

AN ABSTRACT OF THE THESIS OF

David B. Irons for the degree of Master of Science

in Wildlife Science presented on 1 February 1982

Title: FORAGING STRATEGIES OF GLAUCOUS-WINGED GULLS: INFLUENCES OF

SEA OTTER PREDATION.

*Redacted for Privacy*

Abstract approved: \_\_\_\_\_

Robert G. Anthony ✓

Diets and foraging strategies of Glaucous-winged Gulls were studied in areas with and without sea otters in the western Aleutian Islands, Alaska. Gulls foraged on invertebrates (e.g., sea urchins, limpets, chitons, mussels, and others) in the rocky intertidal community and on fish at sea; this study was conducted on gulls foraging intertidally.

Sea otters affected foraging strategies and diets of gulls by reducing the size and density of intertidal prey available to them. In the presence of low densities of sea otters (which had depredated large sea urchins) gulls adjusted their foraging strategies by being more selective while feeding on urchins. In the presence of high densities of sea otters (which had depredated most intertidal prey) gulls shifted their diets from intertidal invertebrates to fish and the diversity of their diets was reduced.

Observations demonstrated that gulls foraged intertidally during low tides and that most foraging occurred in the lowest intertidal zones that were exposed. Consequently, gulls foraged in different zones during spring and neap tides. When all zones were exposed gulls selected the Alaria and Laminaria zones, which offered the highest net rate of energy gain (En). Gulls also selected particular prey species and prey sizes. Selective foraging of gulls increased their En 126% in areas without sea otters and 181% in areas with low densities of sea otters.

Prey preference experiments demonstrated that preferences of gulls for chitons and urchins were significantly correlated to En, but assimilation rate, experience and search images were also influential. Highly preferred prey species (chitons) were not strongly selected for in the field because of their ability to adhere to the substrata.

Foraging behavior of gulls indicated that they hunted by En expectation and left prey patches when a threshold En was reached. Foraging behavior of gulls in the rocky intertidal community supported optimal foraging theory for optimal diets, patch choice, and time allocation to patches.

Foraging Strategies of Glaucous-winged Gulls:  
Influences of Sea Otter Predation

by

David B. Irons

A THESIS

submitted to

Oregon State University

in partial fulfillment of  
the requirements for the  
degree of

Master of Science

Completed 1 February 1982

Commencement June 1982

APPROVED:

*Redacted for Privacy*

---

Associate Professor of Wildlife Ecology ✓  
in charge of major

*Redacted for Privacy*

---

Head of Department; Fisheries and Wildlife

*Redacted for Privacy*

---

Dean of Graduate School

Date thesis is presented 1 February 1982

Thesis typed by David B. Irons for David B. Irons

## ACKNOWLEDGEMENTS

I thank the following for their contributions to this study. The Denver Wildlife Research Center (USFWS) funded this project for which I am very grateful. The Oregon Cooperative Wildlife Research Unit provided additional funding in the final phases. The United States Coast Guard provided transportation to and from Attu Island, and Lt. Karonis furnished logistical support on Attu. John Martin and the employees of the Aleutian Island National Wildlife Refuge helped with logistics, supplied fresh produce, and collected gull pellets on Amchitka Island, all of which was greatly appreciated. John Trapp provided encouragement and stimulating conversations at the beginning of the study. Rick Madigan and Gary Miller worked diligently and provided warm friendship throughout the cold, rainy field season. David Linberg gladly lent some of his expertise in identifying mollusks. Winston Smith took time for several thought provoking conversations during my data analysis. Bill Mannan, Gordon Kruse, and Chris Hundermark were helpful in discussing topics of question during data analysis. Eric Beals shared his vast knowledge of computers cheerfully. Bruce Menge, Robert Jarvis, and Frank B. Issacs provided constructive criticism of my thesis. Bob Anthony and Jim Estes gave invaluable guidance throughout the fieldwork, data analysis, and manuscript preparation. Without them I would not have had the unique opportunity to conduct this study; I am deeply grateful. Finally, I acknowledge my wonderful family and friends, without whom I am nothing.

TABLE OF CONTENTS

I. Introduction..... 1

II. Study Sites..... 4

III. Methods and Materials..... 9

    Definition of terms..... 9

    Field procedures..... 10

    Laboratory procedures..... 13

    Data analysis and statistical methodology..... 14

IV. Results and Discussion..... 20

    Time budgets and foraging patterns..... 20

    Diets..... 25

    Prey selection..... 28

    Benefits of selective foraging..... 40

    Prey preference experiments..... 41

    Prey preference vs selection..... 48

    Foraging behavior..... 49

V. General Discussion..... 55

    Optimal foraging theory..... 59

VI. Literature cited..... 63

VII. Appendices..... 68

## LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	Map of Attu Island indicating study sites and range of sea otters in 1980.	6
2	Percent of gulls feeding in the intertidal zones in relation to tide height, for spring and neap tides (data from observations at Chichagof Harbor, Attu Island, Alaska).	22
3	Frequency of occurrence of prey (%) in diets of gulls at Massacre Bay during spring tides and Chichagof Harbor during spring and neap tides (data from observations on Attu Island, Alaska).	29
4	Frequency of occurrence of prey (%) in regurgitated pellets of gulls during spring and neap tides at Chichagof Harbor and Massacre Bay, Attu Island, Alaska.	30
5	Size class frequency of urchins (%) in intertidal areas and in gull pellets at Massacre Bay and Chichagof Harbor, Attu Island, Alaska.	34
6	Size class frequency of chitons (%) in intertidal areas and in gull pellets at Massacre Bay and Chichagof Harbor, Attu Island, Alaska.	35
7	Size class frequency of mussels (%) in intertidal areas and in gull pellets at Massacre Bay and Chichagof Harbor, Attu Island, Alaska.	36
8	Size class frequency of limpets (%) in intertidal areas and in gull pellets and stomachs at Massacre Bay and Chichagof Harbor, Attu Island, Alaska.	38
9	Hypothesized relationship of diversity and equitability of gulls' diets in relation to density of sea otters in the western Aleutian Islands, Alaska.	57
10	Frequency of selected prey (%) of Glaucous-winged Gulls with data collected from observations, pellets, and stomachs from Chichagof Harbor, Attu Island, Alaska.	71
11	Frequency of selected prey (%) in diets of Glaucous-winged Gulls using observational data (n=158) collected during spring low tides at Chichagof Harbor, Attu Island, Alaska, and three methods of analysis: number of prey, occurrence, and dry weight.	73

## LIST OF TABLES

<u>Table</u>		<u>Page</u>
1	Average densities and sizes of selected intertidal invertebrates according to intertidal zone at Massacre Bay and Chichagof Harbor, Attu, Island, Alaska.	7
2	Percent of gulls that were foraging/resting in each intertidal zone and percent of foraging gulls that used each intertidal zone in relation to study site and tidal cycle on Attu Island, Alaska.	23
3	Frequency of occurrence for all prey in pellets of Glaucous-winged Gulls from two sites on Attu Island and from Amchitka Island, Alaska.	26
4	Percent of foraging gulls and characteristics of intertidal zones at Chichagof Harbor during spring low tides.	32
5	Results of prey preference experiments with adult Glaucous-winged Gulls at Massacre Bay and Chichagof Harbor, Attu Island, Alaska.	43
6	Results of prey preference experiments with juvenile Glaucous-winged Gulls at Massacre Bay and Chichagof Harbor, Attu Island, Alaska.	44
7	Caloric value of selected prey items and their means weighted to the proportion of adult gulls' diet they comprised and parameters describing foraging behavior of gulls at Chichagof Harbor and Massacre Bay, Attu Island, Alaska.	50



FORAGING STRATEGIES OF GLAUCOUS-WINGED GULLS:  
INFLUENCES OF SEA OTTER PREDATION

INTRODUCTION

Glaucous-winged Gulls (Larus glaucescens) are large omnivorous seabirds that breed in coastal environments from Washington to Alaska, including the Aleutian archipelago. Glaucous-winged Gulls are food generalists and are opportunistic (Bent 1963). They molt into adult plumage at three years of age, but do not breed until age four (Vermeer 1963). During summer thousands of these gulls nest on small, fox-free islets in the western Aleutian Islands. During winter few gulls remain in this area (V. DiPietro, U.S.C.G. Attu Island, 1980, personal observation); most migrate south to Asia or North America as far as Baja, California (Devillers et al. 1971).

Gulls on Attu foraged intertidally and at sea. Glaucous-winged Gulls that nested on Williamson Rocks (San Juan Islands, Washington), fed intertidally on invertebrates (crabs, mussels, polychaetes, sea urchins, chitons, and sea cucumbers) and at garbage cans, but their staple food was scraps from fish canneries (James-Veitch and Booth 1954).

Recently, Trapp (1979) found great variation in diets of Glaucous-winged Gulls, based on regurgitated pellets, among islands in the western Aleutians. Gulls ate many sea urchins (79 and 80%) on islands with low densities of sea otters (Enhydra lutris) and fish

made up a large portion (77%) of diets of gulls on an island with a high density of sea otters. Trapp suggested this difference was due to sea otter predation on sea urchins which made it energetically unfeasible for gulls to prey on them.

Dayton (1975:230) argued that "few natural communities are so influenced by one population as is the nearshore marine community dominated by the sea otter". Along the central coast of California Ebert (1968) and Lowry and Pearse (1973), and in Alaska Estes and Palmisano (1974), Palmisano (1975), Estes et al. (1978) and Duggins (1980) have found that sea otters exerted a major influence on the structure of nearshore marine communities by reducing the number of important herbivorous macroinvertebrates (principally sea urchins).

More is probably known about the rocky intertidal than most other communities because of the accessibility of the habitat and the observability of the species (Paine 1974). Avian predators, which consume relatively large, slow moving prey in the rocky intertidal are excellent species for the investigation of foraging strategies. Their foraging behavior, diet, and prey base can be quantified relatively easily allowing many of the predictions of optimal foraging theory to be tested in the field.

Optimal foraging has been discussed in several theoretical papers (see Shoener 1971 and Pyke et al. 1977 for reviews) and empirical papers (Royama 1970, Smith and Dawkins 1971, Willson 1971, Menge 1972, Krebs et al. 1974, Werner and Hall 1974, 1979, Emlen and Emlen 1975, Charnov 1976, Zach and Falls 1976a, b, c, Davis 1977, Eggers 1977, Gill and Wolf 1977, Reichman 1977, and Stein 1977). However, few

studies have attempted to test optimal foraging theory in the field. Those that did, except for Menge (1972), generally worked with simple systems involving one predator and one prey species. The obvious reason for this is that the necessary data to test these theories cannot be collected on most natural communities.

Although much research has been done on the interactions between sea otters and marine communities, none have addressed the effects of sea otters on coastal foraging sea birds. In addition, optimal foraging theories have not been tested in the complex predator-prey system of gulls foraging in the rocky intertidal. The purpose of this study was to investigate foraging strategies of Glaucous-winged Gulls and determine if predation by sea otters and monthly tidal cycles were influential. I also investigated prey preferences of Glaucous-winged Gulls by field experiments and tested predictions of optimal foraging theory.

## STUDY SITES

Most of the research for this study was conducted on Attu Island, Alaska, but additional limited data were collected at Amchitka Island, Alaska. Attu Island is situated at 173°E and 53°N and is the largest (905 km<sup>2</sup>; 254 km of coastline) of the Near Islands. Amchitka Island (295 km<sup>2</sup>; 170 km of coastline) is part of the Rat Island group and is located at 179°E and 52° 30'N. Weather conditions in the Aleutian Islands during summer are characterized by cloudy skies, fog, rain, and occasional high winds with temperatures from 5 to 15°C. The Pacific Ocean which borders the south side of the Aleutian Islands has more ocean swell (causing high wave exposure on the shores) than the smaller Bering Sea which borders the north side of the Aleutian Islands.

The Rat Islands including Amchitka are densely populated with sea otters that have recovered from heavy, unregulated exploitation from 1741 to 1911 (Kenyon, 1969). Based on annual winter mortality Kenyon (1969) and Estes and Smith (1973) suggested that this population has been near equilibrium for several Decades. The Near Islands were recolonized by sea otters about 1965. Initially otters reestablished a population around Chichagof Harbor on Attu Island (Kenyon, 1969). A population of approximately 800 sea otters inhabited the northeastern coastline of Attu in the summer of 1980. Estes (personal communication) suggests that the equilibrium density population size is probably about 10,000 individuals.

Two sites were studied intensively on Attu in order to compare areas with and without sea otters (Fig. 1). Chichagof Harbor on the northeast coast of the island is near the center of the otter's distribution. Massacre Bay on the southeast coast lies beyond the range of sea otter. More limited observations were made at Kirilof Rocks, on the north coast of Amchitka Island, where otters have existed in dense numbers.

The rocky intertidal community at Attu Island is composed of distinct zones dominated by particular species of invertebrates or algae (Table 1). At Chichagof, from highest of lowest, there are the barnacle, mussel, Alaria, and Laminaria zones. The barnacle zone is composed chiefly of the species Balanus glandula. The mussel zone which has a carpet of mussels (Mytilus edulis) with B. glandula growing on many of the mussels; larger barnacles (B. cariosus) grow beneath and adjacent to the mussels. Alaria crispera, a brown upright alga, is associated with several other invertebrate species, the four dominant species being B. cariosus, chitons (Katharina tunicata), and limpets (Notoacmaea scutum and Collisella pelta). The lowest intertidal zone is characterized by brown algae of the Laminaria genera. Laminaria longipes dominates the upper Laminaria zone, and other stipate species (L. groenlandica, L. yezoensis, and L. dentigera), form the lower Laminaria zone. Balanus cariosus, chitons, and urchins plus other less common species of invertebrates occur in the upper Laminaria zone (Appendix I, also see O'Clair 1977). The lower Laminaria zone supports a great diversity of invertebrate species, but by far the most common one is the urchin.

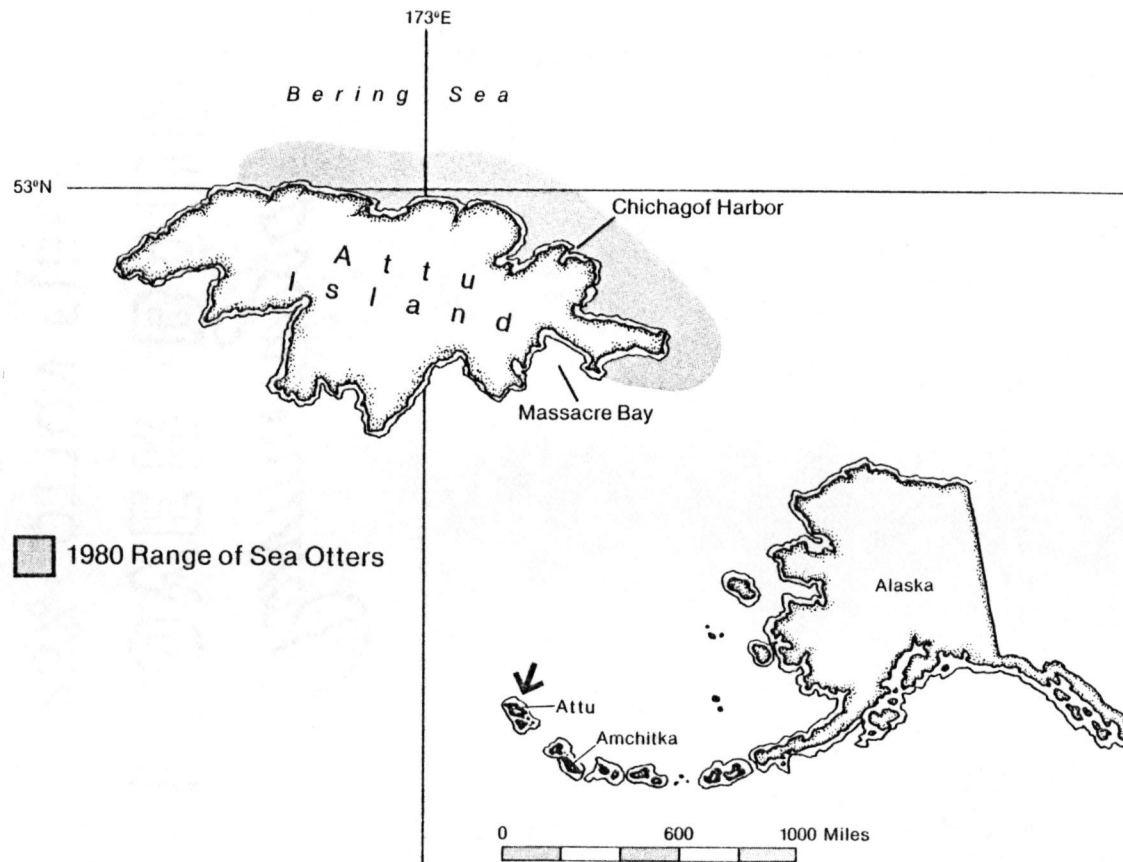


Figure 1. Map of Attu Island indicating study sites and range of sea otters in 1980.

