0.18-0.38
Reproductive success ⁱ	0.09	0.22	0.17
Productivity ^j	0.12	0.17	0.15

^a Mean number of adults observed each visit on breeding ledges surveyed for eggs and chicks, used as proxy for nest attempts.

^b Eggs observed at least once on surveyed ledges, used as proxy for nest w/eggs as well as eggs laid.

^c Eggs hatched out of eggs identified.

^d No growth rates measured.

^e Total chicks fledged = those from identified eggs as well as others for which eggs had not been identified.

^f Clutch assumed to be equal to one.

^g Hatching success = eggs hatched per eggs identified.

^h Fledging success = chicks fledged (jumped) from identified eggs per eggs hatched.

ⁱ Reproductive success = chicks fledged (jumped) from identified eggs per eggs identified.

^j Productivity = total chicks fledged (jumped) per mean number adults.

APPENDIX C

Data Summary, St. George Island 1976-1984

Table C1. Summary of studies on black-legged kittiwakes at St. George Island, 1976-1984.

Parameter	Year								
	1976	1977	1978	1979	1980	1981	1982	1983	1984
Nest attempts (sample size)	34	110	229	146 ^l	106 ^l	102	-	-	57
Nests w/eggs	19	78	68	-	-	59	-	-	32
Clutch size ^a	1.42	1.46	1.20	-	-	1.37	-	-	1.31
Mean date hatching (n, ± S.D.)	7-28 (17,±6.1)	7-27 (63,±4.6)	8-01 (32,±5.0)	-	-	7-22 (43,±4.0)	-	-	-
Chick growth rate ^b (n, ± S.D.)	11.5 (24,±2.6)	13.8 (21,±1.8)	13.0 (16,±2.2)	-	-	10.33 (2,±4.6)	-	-	-
Hatching success ^c	0.70-0.93	0.73-0.94	0.57-0.77	-	-	0.38-0.77	-	-	0.19-0.28
Fledging success ^d	0.60-0.79	0.41-0.53	0.51-0.72	-	-	0.11-0.23	-	-	0.50-0.62 ^{k,l}
Reproductive success ^e	0.79	0.56	0.48	-	-	0.12	0.01 ^{i,l}	0.01 ^{j,l}	0.13 ^{k,l}
Productivity ^f	0.62	0.45	0.22	0.40 ^{g,l}	0.38 ^{h,l}	0.07	0.01 ^{i,l}	0.01 ^{j,l}	0.14 ^{k,l}
Source	Hunt et al. 1981a	Hunt et al. 1981a	Hunt et al. 1981a	This study	This study	This study	Craighead and Oppenheim 1985	Springer, pers. comm.	Johnson and Baker 1985

^a Clutch size = number eggs per nests w/eggs.

^b Growth rate = grams per day

^c Hatching success = eggs hatched per eggs laid, reported as range due to range of eggs hatched.

^d Fledging success = chicks fledged per eggs hatched, reported as range due to range of eggs hatched.

^e Reproductive success = chicks fledged per nests w/eggs.

^f Productivity = chicks fledged per nest attempt.

^g Based upon a two-day visit on August 17, 18 (by Hunt et al.) and calculation with arbitrary survivorship rates.

^h Based upon a two-week visit August 6-20 and calculation with arbitrary survivorship rates.

ⁱ Based upon sighting of only three chicks in hundreds of nests in July-August.

^j Based upon personal communication of A. Merculieff (St. George) to Alan Springer (University of Alaska-Fairbanks).

^k Based upon observations that ceased August 13, before fledging, therefore reported values of breeding performance are not reliable, and likely high.

^l Values represent short-term or qualitative observations.

Table C2. Summary of studies on red-legged kittiwakes at St. George Island, 1976-1984.