Table 1. Average densities and sizes of selected intertidal invertebrates according to intertidal zone at Massacre Bay and Chichagof Harbor, Attu Island, Alaska.<sup>a</sup>

CHICHAGOF HARBOR								
Invertebrate Types	Barnacle Zone (n=8)		Mussel Zone (n=30)		Alaria Zone (n=35)		Laminaria Zone (n=62)	
	number <sub>2</sub> per 1/4 m <sup>2</sup>	size (mm)	number <sub>2</sub> per 1/4 m <sup>2</sup>	size (mm)	number <sub>2</sub> per 1/4 m <sup>2</sup>	size (mm)	number <sub>2</sub> per 1/4 m <sup>2</sup>	size (mm)
Urchins	0	-	0	-	3.9±1.1	19±0.8	23.0±3.0	22±0.3
Chitons	0	-	<0.1±un <sup>c</sup>	18±un <sup>c</sup>	10.3±0.9	38±0.8	5.6±1.6	46±1.1
Limpets	0	-	8.9±0.9	15±0.6	11.9±1.7	17±0.5	3.4±0.9	18±0.8
Mussels	48.6±8.5 <sup>d</sup>	10±1.4 <sup>d</sup>	852.3±76.0	19±0.2	1.7±0.6	25±1.7	0.6±0.6	19±1.6
<i>B. cariosus</i>	0	-	60.4±3.3	14±0.6 <sup>a</sup>	132.9±5.7	14±0.6 <sup>bd</sup>	68.7±5.3	14±0.6 <sup>bd</sup>
<i>B. glandula</i>	2152.0±328.8 <sup>d</sup>	8±0.7 <sup>bd</sup>	168.0±5.6	8±0.7 <sup>b</sup>	0	-	0	-

MASSACRE BAY						
Invertebrate Types	(n=25)		(n=25)		(n=25)	
	number <sub>2</sub> per 1/4 m <sup>2</sup>	size (mm)	number <sub>2</sub> per 1/4 m <sup>2</sup>	size (mm)	number <sub>2</sub> per 1/4 m <sup>2</sup>	size (mm)
Urchins	0	-	0.8±0.43	29±3.4	35.2±6.4	49±0.7
Chitons	<0.1±un <sup>c</sup>	55±un <sup>c</sup>	6.5±0.6	59±1.5 <sup>b</sup>	<0.1±un <sup>c</sup>	59±1.5 <sup>b</sup>
Limpets	9.3±1.9	15±0.4	10.9±2.3	16±0.4	1.9±0.8	21±1.0
Mussels	355.8±71.2	11±0.1	1.5±0.8	17±0.5	0	-
<i>B. cariosus</i>	0	-	41.5±5.2	14±0.6 <sup>bd</sup>	0	-
<i>B. glandula</i>	231.7±18.2	8±0.7 <sup>b</sup>	0	-	0	-

<sup>a</sup>Values are means with 95% confidence intervals.

<sup>b</sup>Sizes of invertebrates were not calculated separately for each zone.

<sup>c</sup>un = confidence intervals were undefined because sample size was one.

<sup>d</sup>From Estes (unpubl. data).

The barnacle, mussel, and Alaria zones at Massacre were structurally similar to those at Chichagof Bay (Appendix 1b). The Laminaria zone, however, showed indications of more intense grazing by sea urchins. Below the Alaria zone few organisms existed besides encrusting coralline algae (Lithothamnion spp.) and urchins. There are two apparent reasons for the differences in structure of the Laminaria zones at Chichagof Harbor and Massacre Bay. First, the specific sampling site at Massacre Bay was somewhat more protected from wave exposure than the site at Chichagof Harbor, thereby, allowing the urchins greater freedom of mobility (J.A. Estes, unpubl. data). Second, sea urchins were larger at Massacre Bay than they were at Chichagof Harbor due to the absence of sea otter predation, and large urchins can consume algae at higher rates than can smaller ones (J.A. Estes, unpubl. data).

Rocky intertidal community structure at Amchitka (the Rat Islands) differs greatly from that at the Near Islands (Palmisano and Estes 1977). Densities of major macroinvertebrates at the Rat Islands are much lower than they are at the Near Islands. For example, a comparison made by Estes and Palmisano (1974) provided the following data for Amchitka vs Shemya islands, respectively: B. glandula 5 vs 1215, mussels 4 vs 772, chitons <1 vs 38, urchins 8 vs 78 per m<sup>2</sup>, and algal cover was much higher at Amchitka. Estes et al. (1978) contended that these basic ecological differences between Amchitka and the Near Islands were due to the presence of sea otters at Amchitka.



## METHODS AND MATERIALS

Definition of terms

Throughout this paper I shall refer to neap and spring tide cycles. During a month there are generally two one week periods with large tidal fluxes, which result in low, low tides called spring tides, these alternate with two one week periods with small tidal fluxes, which result in high, low tides called neap tides.

Prey have often been considered available to predators if they were simply present. However, potential prey species may be present but unavailable to predators because of escape responses, large size, and/or the ability to adhere to the substrata. I refer to available prey as prey that are present and consumable by predators.

When discussing the choice of prey by predators the terms prey selection and prey preference have often been used synonymously. I differentiate between these terms. Prey selection refers to the process of prey choice by predators without regard to availability of prey. Prey preference refers to prey choice when all prey are equally available to the predator.

Most studies have referred to patches as areas where prey were variable in time and space (Shoener 1971), and quality of patches often differed only in densities of one prey species (Krebs et al. 1974, Gibb 1958, Royama 1970, Tullock 1971, MacArthur and Pianka 1966,

and Zach and Falls 1976a,b,c). Empirical studies have generally investigated simple systems with one prey species of the same size. The rocky intertidal community is complicated in that many species of several sizes occur in zones and in clumps or patches within zones. Henceforth, I will recognize two scales of patchiness in rocky intertidal communities: 1) intertidal zones and 2) clumps of prey within zones such as those that occur in tide pools or other physical irregularities in the habitat.

Net rate of energy gain ( $E_n$ ) and giving up time (GUT) (Charnov 1976) were determined for foraging gulls. I define net rate of energy gain as the average caloric value (Kcal) of a prey item divided by the average search and handling time (h) for that prey item. I define giving-up time of a foraging gull to be the time interval of continuous searching between the last capture and when the gull left the intertidal area.

#### Field procedures

Sixty-nine gulls were collected by shooting at Massacre Bay and 82 at Chichagof Harbor during the summer of 1979 and 1980. I collected gulls at or shortly following low tide during both spring and neap tide cycles. I attempted to collect only birds that had been feeding. When not killed instantly gulls often regurgitated food, which was retrieved when possible. All other field work at Attu was conducted in the summer of 1980.

Gulls regurgitate pellets that are composed of large undigestible hard parts of prey. These were collected on Amchitka once in September 1979 and three times in summer 1980. I collected pellets weekly on Attu after spring and neap tidal cycles from areas where gulls were known to congregate. To determine if there were local differences in diets pellets were collected in three types of areas at both Chichagof Harbor and Massacre Bay: a nesting area, proximate to the rocky intertidal, and adjacent to a creek. All areas were within 5km of sites where foraging behavior was observed. Pellets were analyzed for occurrence of prey species, and measurable parts of prey were collected to determine their sizes.

Intertidal invertebrates and algae were sampled on Attu at Chichagof Harbor and Massacre Bay at the same site where foraging behavior was observed. At each site 25 to 35  $1/4 \text{ m}^2$  quadrats were arbitrarily placed in each zone and recorded from each quadrat the density and size of all macroinvertebrates and percent cover of macroalgae.

Spotting scopes were used to observe gulls foraging intertidally during neap and spring tides at Chichagof Harbor and during spring tides at Massacre Bay (in July and August about a week was spent at each location during each tide cycle). At 30 minute intervals, zone occupancy and activity of all gulls in the intertidal were recorded to study time budgets. Individual foraging gulls were selected arbitrarily for observation. During the observations the intertidal zone was noted; search and handling times for each prey item and resting time (i.e. any period interrupting active foraging behavior)

were recorded. I recorded periods of active foraging as search time and the interval from when physical contact was made with the prey until it was swallowed or abandoned as handling time. Prey items were identified to species when possible. Mode of consuming prey (i.e., swallowed intact, pecked-out, or air-dropped), was also recorded. Observations were made from a few hours before to a few hours after low tide at which time birds usually quit foraging.

To determine the prey items that gulls would choose first if all were equally available (i.e., not attached to the substrata) I conducted prey preference experiments at Chichagof Harbor and Massacre Bay. I used three species of prey that appeared relatively important in diets of gulls and selected sizes that represented small, medium, and large prey. The following seven prey types, freshly collected, were used in each experiment: a small, medium, and large urchin (mean test diameter about 15, 35, and 75mm, respectively); a small and large chiton (average lengths about 25 and 55mm, respectively); and a small and large mussel (mean lengths about 25 and 55mm, respectively). Prey items were set out in a triangular grid pattern about 30cm across, with the small items positioned closest to the viewer to facilitate observations. Most of the experiments were carried out on flat rocks in nesting colonies because adult gulls returned quickly to their territory after being disturbed. To test several gulls, locations of experiments were changed after 2-4 repetitions. Foraging birds were observed through a spotting scope from distances of between 10 and 30 meters. Age of gull (i.e., juvenile, 1, 2, or >2 years old), handling time for each prey item, and the sequence that the prey were handled

or consumed were recorded on tape.

To determine if urchins and chitons were equally available in the intertidal to foraging gulls the strength of adhesion of each was estimated by measuring the shear force required to remove organisms from substrata. A spring scale was attached to the center of a metal rod which had one end flattened. The rod was held perpendicular to the substratum and the flattened end was placed against the organism. By pulling the spring scale, pressure was applied to the organism until it was dislodged. The species, size, and force required to remove organisms were recorded.

#### Laboratory procedures

Contents of crops and gizzards of collected gulls were analyzed for occurrence and size of prey species. Length and diameter of intact chitons and urchins, respectively, were regressed on sizes of calcareous parts of these organisms. These relationships were used to estimate sizes of prey items in pellets and stomachs. Size of the thickest portion of the demipyramid, which is part of the Aristotle's lantern (feeding apparatus of urchins), was used to estimate urchin diameter with the linear model  $y = -6.1865 + 19.8134x$  ( $R^2 = .972$ ) where  $y$  = urchin diameter and  $x$  = thickness of demipyramid. The logarithm of body length of chitons was regressed on the width of the exposed portion of the anterior and posterior valves. The relationship between body length ( $y$ ) and the width of the anterior valve ( $x$ ) was defined by the equation  $y = -27.0213 + 35.7879 \ln x$  ( $R^2 = .788$ ). Body

length (y) was related to the width of the posterior valve (x) by the equation  $y = -7.5550 + 34.9374 \ln x$  ( $R^2 = .840$ ). The posterior valve, when present in pellets, was used to estimate chiton length. If not, the anterior valves were used. Sizes of mussels, welks (Nucella), and limpets (Notoacmaea scutum and Collisella pelta) that were collected from pellets were measured directly to determine sizes consumed by gulls. The energetic value of different prey items were estimated from size/dry wt. relationships and caloric values of edible body parts. For sea urchins the size(y)/dry wt.(x) equation was estimated by  $y = 0.000005x^{3.1}$  ( $R^2 = .913$ ). Size to dry weight relationships for all other species were estimated from data provided by B. A. Menge (unpubl. data) (Appendix V). A Parr (model 1101) oxygen bomb calorimeter was used to determine energy (Kcal/g) of edible body parts (Appendix IV). Specimens were collected from the intertidal community at Massacre Bay, frozen, and transported to Oregon State University for analysis. Subsequently, the soft parts were dried to constant weight at 45°C and ground into a powder. Several individuals of small prey species were combined to create more uniform aliquots. Calorimetry procedures from the Parr Instrument Co. (1980) were followed.

#### Data analysis and statistical methodology

Net rate of energy gain (En) was determined for average weights of species of prey that gulls fed on, for average weights of invertebrates that occurred within each intertidal zone, and for prey

items used in prey preference experiments. Mean search times and handling times were used for analysis.

Selection of prey species and prey sizes by gulls was determined by using the odds ratio (Fleiss 1973) which related the proportion of a prey species in the diet to that in the environment:

$$O = p_1q_2/p_2q_1$$

where

$p_1$  = proportion of diet comprised by a given prey taxon

$q_1$  = proportion of diet comprised by all other prey taxa

$p_2$  = proportion of food complex in environment comprised by the given taxon

$q_2$  = proportion of food complex in environment comprised by all other taxa.

The natural log of "O" was used to determine if values were significantly different from zero (Gabrial 1978). Prey base data, pellet contents, and foraging observations of gulls in the intertidal during spring low tides were used to compute the odds ratio.

The consequences of selective foraging on  $E_n$  was determined by comparing a calculated  $E_n$  for hypothetical, randomly foraging birds to the  $E_n$  for selective foraging (i.e., the manner in which gulls actually foraged). Data from observations that were analyzed by percent occurrence were used to quantify diets.  $E_n$  for random

foraging was determined on three scales that I judged to be meaningful. First,  $E_n$  was calculated for gulls assuming they foraged randomly among all intertidal zones and on all prey items. Second,  $E_n$  was calculated for gulls assuming they selected specific zones, but foraged randomly with respect to prey species and size in that zone. Third,  $E_n$  was calculated for gulls assuming they selected zones and species, but foraged randomly with respect to prey sizes.  $E_n$  assuming random foraging between all intertidal zones, was calculated by assuming 25% of the gulls foraged randomly in each of the four intertidal zones.  $E_n$  obtained if gulls selected only intertidal zones was determined by weighting  $E_n$ , obtained by random foraging within each zone, by the proportion of gulls that foraged there (i.e., barnacle, 0.02; mussel, 0.07; Alaria, 0.46; and Laminaria, 0.45). The  $E_n$  that gulls gained if they selected zones and prey species but not specific sizes was calculated using only the Alaria and Laminaria zones (where most foraging occurred during spring tides). The  $E_n$  that gulls obtained by feeding on each major prey species within those zones was calculated using mean weights of prey in the intertidal community and weighting them by the proportion that each species made up of the gulls' diet (i.e., urchins, 0.66; limpets, 0.29; and chitons, 0.05). The  $E_n$  that gulls obtained by foraging selectively for zone, species, and sizes was determined by weighting the  $E_n$  of major prey species and weights selected by gulls by the proportion of each in their diet.

Prey preference of gulls from prey preference experiments was assigned based on the percent of the experiments that an adult gull



handled a particular prey item first. If a prey item was handled twice by a bird in one experiment only the first time was counted. Handling, rather than actual consumption, was used to determine preference, because I assumed that if a prey item was handled the gull intended to consume it.  $E_n$  was calculated for these experiments using only handling time and not search time, because search time was not involved. By using these methods I removed factors that may have had differential effects on the availability of prey in the field, thereby, permitting me to determine prey preference.

To determine  $E_n$  for urchins consumed by gulls in the field by different modes (i.e., swallowed intact, pecked-out, and air-dropped) it was necessary to know the average size weight of urchins that gulls consumed by each of these modes. From observations of gulls foraging and measurements of the width of their bill at the commissural point I estimated that urchins up to about 60mm in diameter could be swallowed intact by gulls. Therefore, I used a weighted mean weight of urchins 60mm or less in diameter that were in pellets for the mean weight of urchins swallowed intact; I used a weighted mean weight of urchins larger than 60mm for the mean weight of urchins that were pecked-out and air-dropped by gulls.

The average GUT was used to calculate the threshold of net rate of energy intake (i.e., the  $E_n$  of a gull at which time it would leave the patch it was foraging in) by substituting GUT for search time in the equation for  $E_n$ .

Species diversity of diets of gulls was calculated by Simpson's (1949) diversity index as modified by Greenberg (1956):

$$D = 1 - \lambda$$

where

$$\lambda = \sum_{i=1}^S p^2$$

$p$  = proportion of individuals of species  $i$

$S$  = total number of species.

An equitability index modified from Heip (1974) was calculated by the formula:

$$\psi = \frac{E}{S}$$

where  $E$

$$E = \frac{1}{\lambda} \text{ (MacArthur 1972),}$$

$S$  and  $\lambda$  are as previously defined.

Student's T-test (McClave and Dietrich 1979) was used to determine significant differences in values of the odds ratio; sizes of chitons, mussels and urchins eaten by gulls at Chichagof Harbor and Massacre Bay; sizes of chitons, mussels, and urchins occurring at Chichagof Harbor and Massacre Bay; and prey preference experiment handling times for adults and juveniles, and for juveniles at Massacre Bay and juveniles at Chichagof Harbor. Data on GUTs, handling times, and search times at Chichagof Harbor and Massacre Bay were normalized

by natural log transformations and tested for differences with Student's T-test. Coefficients of determination were used to determine significance of relationships between prey preferences and net rate of energy gain, between size of prey and handling time, and between size of prey and success rates. Differences were considered significant at the  $P < 0.05$  level.

## RESULTS AND DISCUSSION

Time budgets and foraging patterns

Dietary contents and field observations of gulls indicated that they foraged almost entirely in or near the ocean during the summer months. They fed principally on invertebrates in the intertidal zones and on fish in the neretic zone. There appeared to be advantages and disadvantages to foraging in both of these areas. Fish were much higher in caloric value (1.49 Kcal/g wet wt.) than invertebrates (0.67 Kcal/g wet wt.) (Cummins and Wuycheck, 1971), but casual observations of gulls feeding on fish indicated that they were a spatially and temporally less predictable food resource. Although invertebrates were lower in energy, they were more predictable (i.e., available) in space and time.

Gulls changed their foraging patterns seasonally. Early in the summer when adults were feeding young, few gulls foraged intertidally. Ninety-six percent of the prey regurgitated by juveniles (n=56) was fish, the remaining four percent was zooplankton. Thus, adults fed nestlings fish rather than calcareous intertidal invertebrates that were probably more difficult to digest. When juveniles began to feed themselves many adults and juveniles foraged in intertidal areas on a lower energy but predictable prey resource.

Time budgets and foraging patterns of gulls feeding intertidally were influenced by tidal cycles. During spring and neap tides most

foraging occurred at or near low tide levels (Fig. 2). Most gulls that were observed in the Laminaria zone during spring tides were foraging (Chichagof Harbor 96%, Massacre Bay 99%), and many gulls that were in the Alaria zone during spring tides were foraging (Chichagof Harbor 63%, Massacre Bay 38%) (Table 2). In contrast, most gulls observed in the mussel and barnacle zones during spring tides were resting (Chichagof Harbor 71, 100% and Massacre Bay 100 and 100%, respectively). However, during neap tides more gulls were observed foraging in the Alaria and mussel zones (92 and 74%, respectively; Table 2). Hence, activity patterns of gulls with respect to zones changed with tidal cycles. Generally, the mussel zone and to some extent the Alaria zone were used for resting during spring tides and foraging during neap tides.

Foraging activities did not occupy a large portion of the day. The percent of gulls foraging in the entire intertidal community at a given time was relatively low. During spring low tides a higher percentage of gulls fed at Chichagof Harbor than at Massacre Bay and at Chichagof Harbor a higher percentage of gulls fed during spring low tides than neap low tides. During spring low tides 9% (391 of 4378) of the gulls observed in the intertidal area at Massacre Bay were foraging compared to 27% (798 of 2924) at Chichagof Harbor. Therefore, gulls may have had to forage longer at Chichagof Harbor than at Massacre Bay to obtain the necessary energy requirements. At Chichagof Harbor only 12% (161 of 1320) of the gulls observed in the intertidal zones during neap tides were foraging. There were four possible reasons why I observed a higher percent of gulls foraging

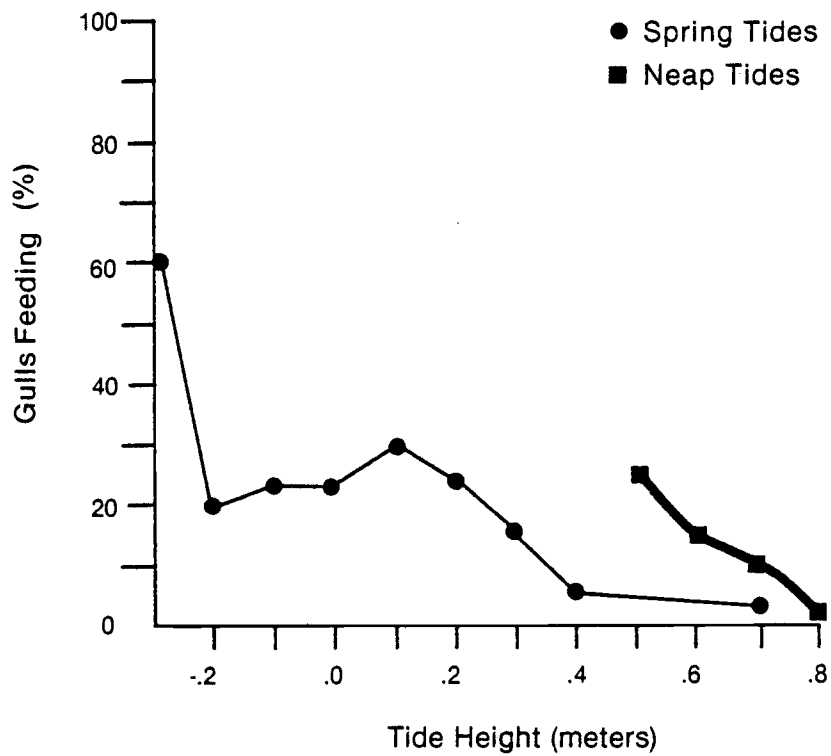


Figure 2. Percent of gulls feeding in the intertidal zones in relation to tide height, for spring and neap tides (data from observations at Chichagof Harbor, Attu Island, Alaska).

Table 2. Percent of gulls that were foraging/resting in each intertidal zone (upper portion of table) and percent of foraging gulls that used each intertidal zone (lower portion of table) in relation to study site and tidal cycle on Attu Island, Alaska.

Study Site (Tide Cycle)	(n)	Intertidal Zone			
		<u>Laminaria</u>	<u>Alaria</u>	Mussel	
Massacre Bay (spring tides)	(4378)	99/1	38/62	<1/100	<1/100
Chichagof Harbor (spring tides)	(2924)	96/4	63/37	29/71	<1/100
Chichagof Harbor (neap tides)	(1320)	0/0	92/8	74/26	<1/100
Massacre Bay (spring tides)	(391)	38	58	2	2
Chichagof Harbor (spring tides)	(778)	45	46	7	2
Chichagof Harbor (neap tides)	(162)	0	53	46	1

during spring tides than neap tides: 1) gulls that foraged at Chichagof Harbor during neap tides obtained food more quickly than when they foraged during spring tides, 2) assimilation time was longer for prey eaten during neap tides, thereby, forcing gulls to wait longer between foraging bouts while food digested, 3) gulls foraged more in the ocean during neap tides and used the intertidal area for resting, 4) prey available during neap tides was lower in food value than prey available during spring tides. Search and handling times for important prey taken during spring tides (urchins, 44s and chitons, 41s) and neap tides (mussels, 22s and barnacles, 16s) support (1). Morphology of prey species eaten during neap and spring tides supports (2) (i.e., mussels have calcareous valves that gulls' gizzards must crush; urchins and chitons do not need to be crushed). Fish remains in pellets differed little between spring (6%, n=512) and neap (5%, n=195) tidal series, refuting (3). Since  $E_n$  for random foraging within the upper intertidal zones (barnacle, 7Kcal/h and mussel, 38Kcal/h) was much lower than for the lower zones (Alaria, 111Kcal/h and Laminaria, 93Kcal/h) (4) is supported. Hence, probable reasons that fewer gulls forage at any given time during neap tides compared to spring tides at Chichagof Harbor are shorter search time, longer assimilation time, and lower food value of prey taken during neap tides. I cannot determine the relative importance of each of these factors.

Gulls utilized intertidal zones unequally for foraging and used particular zones differently during neap and spring tide cycles. During spring low tides when all zones were exposed, most foraging



occurred in the Alaria and Laminaria zones (Table 2). During neap low tides when the Laminaria zone was covered and the Alaria zone was only partially exposed for short periods, foraging occurred in the Alaria and mussel zones. Gulls foraged little in the barnacle zone at any time. Hence, gulls preferred to feed in the lowest intertidal zones exposed during low tide.

### Diets

Results of three methods used to collect data on diets of gulls (i.e., observations, gut contents, and pellet contents) were generally consistent. For a comparative discussion on these methods and on methods used to analyze the data see Appendix II.

Pellet contents indicated that urchins were the most important prey species of gulls and were used in similar amounts at Chichagof Harbor and Massacre Bay (i.e., 70 and 72 percent occurrence, respectively; Table 3). Other important prey included chitons, mussels, limpets, crabs, snails, barnacles, and fish. Mussels (34%) and barnacles (16%) were important secondary prey at Chichagof Harbor, and crabs (16%) and K. tunicata (15%) were similarly important at Massacre Bay. Diets of gulls on Amchitka were grossly different from diets of gulls on Attu in that urchins were more than six times as prevalent in pellets at Attu and fish were 12 times more important at Amchitka. Other invertebrates were of little importance at Amchitka.

Differences in diets of gulls at these locations can be ultimately attributed to predation by sea otters. Sea otters preyed

Table 3. Frequency of occurrence(%) for all prey in pellets of Glaucous-winged Gulls from two sites on Attu Island and from Amchitka Island, Alaska.

Prey item	Study Site		
	Massacre (n=1244)	Chichagof (n=1581)	Amchitka (n=213)
Urchins ( <u>Strongylocentrotus polyacanthus</u> )	69.7	71.9	10.8
Fish <sup>a</sup>	7.5	7.3	90.6
Chitons ( <u>Mopalia</u> spp.)	3.2	1.1	0
Chitons ( <u>Katharina tunicata</u> )	15.0	10.6	0.5
Mussels ( <u>Mytilus edulis</u> )	5.7	33.5	2.8
Limpets <sup>b</sup>	5.1	10.2	2.3
<u>Nucella</u> spp.	1.8	7.5	3.8
<u>Littorina</u> spp.	0	0.7	0
Crabs <sup>c</sup>	15.6	5.6	2.3
Seastars ( <u>Leptasterias</u> spp.)	1.0	0.8	0.0
Cephalopods	0	0	0.5
Fish eggs <sup>d</sup>	1.0	0	0.9
Amphipods	0.1	0	0
Isopods	0	0	0.5
Barnacles ( <u>Balanus glandula</u> and <u>B. cariosus</u> )	8.8	16.0	0
Birds <sup>e</sup>	2.0	0.8	3.8
Scallops ( <u>Chlamys</u> spp.)	0	0	0.5
Crowberries ( <u>Empetrum nigrum</u> )	0.6	3.0	0
Clams ( <u>Hiatella</u> spp.)	0	0.1	0
Blueberries ( <u>Vaccinium</u> spp.)	0.1	0.1	0
Mussels ( <u>Modiolus</u> spp.)	0.3	0.2	0
Unidentified mollusks	0.2	0.2	1.4
Gooseneck barnacles ( <u>Lepas</u> spp.)	0.1	0.1	1.4
Gumboot chitons ( <u>Cryptochiton</u> spp.)	0.2	0	0
Eider eggs ( <u>Somateria mollissima</u> )	0.1	0	0

<sup>a</sup> Ammodytes hexapterus, Clupea harengus, and unidentified species

<sup>b</sup> Collisella pelta and Notoacmaea scutum

<sup>c</sup> Telmessus cheiragonus, Pugettia spp. and unidentified species

<sup>d</sup> Oncorhynchus spp. and Hexagrammos lagocephalus

<sup>e</sup> Larus glaucescens and Somateria mollissima

almost entirely on invertebrates at Attu (Estes et al. 1981) and have reduced the mean size of urchins, but have not yet reduced the density of urchins at Chichagof Harbor (Table 1). Data on subtidal (J. A. Estes unpubl.) and intertidal (Appendix I) crab densities indicated that there were fewer crabs at Chichagof Harbor. Sea otter predation may have decreased crab populations also, because sea otters preyed heavily on crabs in areas where they were available (Estes et al. 1981). The effects of sea otter predation on diets of gulls as noted by Trapp (1979) were evident by comparing Massacre Bay and Amchitka Island (Table 3). At Amchitka, predation by sea otters has reduced the size and density of urchins and other invertebrates (Estes and Palmisano 1974, Palmisano 1975, and Estes et al. 1978), and as a result gulls fed mostly on fish.

Another major difference in the diets of gulls at the two locations at Attu was the amount of mussels consumed. I believe that sea otters had little influence on this, and that the difference was due to a difference in wave exposure between the Bering Sea and the Pacific Ocean. The Pacific Ocean generally had larger ocean swells than the Bering Sea (personal observation). Mytilus edulis, the only intertidal mussel at Attu, prefers quiet waters but occasionally settles on exposed rocks (Ricketts and Calvin 1968). At Chichagof Harbor there was a well developed band of mussels, while at Massacre Bay there was only a narrow, less dense band of small mussels. I suggest that higher wave exposure results in smaller sizes and lower densities of mussels at Massacre Bay, and consequently gulls selected mussels less frequently.