Parameter	Year								
	1976	1977	1978	1979	1980	1981	1982	1983	1984
Nest attempts (sample size)	88	240	235	52 ^k	123 ^l	79	-	-	149
Nests w/eggs	39	168	72	-	-	31	-	-	41
Clutch size ^a	1	1	1	1	1	1	1	1	1
Mean date hatching (n, ± S.D.)	8-05 (35,±6.3)	7-31 (93,±8.3)	8-10 (25,±10.1)	-	7-30 ^{g,n} (12,±5.0)	7-24 (14,±6.8)	-	-	-
Chick growth rate ^b (n, ± S.D.)	10.5 (12,±2.1)	13.1 (42,±2.3)	13.1 (13,±2.2)	-	7.96 (12,±3.5)	-	-	-	-
Hatching success ^c	0.79-0.87	0.78-0.85	0.57-0.81	-	-	0.45-0.87	-	-	0.07-0.37
Fledging success ^d	0.76-0.84	0.79-0.86	0.53-0.76	-	-	0.33-0.64	-	-	0.86-1.00 ^{m,n}
Reproductive success ^e	0.67	0.68	0.43	-	-	0.29	0.01 ^{h,n}	0.01 ^{i,n}	0.07 ^{m,n}
Productivity ^f	0.38 ^j	0.54	0.13	0.18 ^{k,n}	0.27 ^{l,n}	0.11	0.01 ^{h,n}	0.01 ^{i,n}	0.13 ^{m,n}
Source	Hunt et al. 1981a	Hunt et al. 1981a	Hunt et al. 1981a	This study	This study	This study	Craighead and Oppenheim 1985	Springer, pers. comm.	Johnson and Baker 1985

^a Clutch size = number eggs per nests w/eggs.

^b Growth rate = grams per day.

^c Hatching success = eggs hatched per eggs laid, reported as range due to range of eggs hatched.

^d Fledging success = chicks fledged per eggs hatched, reported as range due to range of eggs hatched.

^e Reproductive success = chicks fledged per nests w/eggs.

^f Productivity = chicks fledged per nest attempt.

^g Based upon mean growth rate of 7.96 grams per day and back-calculation to mean date of hatching.

^h Based upon sighting of only three chicks in hundreds of nests in July-August.

ⁱ Based upon personal communication of A. Merculieff (St. George) to Alan Springer (University of Alaska-Fairbanks).

^j Average of reported range in productivity, 0.30-0.45.

^k Based upon a two-day visit on August 17,18 (by Hunt et al.) and calculation with arbitrary survivorship rates.

^l Based upon a two-week visit August 6-20 and calculation with arbitrary survivorship rates.

^m Based upon observations that ceased August 13, before fledging, therefore reported values of breeding performance are not reliable, and likely high.

ⁿ Values represent short-term or qualitative observations.

Table C3. Summary of studies on common murres at St. George Island, 1976-1984.

Parameter	Year								
	1976	1977	1978	1979	1980	1981	1982	1983	1984
Mean number adults ^a	-	-	-	-	-	162 ^m	-	-	-
Eggs identified ^b	-	-	10	-	-	64	-	-	-
Eggs hatched ^c	-	-	-	-	-	44-61	-	-	-
Mean date hatching (n, ± S.D.)	8-03 (9, ±3.7)	8-04 (10, ±7.0)	8-02 (13, ±9.9)	-	-	7-30 (19, ±6.5)	-	-	-
Chick growth rate ^d (n, ± S.D.)	7.0 (4, ±2.9)	6.9 (3, ±1.2)	7.1 (12, ±3.6)	-	-	4.89 (5, ±2.1)	-	-	-
Chicks fledged from identified eggs	-	-	-	-	-	19	-	-	-
Total chicks fledged ^e	-	-	-	-	-	26 ^m	-	-	-
Clutch size ^f	-	-	1	-	-	1	-	-	-
Hatching success ^g	-	-	0.80	-	-	0.69-0.95	-	-	-
Fledging success ^h	-	-	0.87	-	-	0.31-0.43	-	-	-
Reproductive success ⁱ	-	-	0.70	-	-	0.30	Low ^{k,m}	-	-
Productivity ^j	-	-	0.26	-	-	0.16 ^m	Low ^{k,m}	-	-
Source	Hunt et al. 1981a	Hunt et al. 1981a	Hunt et al. 1981a			This study	Craighead and Oppenheim 1985		

^a Mean number of adults observed each visit on breeding ledges surveyed for eggs and chicks, used as proxy for nest attempts.

^b Eggs observed at least once on surveyed ledges, used as proxy for nest w/eggs as well as eggs laid.

^c Eggs hatched out of eggs identified.

^d Growth rate = grams per day.

^e Total chicks fledged = those from identified eggs as well as others for which eggs had not been identified.

^f Clutch assumed to be equal to one.

^g Hatching success = eggs hatched per eggs identified.

^h Fledging success = chicks fledged (jumped) from identified eggs per eggs hatched.

ⁱ Reproductive success = chicks fledged (jumped) from identified eggs per eggs identified.

^j Productivity = total chicks fledged (jumped) per mean number adults.

^k Craighead and Oppenheim (1982) observed few eggs and no chicks in study areas, but believed common murres fared better than thick-billed murres.

^l Johnson and Baker (1985) did not survey common murres on St. George Island.

^m Values represent short-term or qualitative observations.

Table C4. Summary of studies on thick-billed murres at St. George Island, 1976-1984.

Parameter	Year								
	1976	1977	1978	1979	1980	1981	1982	1983	1984
Mean number adults ^a	-	-	-	-	-	74 ^m	-	-	126
Eggs identified ^b	-	51	90	-	-	88	-	-	55
Eggs hatched ^c	-	-	-	-	-	57-77	-	-	42 ^{l,m}
Mean date hatching (n, ± S.D.)	8-03 (26,±9.1)	8-05 (43,±8.3)	7-29 (36,±5.0)	-	-	7-26 (44,±6.3)	-	-	-
Chick growth rate ^d (n, ± S.D.)	6.0 (23,±3.0)	7.9 (34,±3.2)	9.3 (25,±2.2)	-	-	4.50 (8,±2.6)	-	-	-
Chicks fledged from identified eggs	-	-	-	-	-	13	-	-	40 ^{l,m}
Total chicks fledged ^e	-	-	-	-	-	8 ^m	-	-	66 ^{l,m}
Clutch size ^f	-	1	1	-	-	1	-	-	1
Hatching success ^g	-	0.59-0.84	0.61-0.70	-	-	0.65-0.88	-	-	0.76
Fledging success ^h	-	0.35-0.97	0.70-0.86	-	-	0.17-0.23	-	-	0.95 ^{l,m}
Reproductive success ⁱ	-	0.29-0.57	0.49-0.52	-	-	0.15	Low ^{k,m}	-	0.73 ^{l,m}
Productivity ^j	-	-	-	-	-	0.11 ^m	Low ^{k,m}	-	0.52 ^{l,m}
Source	Hunt et al. 1981a	Hunt et al. 1981a	Hunt et al. 1981a			This study	Craighead and Oppenheim 1985		Johnson and Baker 1985

^a Mean number of adults observed each visit on breeding ledges surveyed for eggs and chicks, used as proxy for nest attempts.

^b Eggs observed at least once on surveyed ledges, used as proxy for nest w/eggs as well as eggs laid.

^c Eggs hatched out of eggs identified.

^d Growth rate = grams per day.

^e Total chicks fledged = those from identified eggs as well as others for which eggs had not been identified.

^f Clutch assumed to be equal to one.

^g Hatching success = eggs hatched per eggs identified.

^h Fledging success = chicks fledged (jumped) from identified eggs per eggs hatched.

ⁱ Reproductive success = chicks fledged (jumped) from identified eggs per eggs identified.

^j Productivity = total chicks fledged (jumped) per mean number adults.

^k Craighead and Oppenheim (1982) observed few eggs and only one chick in study areas; characterized year as nesting failure.

^l Based upon observations that ceased on August 13, before fledging, therefore reported values of breeding performance are not reliable, and likely high.

^m Values represent short-term or qualitative observations.

APPENDIX D

Data Summary, Cape Peirce 1970-1984

Table D1. Summary of studies on black-legged kittiwakes at Cape Peirce, 1970-1984.