Monthly tidal cycles had an important temporal effect on the diets of gulls at Attu. During spring low tides all intertidal zones were available to gulls for foraging, but during neap low tides the lower zones were generally covered by water. Consequently, my observations at Chichagof Harbor showed that sea urchins constituted 70% of the prey selected by gulls during spring tides, but only 2% of the prey selected during neap tides (Fig. 3). Similarly, mussels and barnacles comprised 10% of the prey selected by gulls during spring tides and 65% of the prey selected by gulls during neap tides at Chichagof Harbor. Data from pellets which were collected throughout the summer following each tidal cycle at Chichagof Harbor also indicated that urchins were taken at higher frequencies during spring tides than they were during neap tide cycles (Fig. 4). These differences are somewhat less dramatic than those shown by the observational data because the pellet data includes days of intermediate tidal fluxes as tide cycles change from spring to neap and visa versa.

#### Prey selection

During spring tides gulls showed a strong preference to forage low in the intertidal area. At Massacre Bay 96% and at Chichagof Harbor 91% of gulls that I observed foraging were in the Alaria and Laminaria zones (Table 2). Prey density, caloric value, and net rate of energy gain (En) in each intertidal zone were computed to determine if any of these characteristics were correlated with where gulls chose

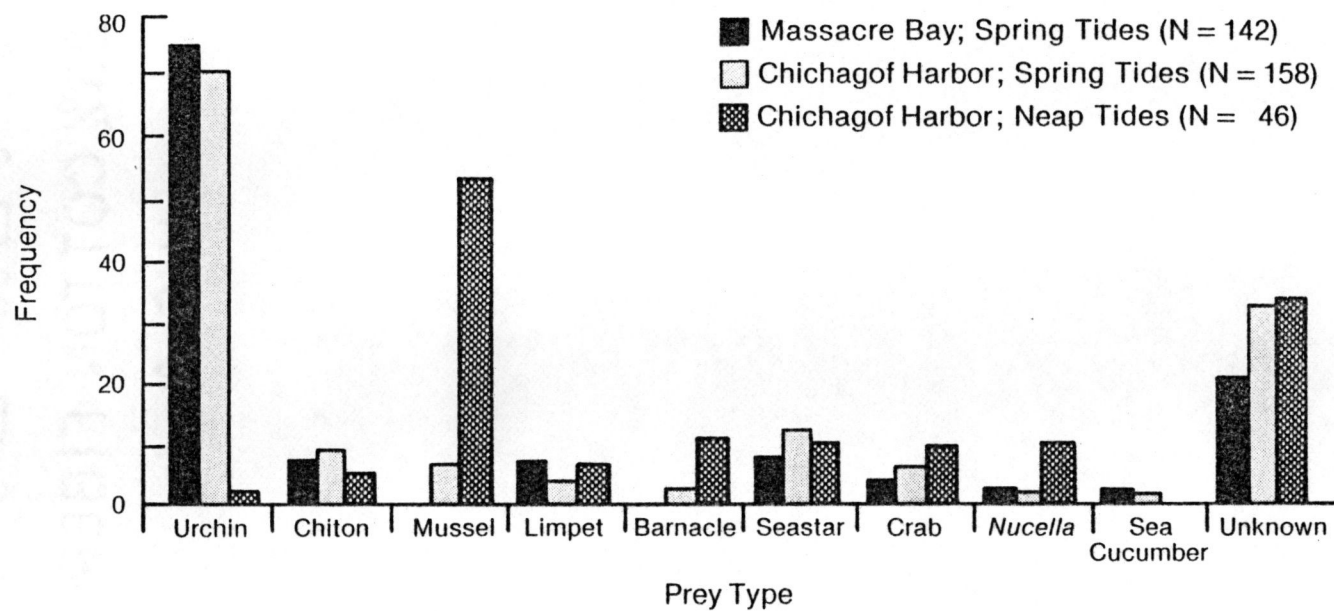


Figure 3. Frequency of occurrence of prey (%) in diets of gulls at Massacre Bay during spring tides and at Chichagof Harbor during spring and neap tides (data from observations at Attu Island, Alaska).

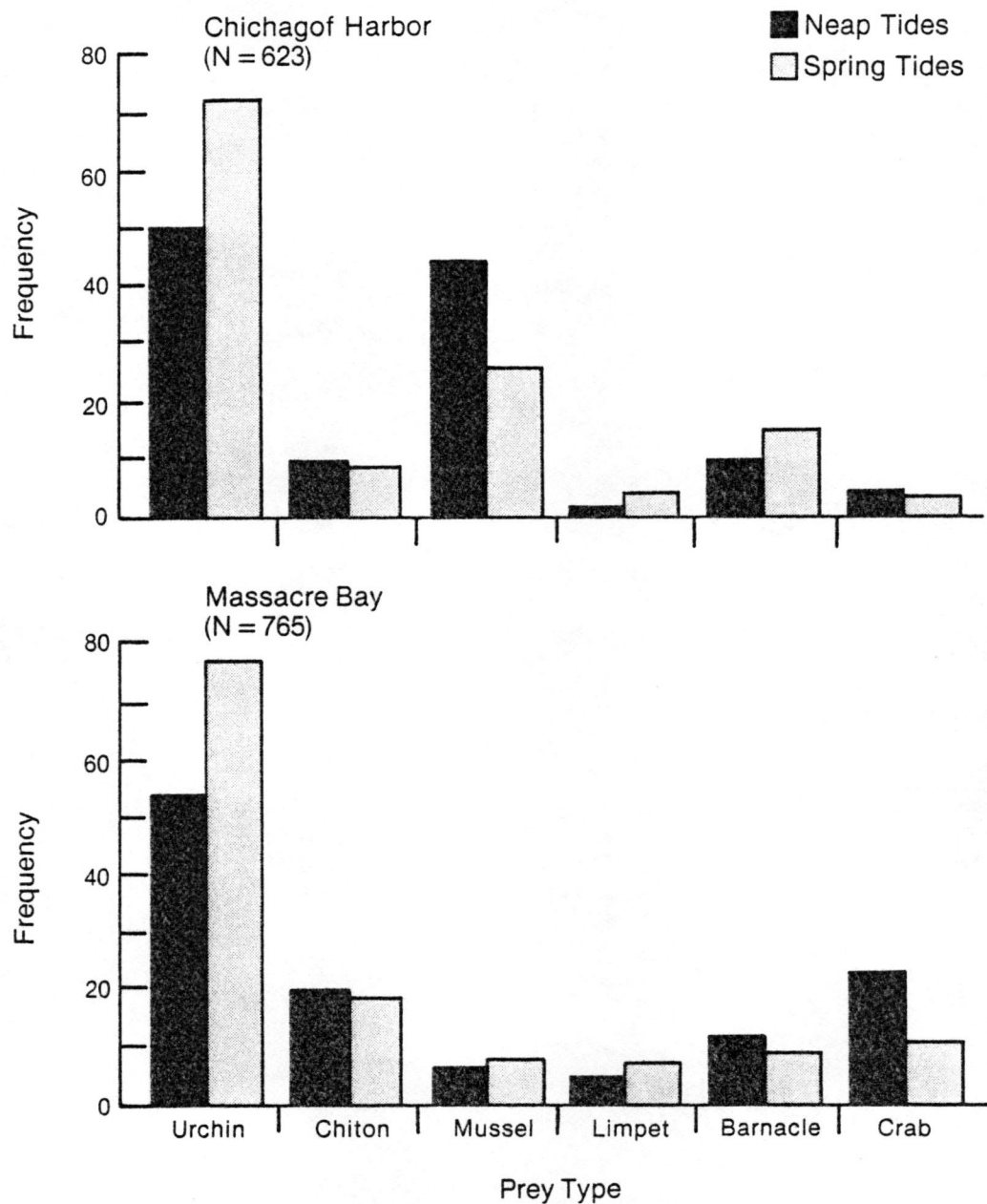


Figure 4. Frequency of occurrence of prey (%) in regurgitated pellets of gulls during spring and neap tides at Chichagof Harbor and Massacre Bay, Attu Island, Alaska.

to forage (Table 4). The mussel and barnacle zones were higher than the lower zones in prey density and Kcalories of prey per unit area and were exposed most of the daylight hours. However, the Alaria and Laminaria zones had higher values of net rate of energy gain (En) assuming gulls fed randomly within each zone. En was higher in the lower zones because, although prey in the upper zones required less search and handling time, prey in the lower zones contained more calories. Total number of prey and caloric value appeared to be unimportant in the choice of gulls for zone; gulls foraged in zones which offered the highest En (i.e., the highest energy gain per unit of search and handling time). If intertidal zones were considered "patches" then gulls selected patches that offered the highest En, as optimal foraging theory predicts.

Gulls selected prey species as well as zones. The odds ratio indicated that at Massacre Bay and Chichagof Harbor, respectively, urchins (+3.8, +4.2), limpets (+2.2, +3.5), and chitons (+1.4, +1.8) were selected, whereas barnacles (-15.5, -5.5) and mussels (-16.3, -1.0) were not selected. All values were statistically significant ( $P < 0.05$ ).

Prey species selected by gulls occurred in highest densities in the Alaria and Laminaria zones, whereas those species that gulls did not select occurred in highest densities in the mussel and barnacle zones. When given a choice gulls selected zones to forage where the selected prey species occurred.

Gulls also chose prey according to size. The selected size range of urchins was about 30-55mm test diameter at both Chichagof Harbor

Table 4. Percent of foraging gulls and characteristics of intertidal zones at Chichagof Harbor during spring low tides.

Intertidal zone	Percent foraging gulls	Percent daylight hours zone exposed	Number prey per 1/4 m <sup>2</sup>	Total Kcalories of prey per 1/4 m <sup>2</sup>	E <sub>n</sub> <sup>a</sup>
Barnacle	2	100	2200.6 <sup>b</sup>	72.0	7.2
Mussel	7	97	1035.6	196.7	37.9
<u>Alaria</u>	46	76	27.8	23.7	111.3
<u>Laminaria</u>	45	15	32.0	31.5	93.2

<sup>a</sup>Kcal/h

<sup>b</sup>From Estes (unpubl. data).



and Massacre Bay. In both cases, the selected size classes occurred in the diet in significantly ( $P < 0.05$ ) different frequencies from those that were available in natural populations residing in the intertidal community (Fig. 5). At Chichagof Harbor, selection was for the largest available prey. At Massacre Bay, selection was for an intermediate range of sizes because the largest size classes have not yet been depredated by sea otters. These data suggest that size selection is constrained by energy limitation at the lower end of the distribution and by physical limitation (probably mouth size) at its upper end.

At both Massacre Bay and Chichagof Harbor gulls ate significantly ( $P < 0.05$ ) more large chitons and fewer small chitons than would be expected from random foraging (Fig. 6). The mean size of chitons that occurred in the intertidal community and those eaten by gulls at Chichagof Harbor were significantly ( $P < 0.05$ ) smaller than chitons that occurred in the intertidal area and those eaten by gulls at Massacre Bay, respectively. Small chitons were not selected at either location. Sea otters fed on chitons (Estes et al. 1981) and may have reduced the number of large chitons from the intertidal at Chichagof Harbor.

Similarly, larger mussels (20-35mm) than the average sizes available in the natural populations were chosen at Massacre Bay and Chichagof Harbor ( $P < 0.05$ ), although the few very large mussels were not consumed (Fig. 7). Mussels 5 to 15mm long were eaten less than expected ( $P < 0.05$ ) at Massacre Bay and Chichagof Harbor. Although the mussels that occurred at Chichagof Harbor were larger ( $P < 0.05$ ) than

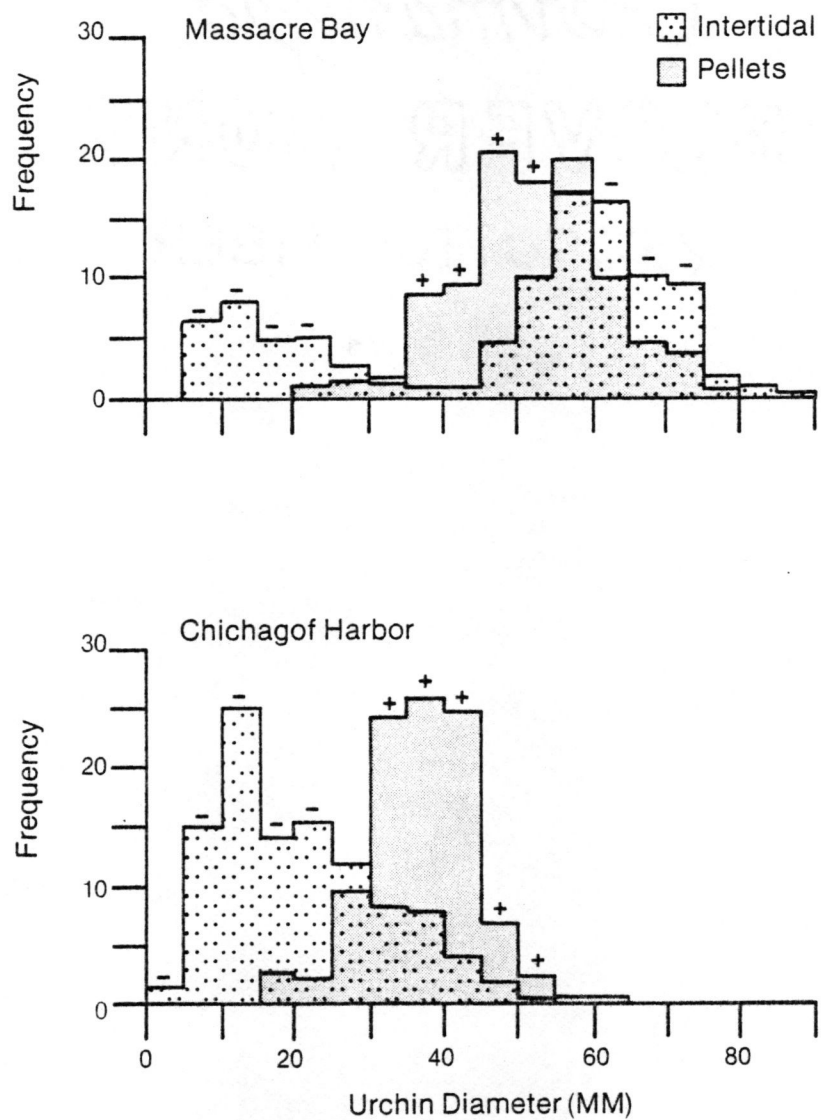


Figure 5. Size class frequency of urchins (%) in the intertidal areas and in gull pellets at Massacre Bay and Chichagof Harbor, Attu Island, Alaska (+ and - indicates significant ( $P < 0.05$ ) positive or negative selection, respectively, for size class).

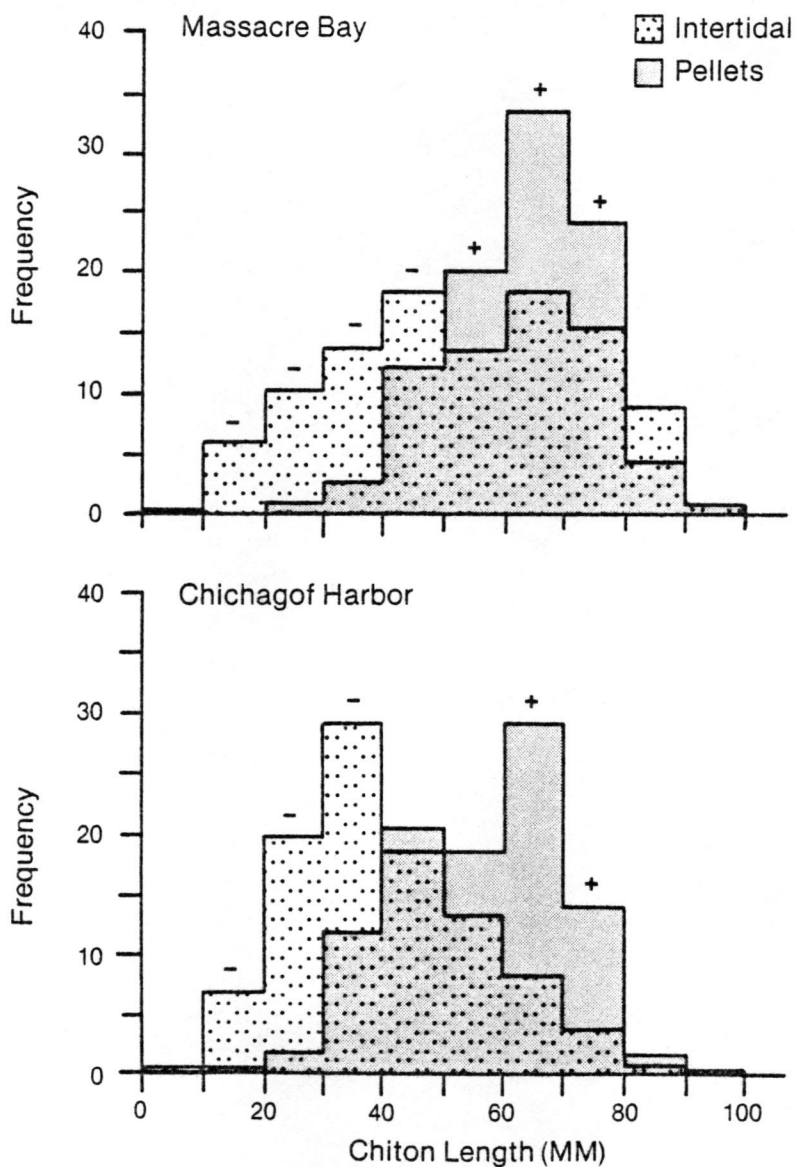


Figure 6. Size class frequency of chitons (%) in the intertidal areas and in gull pellets at Massacre Bay and Chichagof Harbor, Attu Island, Alaska (+ and - indicates significant ( $P < 0.05$ ) positive or negative selection, respectively, for size class).

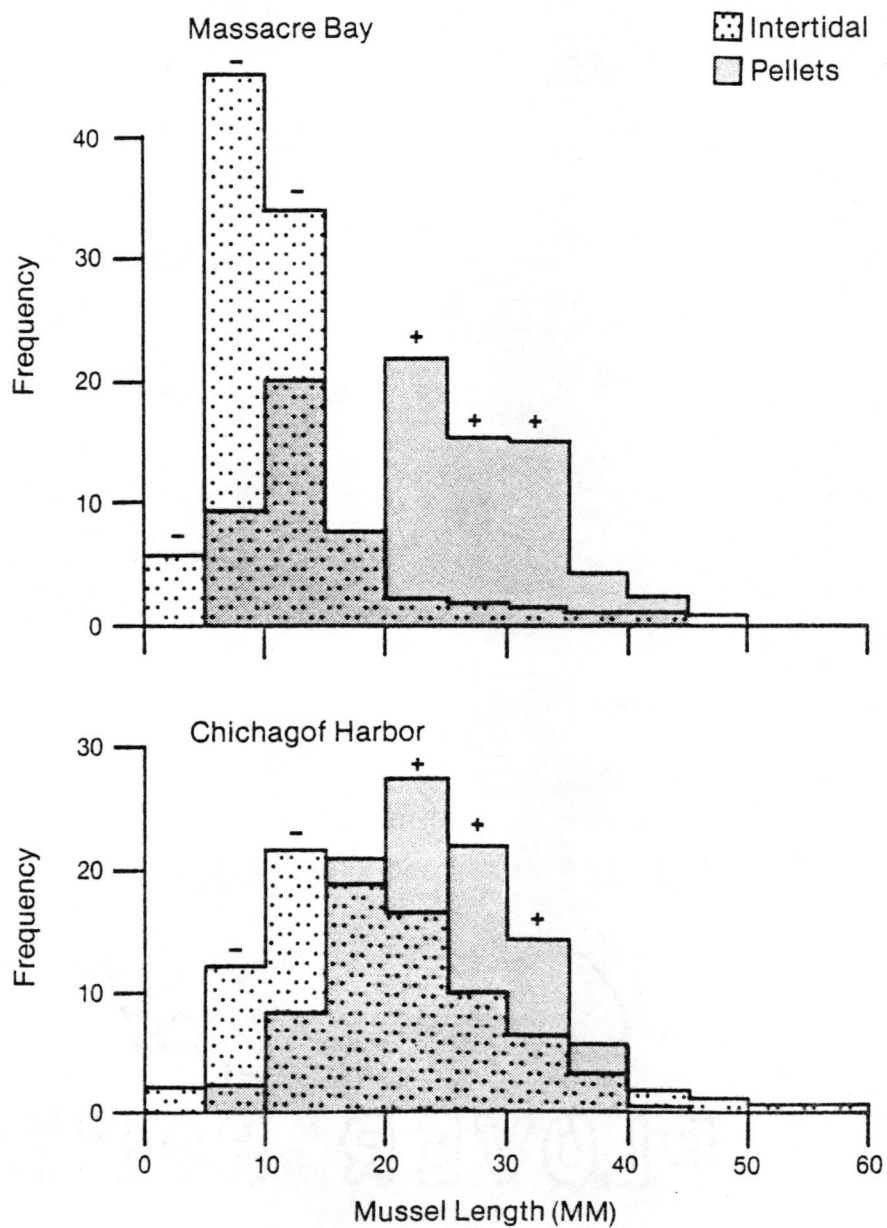


Figure 7. Size class frequency of mussels (%) in the intertidal areas and in gull pellets at Massacre Bay and Chichagof Harbor, Attu Island, Alaska (+ and - indicates significant ( $P < 0.05$ ) positive or negative selection, respectively, for size class).

those at Massacre Bay, the sizes of mussels selected by gulls at each study area were not significantly ( $P < 0.05$ ) different.

Most sizes of limpets were eaten in proportion to their occurrence in the intertidal zones (Fig. 8). However, 15-20mm long limpets at Massacre Bay and 40-45mm long limpets at Chichagof Harbor were eaten significantly ( $P < 0.05$ ) more than expected from random foraging. I suspect these differences in size selection between the two areas are explained by sampling bias combined with different foraging modes.

Limpets occurred on the substrata and on the blades of intertidal algae. Limpets on algae appeared to be much more vulnerable to predation by gulls (I observed one gull that removed over 60 limpets from an algae plant in less than 2 minutes), and most limpets on algae were medium or small sized (personal observation). Although my sample sizes for length of individual limpets eaten were quite large ( $n=109$  at Chichagof Harbor,  $n=203$  at Massacre Bay), the number of pellets and stomachs that contained limpets was much smaller. A few of the pellets from Massacre Bay contained several (e.g., 15, 11, 11, 14) limpets of medium sizes (10-25mm). No pellets from Chichagof Harbor contained more than five limpets, but one stomach contained several medium sized limpets. Apparently, when gulls fed on limpets that were attached to algae they ate many medium sized individuals in one foraging bout, but when they fed on limpets that were attached to rock substrata they ate fewer but selected larger individuals. The pellet samples at Massacre Bay probably contained more pellets by chance from gulls that had fed on limpets that were on algae than did the pellets

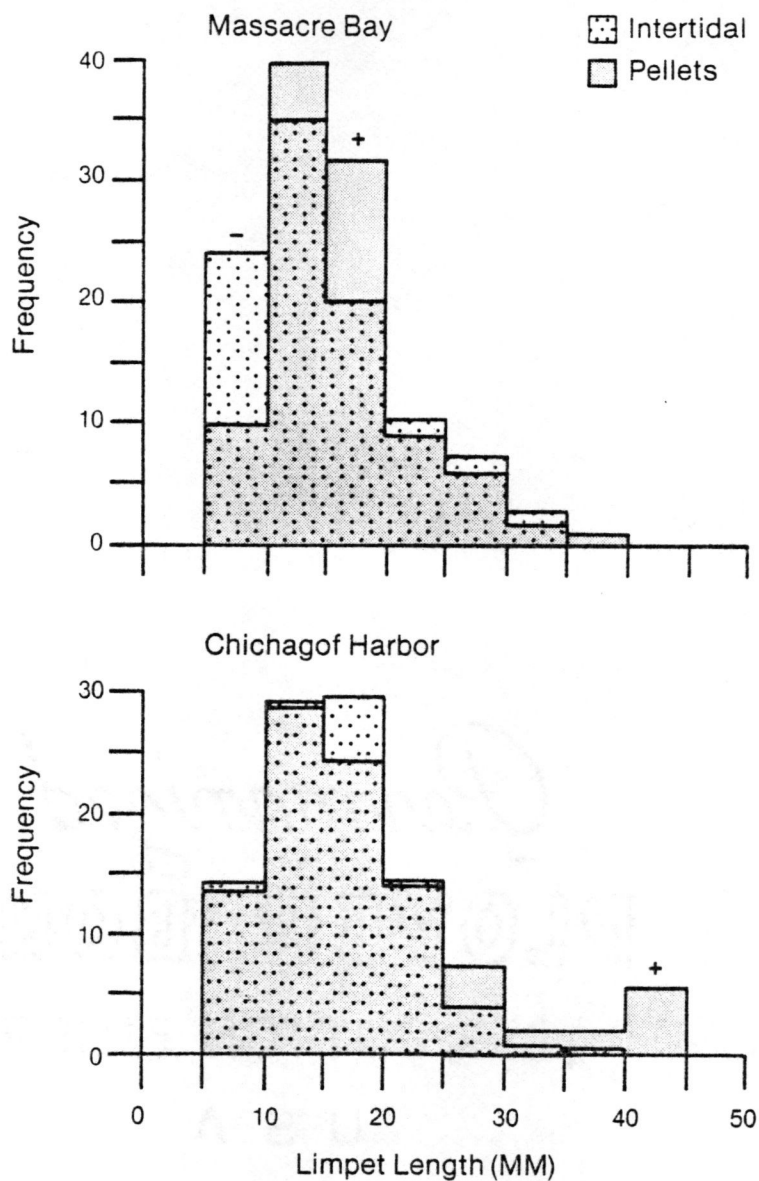


Figure 8. Size class frequency of limpets (%) in the intertidal areas and in gull pellets and stomachs at Massacre Bay and Chichagof Harbor, Attu Island, Alaska (+ and - indicates significant ( $P < 0.05$ ) positive or negative selection, respectively, for size class).

from Chichagof Harbor. Observations of foraging gulls demonstrated an opposite difference (i.e., more gulls at Chichagof Harbor than at Massacre were observed eating limpets that were on algae), which reduced the mean search time and therefore, raised the En for limpets at Chichagof Harbor. Finally, though there were hundreds of tiny (< 5mm) limpets in the intertidal (Appendix I), they were not included in the analyses because gulls did not feed on them.

Frequency distributions of size classes of chitons and mussels occurring in the intertidal region at Massacre Bay and Chichagof Harbor differed, but selection for specific sizes was similar (Fig. 6 & 7). Gulls selected chitons in the 60-70mm size class at Massacre Bay and Chichagof Harbor to similar extents (18 and 22% more than they occurred in the intertidal, respectively). However, the proportion of chitons that occurred in the intertidal community was different (0.17 and 0.07 at Massacre Bay and Chichagof Harbor, respectively). Therefore regardless of the proportion of chitons in the habitat, gulls select them about 20% more often than expected from random foraging. This pattern appeared for several size classes of chitons and mussels.

Hence, gulls selectivity for size classes of prey was independent of the relative abundance of those size classes. Therefore, the number of prey eaten was dependent on the absolute number that were available. When prey of size classes that were selected for were scarce fewer of these prey and more prey of the sizes that were not selected were eaten. Gulls selected large prey that had high En and did not select small prey that had low En. Therefore, the frequency

of prey with low food value in the diets of gulls was dependent upon the number of prey with higher food value, which supports a prediction of optimal diet theory (Pyke et al. 1977).

If gulls generally selected larger than average prey to increase their energy (Kcal) intake, why did they not select large urchins at Massacre Bay? To answer such a question, mode of consuming prey and  $E_n$ , rather than caloric value, must be considered. Most prey that gulls ate were swallowed intact. However, large urchins were too large to be ingested whole. Instead, gulls air-dropped them to break the tests of the urchins or pecked-out the Aristotle's lantern to extract the viscera and energy-rich gonads. Both methods required much more time than when one was swallowed whole; average handling time for the three modes of consuming urchins at Massacre Bay were: swallowed intact, 17s, air-dropped, 128s, and pecked-out, 310s. A longer handling time reduced  $E_n$  (by definition) and furthermore, increased vulnerability to piracy by other gulls (personal observation). Consequently, gulls appeared to select for the largest urchins that could be swallowed whole, thereby, maximizing net rate of energy gained.

#### Benefits of selective foraging

Gulls selected particular Intertidal zones to forage in and specific prey species and prey sizes to eat. What benefit did they derive by foraging selectively in this way? An obvious potential benefit was an increase in net rate of energy gain ( $E_n$ ). A comparison



of mean  $E_n$  for completely random foraging versus selective foraging for zones, species, and size supports this conclusion. Completely random foraging in the intertidal region at Massacre Bay and Chichagof Harbor, respectively, yielded 78 & 62 Kcal/h for a gull. For hypothetical gulls that selected zones but foraged randomly for species and sizes, values were 135 & 96 Kcal/h. The calculated  $E_n$  for gulls selecting zones and species but foraging randomly for sizes was 116 & 63 Kcal/h. The value of  $E_n$  for gulls foraging selectively in Alaria and Laminaria zones with respect to prey species and sizes was 176 & 174 Kcal/h which was a 126 & 181% increase over the  $E_n$  for gulls foraging randomly. Selecting intertidal zones raised  $E_n$  more at Massacre Bay (73%) than at Chichagof Harbor (54%) because prey were larger at Massacre Bay. Selecting zones and species increased  $E_n$  less than selecting only zones because few chitons, which were high in caloric value, were eaten by gulls. Foraging selectively for zones, species, and sizes yielded an increase in  $E_n$  at Chichagof Harbor that was 44% higher than at Massacre Bay. Therefore, gulls at Chichagof Harbor must be more selective in order to maintain a high  $E_n$ .

#### Prey preference experiments

Field experiments demonstrated definite preference by gulls for prey species and sizes, independent of any extrinsic factors that might make different species or sizes easier or more difficult to obtain. Large (50-60mm) chitons were most highly preferred followed by medium urchins (30-40mm) at both Chichagof Harbor and Massacre Bay

(Table 5). Large urchins (70-80mm) were ranked higher at Chichagof Harbor than at Massacre Bay but were not highly preferred at either area. Attraction to an oddity (Smith and Dawkins 1971 and Mueller 1977) may explain the higher use of large urchins at Chichagof harbor since urchins of that size class do not occur in the intertidal community there. Small urchins and small chitons were preferred more than large urchins and mussels.