Parameter	Year					
	1970	1973	1976	1977	1981	1984
Nest attempts (sample size)	60	190 ^k	1986	136 ^k	308	272
Nests w/eggs	-	-	-	-	209	99
Clutch size ^a	-	-	-	-	1.64	1.35
Mean date hatching (n, ± S.D.)	-	-	7-15 ^g (45,-)	-	6-26 (139,±4.9)	-
Chick growth rate ^b (n, ± S.D.)	-	-	-	-	10.93 (9,±1.4)	-
Hatching success ^c	-	-	0.39 ^{h,k}	-	0.59-0.89	0.01
Fledging success ^d	<<1.00 ^k	-	0.63	0 ^{i,k}	0.16-0.24	0.50 ^k
Reproductive success ^e	-	-	-	0 ^{i,k}	0.23	0.01 ^k
Productivity ^f	0.15	0.09 ^k	0.25	0 ^{i,k}	0.16	<0.01 ^{j,k}
Source	Dick and Dick 1971	Dick, pers. comm.	Petersen and Sigman 1977	Petersen, pers. comm.	This study	Johnson and Baker 1985

^a Clutch size = number eggs per nests w/eggs.

^b Growth rate = grams per day.

^c Hatching success = eggs hatched per eggs laid, reported as range due to range of eggs hatched.

^d Fledging success = chicks fledged per eggs hatched, reported as range due to range of eggs hatched.

^e Reproductive success = chicks fledged per nests w/eggs.

^f Productivity = chicks fledged per nest attempt.

^g This value is actually modal date of hatching.

^h This value is not strictly comparable to other hatching success, since it equals proportion of nests from which eggs hatched.

ⁱ Based upon a one day visit on August 21, 1977 during which no chicks were seen.

^j Based upon observations that ceased on July 16, before fledging, however hatching success was so poor that low reproductive success and productivity values are realistic.

^k Values represent short-term or qualitative observations.

Table D2. Summary of studies on common murrelets at Cape Peirce, 1970-1984.

Parameter	Year					
	1970	1973	1976	1977	1981	1984
Mean number adults ^a	-	-	-	104 ⁿ	290	487
Eggs identified ^b	-	-	-	-	88	161
Eggs hatched ^c	-	-	-	-	39-82	22 ^{l,n}
Mean date hatching (n, ± S.D.)	-	-	7-21 ^k (8,-)	-	7-12 (19,±6.4)	-
Chick growth rate ^d	-	-	-	-	-	-
Chicks fledged from identified eggs	-	-	-	-	15	21 ^{l,n}
Total chicks fledged ^e	-	-	-	-	46	26 ^{l,n}
Clutch size ^f	-	-	-	1	1	1
Hatching success ^g	-	-	-	-	0.44-0.93	0.14 ^{l,n}
Fledging success ^h	-	-	-	-	0.18-0.38	0.95 ^{l,n}
Reproductive success ⁱ	-	-	0.20 ⁿ	0.01 ⁿ	0.17	0.13 ^{l,n}
Productivity ^j	-	-	0.20 ^{l,n}	0.01 ^{m,n}	0.15	0.05 ^{l,n}
Source	Dick and Dick 1971	Dick pers. comm.	Petersen and Sigman 1977	Petersen, pers. comm.	This study	Johnson and Baker 1985

^a Mean number of adults observed each visit on breeding ledges surveyed for eggs and chicks, used as proxy for nest attempts.

^b Eggs observed at least once on surveyed ledges, used as proxy for nest w/eggs as well as eggs laid.

^c Eggs hatched out of eggs identified.

^d No growth rates measured.

^e Total chicks fledged = those from identified eggs as well as others for which eggs had not been identified.

^f Clutch assumed to be equal to one.

^g Hatching success = eggs hatched per eggs identified.

^h Fledging success = chicks fledged (jumped) from identified eggs per eggs hatched.

ⁱ Reproductive success = chicks fledged (jumped) from identified eggs per eggs identified.