Large chitons, which were most preferred, offered the highest net rate of energy gain ( $E_n$ ) (i.e., Kcal of prey/handling time) to gulls and medium sized urchins, which were second in preference, provided the second highest  $E_n$  (Table 5). If only chitons and urchins were considered, prey preference of gulls was significantly correlated ( $R^2=0.78$ ) with  $E_n$  of the prey items, but if small mussels were included the correlation was not significant ( $R^2=0.22$ ). Mussels ranked higher in  $E_n$  than in preference (see juvenile experiment data for  $E_n$  of large mussels; Table 6). Unlike urchins and chitons, mussels have a solid calcareous shell that encloses the edible portion. For a gulls to obtain the palatable part their gizzard crushes the hard shell. Gulls, like other carnivorous and piscivorous birds have a small, weak gizzard compared to granivores or molluscivores (Welty 1975). Thus, a greater time cost is probably required for gulls to assimilate energy from mussels than urchins or chitons, thereby reducing net rate of energy gain for mussels in a manner that is not accounted for in my calculation of  $E_n$ .

Apparently  $E_n$  was an important factor in determining prey preference by gulls. However, a higher correlation between preference

Table 5. Results of prey preference experiments with adult Glaucous-winged Gulls at Massacre Bay and Chichagof Harbor, Attu Island, Alaska.

	Percent Chosen First and Second				Net rate of energy gain $K_p$		Average handling time (s)		Success rates (%)	
	MASSACRE		CHICHAGOF		Mass <sup>b</sup>	Chic <sup>b</sup>	Mass <sup>b</sup>	Chic <sup>b</sup>	Mass <sup>b</sup>	Chic <sup>b</sup>
	1st <sup>a</sup> (n=96)	2nd <sup>a</sup> (n=70)	1st (n=66)	2nd (n=66)						
Ig. Chiton	59	11	42	18	1699	1774	9.5±1.5	9.1±2.0	77	66
Med. Urchin	24	11	35	21	739	1150	5.6±0.7	3.6±0.6	77	89
Sm. Chiton	6	43	4	12	729	344	1.7±0.1	3.6±1.0	88	85
Sm. Urchin	5	29	8	43	112	195	2.8±0.6	1.6±0.2	98	98
Ig. Urchin	3	1	11	6	137	186	310.7±62.4	229.1±36.9	42	20
Sm. Mussel	2	1	0	0	339 <sup>d</sup>	339 <sup>d</sup>	3.8±0.8	1.2±un <sup>e</sup>	67	13
Ig. Mussel	0	3	0	0	-f	-f	-f	-f	0	0

<sup>a</sup>Column does not add up to 100 because of rounding error.

<sup>b</sup>Mass = Massacre Bay and Chic = Chichagof Harbor.

<sup>c</sup>Mean 195% confidence interval.

<sup>d</sup>Combined handling times for Chichagof Harbor and Massacre Bay to increase small sample size (n = 1 & 6, respectively).

<sup>e</sup>un = confidence intervals were undefined because sample size was one.

<sup>f</sup>No data were available because large mussels were not eaten by adult gulls in experiments.

Table 6. Results of prey preference experiments with juvenile Glaucous-winged Gulls at Massacre Bay and Chichagof Harbor, Attu Island, Alaska.

	Percent Handled First and Second				Net rate of energy gain $E_h$		Average Handling time (s)		Success rates (%)	
	MASSACRE		CHICHAGOF		Mass <sup>a</sup>	Chic <sup>a</sup>	Mass <sup>a</sup>	Chic <sup>a</sup>	Mass <sup>a</sup>	Chic <sup>a</sup>
	1st (n=22)	2nd (n=22)	1st (n=69)	2nd (n=66)						
Lg. Chiton	43	30	33	17	606	1021	26.6	15.8	42	37
Med. Urchin	19	8	16	27	161	752	25.7	5.5	55	75
Sm. Chiton	23	35	6	11	210	149	5.9	8.3	77	41
Sm. Urchin	0	8	19	25	89	149	3.5	2.1	82	85
Lg. Urchin	5	0	23	11	90	195	471.9	218.3	27	15
Sm. Mussel	5	0	3	1	262	320	4.4	3.6	29	20
Lg. Mussel	5	19	0	8	- <sup>b</sup>	544	- <sup>b</sup>	23.2	0	7

<sup>a</sup>Mass = Massacre Bay and Chic = Chichagof Harbor.

<sup>b</sup>No data were available because large mussels were not eaten by gulls in experiments.

and  $E_n$  than observed here might be expected if it were the only factor. There are at least two additional factors not accounted for by  $E_n$ , that may have affected prey preference of gulls, these are 1) assimilation time and/or energy, and 2) experience and the formation of a search image. Effects of long assimilation time and/or high energy cost on prey preferences were apparent in gulls' low preference for mussels, which have a high  $E_n$ . Rabinowitch (1969) conducted experiments with zebra finches and found that experience influenced preferences. Birds were conditioned on a particular prey then given a choice between that prey and a prey type with higher energy value. The conditioned birds chose the type they had previously eaten rather than the high energy type. Comparing Massacre Bay (where gulls ate many large urchins and few medium and small ones) and Chichagof Harbor (where gulls ate many medium and small urchins; Fig. 5), medium and small urchins were preferred more at Chichagof Harbor than at Massacre Bay (Table 5). Handling times for medium and small urchins were lower at Chichagof Harbor than at Massacre Bay, and success rates for medium urchins were higher at Chichagof Harbor. Higher preference for a particular prey item was, therefore, associated with shorter handling times and higher success rates. These observations suggest that handling times were lower and success rates were higher for gulls that had more experience foraging on a particular prey item.

Prey preference experiments indicated that adult gulls have search images and that those with more experience foraging on particular prey items had apparently formed stronger search images for those prey than birds with less experience (e.g., gulls at Chichagof

Harbor appeared to have had stronger search images for small urchins than gulls at Massacre Bay). Eighty-four percent of the gulls that handled a medium urchin first at Chichagof Harbor handled a small urchin second, while only 52% of the gulls at Massacre Bay chose the small urchin after choosing the medium one. The small chiton was handled after the large chiton in 39 and 42% of the experiments at Chichagof Harbor and Massacre Bay, respectively. Two points should be noted from these observations. First, gulls sequentially chose the same species, although more preferred prey were present, more than expected assuming random foraging (17%) (i.e., with six prey items remaining in an experiment the probability of choosing any one is 17%). I suggest this indicates that gulls have search images for particular prey items. Second, gulls chose the medium and small urchins sequentially more often at Chichagof Harbor than at Massacre Bay, which demonstrates that search images were probably stronger in gulls that had had more experience foraging on small urchins. If gulls at Chichagof Harbor have stronger search images for small urchins than gulls at Massacre Bay, then size of prey items must be important in the formation of a search image. Being size selective was extremely beneficial in terms of increasing  $E_n$  at Chichagof Harbor, thus it is reasonable to argue that size should be an important factor in the formation of search images. Pellet contents indicated that gulls ate about 70% urchins at both Chichagof Harbor and Massacre Bay, but at Chichagof Harbor 94% of the urchins eaten were 40mm or less in diameter compared to 29% at Massacre Bay. I suggest that gulls at Massacre Bay had weaker search images for small

urchins than did at Chichagof Harbor, because, at Massacre Bay the smaller prey items were less common, and therefore, gulls were less experienced in feeding on them.

Gulls often chose two urchins sequentially, even though a large chiton with much higher  $E_n$  was present. Therefore, I suggest that gulls form search images that influence their choice of prey in a manner that results in suboptimal  $E_n$  in these experiments. However, this does not necessarily mean that search images cause gulls to forage suboptimally in natural conditions. This is relevant to other manipulative studies involving foraging behavior because artificial conditions may cause animals to alter their foraging behavior, or cause optimal foraging behavior to appear suboptimal.

In summary, three factors appeared to influence prey preferences of gulls: i) net rate of energy gain, ii) assimilation rate, and iii) previous experience and search images.

Handling times and success rates for prey items in prey preference experiments were significantly correlated to prey size ( $R^2=0.71$  and  $0.74$ ), respectively). Handling times increased with prey size and success rates decreased as prey size increased (Table 5) indicating that gulls were more efficient eating small than large prey. There appeared to be a trade-off of efficiency for calories as prey size increased, which may have caused very large prey to have had lower  $E_n$  than medium sized prey. Therefore, gulls may have been optimizing their  $E_n$  by selecting medium to large prey rather than very large prey.

Juvenile gulls exhibited similar but weaker prey preferences than adults (Table 6). Chitons were preferred more at Massacre Bay than at Chichagof Harbor and urchins were preferred more at Chichagof Harbor than at Massacre Bay. Handling times of juveniles were significantly ( $P < 0.05$ ) longer than those of adults, and handling times for juveniles at Massacre Bay were significantly longer than those at Chichagof Harbor. Why did these differences occur? Two factors may have increased experience of juveniles at Chichagof Harbor, which may have decreased handling times: 1) there were more medium and small urchins at Chichagof Harbor so gulls there probably ate more and therefore had more experience than birds at Massacre Bay, 2) experiments were conducted later in the season at Chichagof Harbor so juveniles were a few weeks older than those at Massacre Bay, consequently, they had more experience eating intertidal prey. Success rates for juveniles were an average of 27% lower than for adults, and as with adults, highest success was with small prey items. Juvenile feeding behavior in prey preference experiments indicated that juveniles had less defined preferences and were less efficient foragers than adults. Consequently, experience was correlated with stronger prey preferences and increased foraging efficiency.

#### Prey preference vs selection

Prey preference experiments demonstrated that gulls preferred large chitons over urchins. However, in the field gulls selected urchins more strongly than chitons. This discrepancy can be explained



by differential availability of these organisms in the field. The shear force required to remove chitons (20.8kg, mean length=53mm, n=103) from the substratum was significantly ( $P<0.05$ ) higher than for urchins (3.7kg, mean diameter=47mm, n=105). Thus, even though chitons were abundant in the intertidal community most of them were unavailable to gulls because of their ability to adhere so strongly to the substratum. To investigate preference of predators availability must be equal, consequently, preference can rarely be determined in natural conditions.

#### Foraging Behavior

Foraging behavior of gulls and net rate of energy gained (En) for prey items differed at Chichagof Harbor and Massacre Bay. Mean search times for gulls at Chichagof Harbor and Massacre Bay were not significantly different ( $P<0.05$ ), but combined mean handling times for prey items were longer ( $P<0.05$ ) at Massacre Bay (Table 7). Giving-up time (GUT) (the period of continuous searching between the last capture and when the gull left the intertidal) was significantly longer at Massacre Bay than at Chichagof Harbor. En, combined, for the proportions of selected prey (i.e., urchins, chitons, and limpets) that occurred in gulls' diets, was lower at Chichagof Harbor than at Massacre Bay.

Differences in foraging behavior of gulls at Chichagof Harbor and Massacre Bay appeared to result largely from large urchins having been removed from the population at Chichagof Harbor by sea otters. Large

Table 7. Caloric value of selected prey items and their means weighted to the proportion of adult gulls' diet they comprised and parameters describing foraging behavior of gulls at Chichagof Harbor and Massacre Bay, Attu Island, Alaska.

Study area and prey item	N	Search time <sup>a</sup> (s)	Handling time <sup>a</sup> (s)	Kcal per prey	E <sub>n</sub> (Kcal/h)	GUT <sup>ab</sup> (s)	Threshold E <sub>n</sub> (Kcal/h)	Percent E <sub>n</sub> <sup>c</sup> of diet for U, C, & L <sup>d</sup>
<b>CHICHAGOF</b>								
Urchins	252	35.8±2.6	8.3±1.6	1.78	145.0		61.3	49.9
Chitons	19	37.9±12.7	3.1±0.4	5.86	514.8		213.0	13.4
Limpets	111	9.9±1.1	1.5±0.1	0.70	243.9		26.0	36.7
Mussels	59	18.9±2.8	2.9±0.7	0.34	56.0			
Barnacles <sup>g</sup>	14	14.1±3.3	2.1±0.3	0.03	6.6			
U, C, & L <sup>d</sup> weighted mean	382	28.4 <sup>h</sup>	6.1 <sup>g</sup>	1.67	174.3	96±14.6 <sup>fh</sup>	58.9	
<b>MASSACRE</b>								
Urchins (intact) <sup>e</sup>	100	45.8±5.5	16.9±1.8	3.49	200.1			
Urchins (air-dropped) <sup>e</sup>	38	22.1±6.9	127.7±8.2	8.25	198.4			
Urchins (pecked out) <sup>e</sup>	9	54.6±20.6	310.1±51.7	8.25	81.5			
Urchins weighted mean	147	40.2	63.3	5.35	186.0		85.1	77.2
Chitons	8	123.7±47.0	3.0±1.0	7.86	223.3		170.5	8.6
Limpets	50	15.5±2.6	1.7±0.3	0.37	76.9		8.0	14.2
U, C & L <sup>d</sup> weighted mean	205	37.7 <sup>i</sup>	45.5 <sup>g</sup>	4.06	175.5	163±18.8 <sup>fi</sup>	70.1	

<sup>a</sup> Values are means with 95% confidence intervals.

<sup>b</sup> Giving up time (GUT) = period from last successful encounter until gull left intertidal area.

<sup>c</sup> Kcal/h

<sup>d</sup> U=urchins, C=chitons, L=limpets.

<sup>e</sup> Mode of consumption.

<sup>f, g, h, i</sup> Values footnoted with same letter were significantly different at P<0.05.

urchins (>60mm) at Massacre Bay required longer handling times for gulls to consume them, but they provided a higher  $E_n$  than those at Chichagof Harbor (Table 7). Giving-up time (GUT) was longer where urchins had a higher  $E_n$  (Massacre Bay), which would be expected if gulls fed optimally (i.e., a predator may use more energy to find a prey if the prey is high in Kcal).

GUTs at Chichagof Harbor and Massacre Bay were significantly ( $P < 0.05$ ) longer than search time, which suggests that gulls hunted by expectation (i.e., they hunted in a patch until a threshold level, measured in units such as time, number, or  $E_n$ , was attained). Gulls searched unsuccessfully in an area two to three times as long as their average search time before they gave up. Presumably, gulls left a search area or patch after a threshold was reached.

Hunting by expectation has been discussed by other investigators interested in when predators leave one patch and go to another (Gibb 1958, Krebs et al. 1974, and Zach and Falls 1976a, b, c). Gibbs (1958) conducted a field study of titmice and concluded that they hunted by number expectation (i.e., they left a patch after finding a certain number of prey regardless of the number of remaining prey) and postulated the hypothesis of "hunting by expectation". Subsequently, his conclusions have been criticized by others who argued that the data provided equivocal support for his hypothesis. Krebs et al. (1974) concluded from laboratory experiments that chickadees did not hunt by number or time expectation (i.e., leave a patch after a particular time of hunting). Laboratory experiments on ovenbirds demonstrated that they did not hunt by number or time expectation, but

rather they seemed to expect where to find food and hunted in those areas (Zach and Falls 1976c). On the other hand, laboratory experiments by Smith and Dawkins (1971) indicated that great tits hunted by expectation. After several experiments, patches with high prey densities were switched with patches with low prey densities. For several trials great tits continued to spend longer periods of time in the patches of previously high density than normally spent in patches of low density. I conclude from the literature on hunting by expectation that birds do hunt by expectation but not by number or time expectation. All studies discussed previously involved only one prey type with patches differing only in density of prey. My study of gulls foraging in the intertidal differ from the designs of the other studies in that gulls forage on different species and different sizes of prey. Also, different sizes of prey occur in different areas (i.e., Chichagof Harbor vs Massacre Bay). GUTs were dissimilar at Chichagof Harbor and Massacre Bay, which indicated gulls develop different expectations at each location. The manner in which gulls forage on Attu suggests that they hunt to maximize net rate of energy gain and when the expected  $E_n$  for a patch decreased to a threshold level gulls left the patch. The threshold  $E_n$  (i.e., average kcal of prey in a habitat/average handling time + the GUT for that habitat) differed in areas with respect to average  $E_n$  of important prey species (i.e., threshold  $E_n$  for urchins was higher at Massacre Bay where the  $E_n$  was higher) (Table 7).

What determined the threshold of GUT relative to  $E_n$ ? The GUTs for gulls foraging at Chichagof Harbor and Massacre Bay indicated that

gulls gave up searching in a patch when the expected En from consuming urchins decreased 80 to 100 Kcal/h below the average En for the habitat (Table 7). Using the En for urchins the threshold En was 101.1Kcal/h at Massacre Bay 83.7Kcal/h at Chichagof Harbor below expected En for urchins in the habitats. What is the significance of a decrease in En of 80-100 Kcal/h? Using the cost of flight of Laughing Gulls (Larus atricilla) (which are much smaller than Glaucous-winged Gulls) at 31km/h (Gordon et al. 1977) and weights of gulls collected on Attu, I calculated the cost of flight for Glaucous-winged Gulls to be 76 Kcal/h and 60 Kcal/h for males and females, respectively. Schnell and Hellack (1979) measured birds flight speeds in nature and found that the average speed for Herring Gulls (Larus argentatus) and California Gulls (Larus californicus) (both slightly smaller than Glaucous-winged Gulls) was 38.8 km/h. If Glaucous-winged Gulls also fly about 39km/h, then then cost of flight for them in nature would be higher than the cost of flying at 31 km/h. I suggest that gulls left patches when the cost of traveling to a new patch became less than the expected En for the habitat. The cost of traveling to a new a patch involves two factors: 1) the loss of the En from the patch the animal is in, and 2) the energy used for travel to a new patch. For example, if the energy used for travel was 100Kcal/h and the expected En for the habitat was 180Kcal/h, then a animal gaining 150Kcal/h in a patch would stay because  $150 + 100 > 180$ , but a bird gaining only 50Kcal/h in a patch would leave because  $50 + 100 < 180$ . More formally, gulls left patches when

$$E_n \text{ patch} + |E_c| \text{ travel} < E_n \text{ habitat}$$

where

$E_c$  = cost of flying (Kcal/h)

$E_n$  = Kcal of prey/search & handling time (h)

The model uses only rates of energy gained and lost. Therefore, it will probably be best suited to predict threshold  $E_n$  for predators that have substantial energy losses due to travel between patches.

Charnov (1976) developed a model to predict GUT for patches. He predicted that "a predator should leave a patch when the marginal capture rate in the patch drops to the average capture rate for the habitat" (Charnov, 1976:133) (marginal capture rate is equivalent to threshold  $E_n$ ). Charnov took into account travel cost in the capture rate for the habitat. Stating his prediction in relation to mine, a predator should leave a patch when the marginal capture rate in the patch drops to the average capture rate for the habitat minus the cost of travel. The general prediction of Charnov's and my model was the same, but he used actual times and energy values and I used rates of energy gained or lost. Charnov's model may be predictive for more different types of habitats (i.e., for habitats with patches very close as well as far from one another), but mine may provide for easier data collection in the field.

## GENERAL DISCUSSION

Predation by sea otters influenced diets and foraging behavior of Glaucous-winged Gulls by altering their prey base. Gulls preyed mostly on invertebrates on Attu and fish at Amchitka. These changes probably occurred gradually over many years after Amchitka was recolonized by sea otters. The effects that sea otter predation had on the diets and foraging strategies of gulls on Attu included: i) a reduction in the mean urchin size eaten by gulls, which in turn decreased handling time,  $E_n$ , and GUT; ii) an increase in the relative importance of other prey species, with reference to  $E_n$ ; iii) a possible reduction in number of crabs and size of chitons eaten by gulls; and iv) an increase in diversity of diet. Gulls altered their foraging strategy in relation to the availability of prey to maximize  $E_n$ . For example, they fed in a fashion that increased their  $E_n$ , however, to do this they fed more selectively on urchins at Chichagof Harbor than at Massacre Bay (Fig. 5). The manner in which gulls foraged on Attu indicated that their foraging strategies were flexible and were probably learned rather than innate.

Field experiments indicated that gulls preferred prey that maximized  $E_n$ . However, there were other factors not accounted for in my definition of  $E_n$  (e.g., assimilation rate, experience and search images) that also influenced prey preferences. To accommodate all these factors,  $E_n$  would have to have been defined in a complex equation with variables that could not be measured in most natural systems.

In the field gulls selected medium urchins most; in experiments gulls preferred large chitons most. This discrepancy results because prey are not equally available to predators. Therefore, I believe that the terms selection and preference should be used as defined herein. Preference is difficult if not impossible to determine under natural conditions and may never be determined exactly, while selection can be easily determined in some field situations.

The diversity of prey consumed by gulls was related to sea otter density by a convex functional form (Fig. 9). That is, the dietary diversity of gulls was lowest at Amchitka where otter density was high. At Massacre Bay (otters absent) the dietary diversity was higher than at Amchitka, but lower than at Chichagof Harbor (low otter density). High diversity was a result of high evenness of prey in the diet. This can be explained as follows: where otters are absent, intertidal invertebrates are abundant and gulls forage selectively on high energy forms. As otter populations increase, gulls will continue to feed on invertebrates, but will also feed more on fish, thereby, increasing the diversity of their diets through increasing evenness. Eventually, at yet higher otter densities, the gull diets will decrease in diversity because of reduced availability of intertidal invertebrates and increased consumption of fish. When the otter population at Attu reaches equilibrium, I predict that the gulls will feed almost entirely on fish (as is the case at Amchitka presently) and consequently, the diversity of their diets will be low. This pattern is similar to that observed for other consumer/prey systems. For example density of Littorina littorea in tidepools (Lubchenco



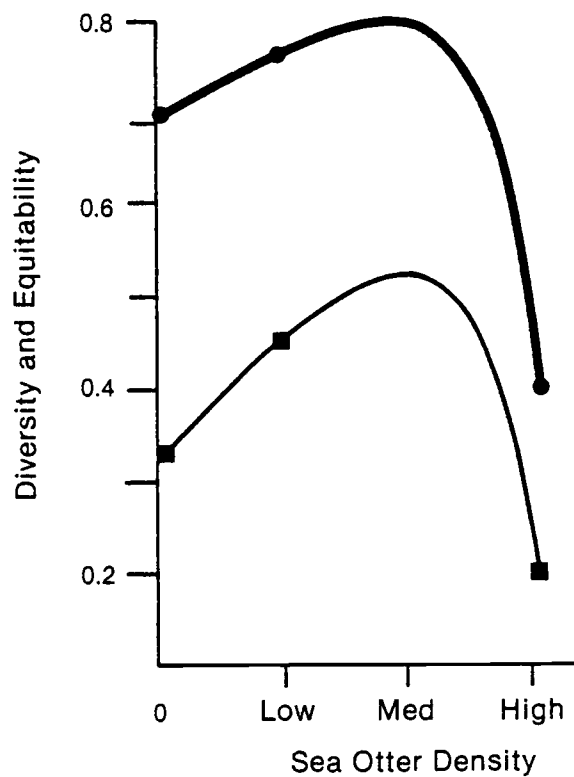


Figure 9. Hypothesized relationship of diversity (●) and equitability (■) of diets of gulls (data from pellets) in relation to density of sea otters (0-Massacre Bay, low-Chichagof Harbor, high-Amchitka Island) in the western Aleutain Islands, Alaska.

1978) and urchins (Strongylocentrotus spp.) (Paine and Vadas 1969 and Duggins 1980) has been correlated to diversity of algae such that algae diversity was high with intermediate densities of herbivores and low with low and high densities of herbivores.

Two factors indicate that gulls and otters may compete for intertidal prey. First, in the presence of high densities of otters, gulls fed less on spatially and temporally predictable intertidal invertebrates and more on less predictable fish at sea. Second, diversity of diets of gulls was lower in areas with high densities of otters (Massacre Bay, 0.70 and Amchitka, 0.41), which may indicate a constriction in the foraging niche of gulls as a result of competition with otters.

The differences in the proportions of overlap of feeding habitats of gulls and otters suggests that adverse affects of competition may be greater on gulls than on otters. The overlap of feeding niches of gulls and otters composes a large proportion of important feeding habitat of gulls, but only a small proportion of the feeding habitat of otters. Sea otters feed subtidally and intertidally, while gulls feed primarily intertidally and on the surface of the ocean. Gulls obtain a major portion of their food from the intertidal area, but sea otters probably gain only a small portion of their food from the intertidal region since the area of the intertidal zones is much less than the subtidal area they feed in. Because a major portion of the feeding niche (intertidal areas) of gulls is exploited by sea otters, any competition probably would be more detrimental to gulls than to sea otters. Adverse affects of competition to gulls could be tested

by comparing fitness and productivity of gulls at Massacre Bay before and after otters recolonize the area.

#### Optimal foraging theory

Optimal foraging theory (Pyke et al. 1977) predicts how consumers should feed to maximize their inclusive fitness. One prediction is that the decision whether or not to include a prey type in a diet is not dependent upon the absolute abundance of that prey type but only on the absolute abundance of prey types of higher En. Prey types at Attu with high En (urchins, chitons, and limpets) occurred in the lower intertidal zones and prey types of low En (mussels and barnacles) occurred in the higher zones. During neap low tides the lower intertidal zones were only partially exposed or not at all. Consequently, the abundance of prey types with higher En was reduced. This change in prey availability as influenced by tides created a "natural" situation to test the prediction that the inclusion of a prey type in a diet is dependent only upon the absolute abundance of prey types of higher En (Pyke et al. 1977). [Note: Because of the irregularity of the tidal cycles on Attu some of the observations during spring low tides occurred during relatively high, low tides. To resolve this problem in testing the above prediction I included data from low spring tides only when the water level was low enough to expose all intertidal zones (i.e., <0.5ft.). Percent occurrence of prey items under this circumstance was: urchins, 67; chitons, 7; limpets, 3; mussels, 0; and barnacles, 0.] Prey types with

low En were not eaten during low spring tides, but they comprised 65% (Fig. 3) of diets of gulls during neap low tides. Thus, foraging by gulls supports the prediction that the decision whether or not to include a prey type in the diet is not dependent upon absolute abundance of that prey type but only on the absolute abundance of prey types of higher En. When the abundance of prey types with high En (urchins, chitons, and limpets) was low, gulls fed on prey types with lower En (mussels and barnacles). Whereas, when the abundance of prey types with high En was high, gulls completely excluded prey types of lower En from their diets. This prediction of optimal diets also was qualitatively supported by the manner in which gulls selected prey sizes in areas that varied in size class distributions. At Chichagof where there were fewer chitons of the sizes that were selected than at Massacre, more small chitons were eaten than at Massacre. Therefore, the abundance of prey that were selected (i.e., prey with high En) influenced the number of secondary prey (i.e., prey with low En) that were eaten.

A second prediction of optimal diets (Pyke et al. 1977) is that "as the abundance of a preferred food type included in the diet increases, the number of less preferred food types included in the optimal diet will shrink... If the diet of an animal does change then items should be added to or dropped from the diet in their rank order." (Pyke et al. 1977:141). Thus, during periods when preferred prey items were abundant, mussels and barnacles were dropped from the diets of gulls (% occurrence of prey was: urchins, 67; chitons, 7; limpets, 3; mussels, 0; and barnacles, 0). I do not know the order in

which mussels and barnacles were dropped from the diets of gulls, but mussels which have a much higher  $E_n$  than barnacles were eaten much more often than barnacles during neap tides (52 and 13%, respectively) even though barnacles were more abundant (Table 1). Gulls foraged in the complex rocky intertidal community in a manner that supported predictions of optimal diet theory. Therefore, the theory of optimal diets applies to complex environments as posed by Schluter (1981:139).

Optimal choice of patch is the second general question discussed by Pyke et al (1977). Although intertidal zones are not consistent with many other authors' formal definition of patches and how they differ, I believe it is meaningful to discuss the question in relation to these zones. Intertidal zones are adjacent to one another but have different species and yield different net rate of energy gain ( $E_n$ ) to gulls. When all patches were available gulls foraged almost entirely (Chichagof, 91% and Massacre, 96%) in the Alaria and Laminaria zones, which had prey that offered much higher  $E_n$  than the mussel and barnacle zones. Therefore, gulls foraged in patches that yielded higher  $E_n$  and did not forage in patches that yielded low  $E_n$ , which would be expected by an optimal forager.

The question of when a predator should leave a patch and move to another was discussed by Charnov (1976); Gibb (1958) postulated the "hunting by expectation" hypothesis to explain when animals should leave a patch. According to Charnov (1976) "the predator should leave a patch it is presently in when the marginal capture rate in the patch drops to the average capture rate for the habitat". Krebs et al. (1974) made several assumptions and revised the prediction such that

"(a) the predator should have a constant giving-up time for all patch types within a habitat... (b) giving-up time should be shorter in better habitats, where the average capture rate is higher". This prediction assumes that prey in different patches and habitats are the same species and size, which is not the case for gulls foraging intertidally.

Foraging behavior of gulls indicated that they hunted by expectation of  $E_n$  and that they left a patch when their  $E_n$  decreased to the average  $E_n$  for the habitat, minus the cost of travel, which is essentially what others have predicted. However, because prey size and therefore  $E_n$  was different in different habitats the giving-up time (GUT) was longer in richer habitats (i.e., with larger prey) (Table 7), but the giving-up threshold  $E_n$  was higher in richer habitats as predicted by Krebs et al. (1974). Foraging behavior of gulls in the rocky intertidal community apparently supports predictions from three important areas of optimal foraging theory. However, optimal foraging theory may not account for important factors that affect foraging behavior, and unnatural conditions (i.e., experimental manipulations) may cause animals to feed in a manner that appears suboptimal even though they may feed optimally in the field.

## LITERATURE CITED

- Bent, A. C. 1963. Life Histories of North American Gulls and Terns. Dover Publ., N.Y. 337 pp.
- Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.* 9:1-8.
- Cummins, K. W. and J. L. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. *Mitt. Internat. Verein. Limnol.* 18. 161pp.
- Davies, N. B. 1977. Prey selection and the search strategy of the spotted flycatcher (Muscicapa striata): a field study on optimal foraging. *Anim. Behav.* 25:1016-1033.
- Dayton, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.* 45:137-159.
- Devillers, P., G. McCaskie, and J. R. Jehl, Jr. 1971. The distribution of certain large gulls (Larus) in southern California and Baja California. *California Birds* 2:11-26.
- Duggins, D. O. 1980. Kelp beds and sea otters: and experimental approach. *Ecology* 61:447-453.
- Ebert, T. A. 1968. Growth rates of the sea urchin Strongylocentrotus purpuratus related to food availability and spine abrasion. *Ecology* 49:1075-1091.
- Eggers, D. M. 1977. The nature of prey selection by planktivorous fish. *Ecology* 58:46-59.
- Emlen, J. M. and M. G. R. Emlen. 1975. Optimal choice in diet: test of a hypothesis. *Am. Nat.* 109: 427-435.
- Estes, J. A. and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. *Science* 185:1058-1060.
- Estes, J. A. and N. S. Smith. 1973. Amchitka Bioenvironmental Program Research on the sea otter, Amchitka Island, Alaska, Final Report, October 1970-December 1972. United States Atomic Energy Commission Report AT(261)-520.
- Estes, J. A., N. S. Smith, and J. F. Palmisano. 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. *Ecology* 59:822-833.