^j Productivity = total chicks fledged (jumped) per mean number adults.

^k This value is actually modal date of hatching

^l Based upon observations that ceased July 16; 45 out of 161 identified eggs are reported as still unhatched; observations did not extend to time of fledging (jumping) therefore reported values of breeding performance are not reliable.

^m Based upon a one day visit on August 21, 1977 during which one chick was seen.

ⁿ Values represent short-term or qualitative observations.

APPENDIX E

Food Samples: St. George Island 1980-1981

Cape Peirce 1981

Table E1. Analysis of food samples for kittiwakes and murre, St. George Island 1980-1981.

Species	Sample type, sample size	Prey type	Frequency of occurrence
<u>1980</u>			
BLKI	Chick regurgitation n = 1	Unidentified fish	100%
RLKI	Chick regurgitation n = 5	<u>Thysanoessa raschii</u> Unidentified fish Myctophid Walleye pollock Arctic cod	60% 60% 20% 20% 20%
COMU	None	-	-
TBMU	None	-	-
<u>1981</u>			
BLKI	Adult stomach n = 7	<u>Thysanoessa raschii</u> Squid Unidentified fish Sandlance	86% 14% 43% 14%
	Chick regurgitation n = 3	<u>Thysanoessa raschii</u> Unidentified fish	33% 100%
RLKI	None	-	-
COMU	Chick regurgitation n = 1	Squid Unidentified fish	100% 100%
TBMU	Adult stomach n = 3	<u>Thysanoessa raschii</u> Squid Sandlance	67% 67% 33%

Table E2. Analysis of food samples for kittiwakes and murre, Cape Peirce 1981.

Species	Sample type, sample size	Prey type	Frequency of occurrence	
BLKI	Adult stomach n = 10	Copepod	30%	
		Mysid	30%	
		Unidentified fish	10%	
		Walleye pollock	10%	
		Sandlance	80%	
	Chick regurgitation n = 10	Copepod	20%	
		Mysid	20%	
		Sandlance	100%	
	COMU	Adult stomach n = 5	Copepod	80%
			Mysid	40%
Decapod			20%	
Gammarid			20%	
Rainbow smelt			20%	
Sandlance			80%	

APPENDIX F

Definition of Abbreviations

Table F. Definition of abbreviations used in figures and tables.

BLKI	Black-legged kittiwake
RLKI	Red-legged kittiwake
COMU	Common murre
TBMU	Thick-billed murre
BLKI-P	Productivity of black-legged kittiwakes
BLKI-R	Reproductive success of "
RLKI-P	Productivity of red-legged kittiwakes
RLKI-R	Reproductive success of "
COMU-R	Reproductive success of common murres
TBMU-R	Reproductive success of thick-billed murres
SST-MY	Sea surface temperature - May
SST-JN	" - June
SST-JL	" - July
SST-AG	" - August
SST-MG	" - mean for May-August
SST-SG	" - mean for September-August
WIND-10	Proportion of days during summer with maximum wind speeds equal to or exceeding 10 miles per hour
WIND-15	" 15 "
WIND-20	" 20 "
WIND-25	" 25 "
WIND-30	" 30 "
WIND-35	" 35 "
WIND-40	" 40 "
PREC-.01	Proportion of days during summer with daily precipitation equal to or exceeding 0.01 inches
PREC-.05	" .05 "
PREC-.1	" .1 "
PREC-.2	" .2 "
PREC-.3	" .3 "
PREC-.4	" .4 "
PREC-.5	" .5 "
PREC-T	Accumulated total summer precipitation
HDD-MY	Heating degree days - May
HDD-JN	" - June
HDD-JL	" - July
HDD-AG	" - August
HDD-ST	" - September
HDD-T	" - total May-September
VAR	Variance
r	Pearson product moment correlation coefficient
r _s	Spearman rank correlation coefficient
p	Probability of rejecting null hypothesis when the null hypothesis is true
ns	not significant
na	not applicable
n	sample size
StG	St. George Island
CP	Cape Peirce

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