- Estes, J. A., R. J. Jameson, and A. M. Johnson. 1981 Food selection and some foraging tactics of sea otters. pp. 606-641. in J. Chapman and D. Pursey, editors. Proc. Inter. Conf. Biol. Furbearers. Frostburg, Maryland.
- Fleiss, J. L. 1973. Statistical methods for rates and proportions. John Wiley and Sons, New York. 223pp.
- Gabrial, W. L. 1978. Statistics of selectivity. pp. 62-66. in S. J. Lipovsky and C. A. Simenstad, eds. Fish food habits studies. Proc. Pacific Northwest Tech. Workshop 2. University of Washington, Seattle.
- Gibb, J. A. 1958. Predation by tits and squirrels on the eucosmid, Ernarmonia conicolana (Heyl.). J. Anim. Ecol. 27:376-396.
- Gill, F. B. and L. L. Wolf. 1977. Nonrandom foraging by sunbirds in a patchy environment. Ecology 58:1284-1296.
- Gordon, M. S., G. A. Bartholomew, A. D. Grinell, C. B. Jorgensen, and F. N. White. 1977. Animal physiology: principals and adaptations. Macmillan Pub. Co. Inc. New York. 695pp.
- Greenberg, J. H. 1956. The measurement of linguistic diversity. Language 32:109-115.
- Heip, C. 1974. A new index measuring evenness. J. Mar. Biol. U.K. 54:555-557.
- James-Veitch, E. and E. S. Booth. 1954. Behavior and life history of the Glaucous-winged Gull. Walla Walla College Publ. 12. College Place, Wash. 39pp.
- Kenyon, K. W. 1969. The sea otter in the eastern Pacific Ocean. United States Department of the Interior, Bureau of Sport Fisheries and Wildlife, North American Fauna Number 68. 352pp.
- Krebs, J. R., J. C. Ryan, and E. L. Charnov. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. Anim. Behav. 22:30-38.
- Lowry, L. F. and J. S. Pearse. 1973. Abalone and sea urchins in an area inhabited by sea otters. Marine Biol. 23:213-219.
- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Nat. 112:23-39.



- MacArthur, R. H. 1972. Geographical ecology. Harper and Row, New York. 269pp.
- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *Am. Nat.* 100:603-609.
- McClave, J. T. and F. H. Dietrich, II. 1979. Statistics. Dellen Publ. Co. San Francisco, Calif. 681pp.
- Menge, B. A. 1972. Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. *Ecol. Monogr.* 42:25-50.
- Mueller, H. C. 1977. Prey selection in the American Kestrel: experiments with two species of prey. *Am. Nat.* 111:25-29.
- O'Clair, C. E. 1977. Marine invertebrates in rocky intertidal communities. pp. 395-450 in M. L. Merritt and R. G. Fuller, eds. The environment of Amchitka Island, Alaska. T1D-26712, National Technical Information Service, United States Department of Commerce, Springfield, Virginia, USA.
- Paine, R. T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia (Berlin)* 15:93-120.
- Paine, R. T. and R.L. Vadas. 1969. The effects of grazing by sea urchins, Strongylocentrotus spp., on benthic algal populations. *Limnol. Oceanogr.* 14:710-719.
- Palmisano, K. F. 1975. Sea otter predation: Its role in rocky intertidal community structure at Amchitka and other Aleutian Islands. Ph.D. dissertation. University of Washington, Seattle, Wash. USA. 207pp.
- Palmisano, J. F. and J. A. Estes 1977. Ecological interactions involving the sea otter. pp. 527-568. in M. L. Merritt and R. G. Fuller, eds. The environment of Amchitka Island, Alaska. T1D-26712, National Technical Information Service, United States Department of Commerce, Springfield, Virginia, USA.
- Parr Instrument Co. 1960. Oxygen bomb calorimetry and combustion methods. Tech. Manual No. 130. Moline, Illinois. 56pp.
- Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* 52:137-154.

- Rabinowitch, V. 1969. The role of experience in the development and retention of seed preferences in zebra finches. *Behaviour* 33:222-236.
- Reichmann, O. J. 1977. Optimization of diets through food preferences by heteromyid rodents. *Ecology* 58:454-457.
- Ricketts, E. F. and J. Calvin. 1968. *Between Pacific tides*. 4th ed., revised by J. W. Hedgepath. Stanford, Calif. Stanford University Press. 614pp.
- Royama, T. 1970. Factors governing the hunting behavior and selection of food by the great tit (Parus major L.). *J. Anim. Ecol.* 39:619-668.
- Schluter, D. 1981. Does the theory of optimal diets apply in complex environments? *Am. Nat.* 118:139-147.
- Schnell, G. D. and J. J. Hellack. 1979. Bird flight speed in nature: optimized or a compromise? *Am. Nat.* 113:53-66.
- Schoener, T. W. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* 2:396-404.
- Simpson, E. H. 1949. Measurement of diversity. *Nature* 163:688.
- Smith, J. N. M. and R. Dawkins. 1971. The hunting behaviour of individual great tits in relation to spatial variations in their food density. *Anim. Behav.* 19:695-706.
- Stein, R. A. 1977. Selective predation, optimal foraging and the predator-prey interaction between fish and crayfish. *Ecology* 58:1237-1253.
- Sutton, G. M. and R. S. Wilson. 1946. Notes on the winter birds of Attu. *Condor*. 44:83-91.
- Trapp, J. L. 1979. Variation in summer diet of Glaucous-winged Gulls in the western Aleutian Islands: an ecological interpretation. *Wilson Bull.* 91:412-419.
- Tullock, G. 1971. The coal tit as a careful shopper. *Am. Nat.* 105:77-80.
- United States Department of the Interior, Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife. 1966. Aleutian Islands National Wildlife Refuge, RL-522. United States Government Printing Office, Washington, District of Columbia, USA, Pamphlet.

- Vermeer, K. 1963. The breeding ecology of the Glaucous-winged Gull (Larus glaucescens) on Mandarte Island, B. C. Occ. Pap. B. C. Prov. Mus. No. 13. 92pp.
- Welty, J. B. 1975. The life of birds, 2nd edition. W. B. Saunders, Philadelphia. 623pp.
- Werner, E. E. and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (Lepomis macrochirus). Ecology 55:1042-1052.
- Werner, E. E. and D. J. Hall. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology 60:256-264.
- Willson, M. F. 1976. Seed selection in some North American finches. Condor 73:415-427.
- Zach, R. and J. B. Falls. 1976a. Ovenbird (Aves: Parulidae) hunting behavior in a patchy environment: an experimental study. Can. J. Zool. 54:1863-1879.
- Zach, R. and J. B. Falls. 1976b. Foraging behavior, learning and exploration by captive ovenbirds (Aves: Parulidae). Can. J. Zool. 54:1880-1893.
- Zach, R. and J. B. Falls. 1976c. Do ovenbirds (Aves: Parulidae) hunt by expectation? Can. J. Zool. 54:1894-1903.

APPENDIX

## APPENDIX Ia

Average densities and sizes of intertidal invertebrates according to intertidal zone at Chichagof Harbor, Attu Island, Alaska.<sup>a</sup>

	Barnacle (n=8)		Mussel (n=30)		Alaria (n=35)		Laminaria longipes (n=32)		Stipitate Laminaria spp. (n=30)	
	number <sub>2</sub> per 1/4 m	size (mm)	number <sub>2</sub> per 1/4 m	size (mm)	number <sub>2</sub> per 1/4 m	size (mm)	number <sub>2</sub> per 1/4 m	size (mm)	number <sub>2</sub> per 1/4 m	size (mm)
Urchins ( <i>Strongylocentrotus polyacanthus</i> )	0	-	0	-	3.9±1.1	19±0.8	18.0±0.8	21±0.4	28.1±0.8	22±0.4
Mussels ( <i>Mytilus edulis</i> )	48.6±18.5 <sup>a</sup>	10±1.4 <sup>c</sup>	852.3±76.0	19±0.2	1.7±0.6	25±1.7	1.1±0.6	19±1.6	0	-
Mussels ( <i>Mytilus edulis</i> ) (<6mm)	0	-	500.0±un <sup>d</sup>	<6	0	-	0	-	0	-
Chitons ( <i>Katharina tunicata</i> )	0	-	<0.1±un <sup>d</sup>	18±un <sup>d</sup>	10.3±0.9	38±0.8	9.7±0.7	46±1.1	1.4±0.4	44±2.2
Chitons ( <i>Mopalia</i> spp.)	0	-	0	-	0.2±0.2	-	0.3±0.2	-	0.1±0.2	-
Barnacles ( <i>Balanus glandula</i> )	2152.0±329.2 <sup>c</sup>	8±0.7 <sup>bc</sup>	168.0±5.6 <sup>c</sup>	8±0.7 <sup>bc</sup>	0	-	0	-	0	-
Barnacles ( <i>B. cariosus</i> )	0	-	60.4±3.3	14±0.6 <sup>bc</sup>	132.9±5.7	14±0.6 <sup>bc</sup>	103.3±0.7	14±0.6 <sup>bc</sup>	34.1±1.3	14±0.6 <sup>bc</sup>
Limpets <sup>c</sup>	0	-	8.9±0.9	15±0.6	11.9±1.7	17±0.5	3.6±0.7	16±1.5	3.1±0.5	19±1.5
Limpets (<6mm) <sup>c</sup>	159.0±43.1 <sup>c</sup>	<6 <sup>c</sup>	500.0±un <sup>d</sup>	<6	0	-	0	-	0	-
<i>Nucella emarginata</i>	0	-	1.6±0.2	17±0.9	0.6±0.2	26±0.9	0.9±0.2	23±0.7	0.1±0.2	14±0.7
<i>Littorina</i> spp.	0	-	0.5±0.2	6±0.6	0	-	0	-	0	-
<i>Littorina</i> spp. (<3mm) <sup>c</sup>	156.5±36.7 <sup>c</sup>	<3 <sup>c</sup>	0	-	0	-	0	-	0	-
<i>Buccellium baerii</i>	0	-	0	-	0	-	0.2±0.2	20±2.6	0.1±0.2	20±1.2
Sea cucumbers ( <i>Cucumaria</i> spp.)	0	-	0	-	0.8±0.4	16±1.0	<0.1±0.3	25±0.6	0	-
Seastars ( <i>Leptasterias</i> spp.)	0	-	<0.1±un <sup>d</sup>	72.0±un <sup>d</sup>	0.4±0.2	28±3.5	1.3±0.2	48±3.9	0.5±0.3	58±4.1
Seastars ( <i>Pisaster</i> spp.)	0	-	0	-	0	-	0.1±0.2	227±28.9	<0.1±un <sup>d</sup>	308±un <sup>d</sup>
Seastars ( <i>Urosalpinx</i> spp.)	0	-	0	-	0	-	0.3±0.2	36±5.6	0.3±0.2	29±3.1
Seastars, unidentified	0	-	0	-	0.1±0.2	20±4.4	0.3±0.2	25±2.7	<0.1±un <sup>d</sup>	24±un <sup>d</sup>
Hermit crabs ( <i>Pagurus</i> spp.)	0	-	0	-	<0.1±un <sup>d</sup>	12±un <sup>d</sup>	<0.1±0.2	22±7.0	<0.1±un <sup>d</sup>	21±1.0
Crabs ( <i>Pugettia</i> spp.)	0	-	0	-	0	-	0.2±0.2	19±1.3	0.1±0.2	17±0.9
Gastropods, unidentified	0	-	0	-	0	-	0.13±un <sup>d</sup>	7±un <sup>d</sup>	<0.1±un <sup>d</sup>	7±un <sup>d</sup>

<sup>a</sup>Values are means with 95% confident intervals.<sup>b</sup>Sizes of invertebrates were not calculated separately for each zone.<sup>c</sup>From Estes (unpubl. data).<sup>d</sup>un = confidence intervals were undefined because sample size was one or was estimated.

## APPENDIX Ib

Average densities and sizes of intertidal invertebrates according to intertidal zone at Massacre Bay, Attu Island, Alaska.<sup>a</sup>

	Mussel (n=25)		Alaria (n=25)		Laminaria (n=25)	
	number <sub>2</sub> per 1/4 m <sup>2</sup>	size (mm)	number <sub>2</sub> per 1/4 m <sup>2</sup>	size (mm)	number <sub>2</sub> per 1/4 m <sup>2</sup>	size (mm)
Urchins ( <u>Strongylocentrotus polyacanthus</u> )	0	-	0.8±0.4	29±3.4	35.2±6.4	49±0.7 <sup>b</sup>
Mussels ( <u>Mytilus edulis</u> )	355.8±71.2	11±0.1	1.5±0.8	17±0.5	0	-
Mussels ( <u>Mytilus edulis</u> ) (<6mm)	20.0±un <sup>d</sup>	<6	0	-	0	-
Chitons ( <u>Katharina tunicata</u> )	<0.1±un <sup>d</sup>	55±un <sup>d</sup>	6.5±0.6	59±1.5 <sup>b</sup>	<0.1±un <sup>d</sup>	59±1.5 <sup>b</sup>
Chitons ( <u>Mopalia</u> spp.)	0	-	<0.1±un <sup>d</sup>	-	<0.1±un <sup>d</sup>	-
Barnacles ( <u>Balanus glandula</u> )	231.7±18.2 <sup>c</sup>	8±0.7 <sup>bc</sup>	0	-	0	-
Barnacles ( <u>B. cariosus</u> )	0	-	41.5±5.2	14±0.6 <sup>bc</sup>	0	-
Limpets <sup>c</sup>	9.3±1.9	15±0.4	10.9±2.3	16±0.4	1.9±0.8	21±1.0
Limpets (<6mm) <sup>c</sup>	370.0±un <sup>d</sup>	<6	8.0±un <sup>d</sup>	<5	0	-
<u>Nucella emarginata</u>	1.2±0.4	16±0.9	0.1±0.3	25±1.3	0	-
<u>Littorina</u> spp.	3.2±0.6	6±0.2	0.3±0.3	7±0.8	0	-
<u>Littorina</u> spp. (<3mm)	60.0±un <sup>d</sup>	<3	0	-	0	-
<u>Buccinum baerii</u>	0	-	0	-	<0.1±un <sup>d</sup>	27±un <sup>d</sup>
Sea cucumbers ( <u>Cucumaria</u> spp.)	0.3±0.4	15±0.9	0.2±0.6	14±1.3	0	-
Seastars ( <u>Leptasterias</u> spp.)	0	-	0.2±1.8	22±6.7	<1.0±0.4	28±4.0
Seastars ( <u>Pisaster</u> spp.)	0	-	0	-	0	-
Seastars, unidentified	0	-	<0.1±un <sup>d</sup>	14±un <sup>d</sup>	0	-
Hermit crabs ( <u>Pagurus</u> spp.)	<0.1±2.6	11±0.5	1.2±0.4	11±0.7	0	-
Gastropods, unidentified	0	-	0	-	0.2±0.2	6±0.1

<sup>a</sup> Values are means with 95% confident intervals.

<sup>b</sup> Sizes of invertebrates were not calculated separately for each zone.

<sup>c</sup> From Estes (unpubl. data).

<sup>d</sup> un = confidence intervals were undefined because sample size was one or was estimated.

## APPENDIX II

The three methods that were used to collect data on the diets of Glaucous-winged Gulls (crop and gizzard contents, observations of feeding birds, and regurgitated pellet contents) were compared. Examination of crops and gizzards had the advantage that prey could be identified and for prey size, weight, and volume could be measured. However, collections required much time, made it difficult to obtain large sample sizes, and gulls often regurgitated their crop contents after being shot. Observations offered the advantages of 1) obtaining large sample sizes without diminishing the population, 2) obtaining dietary data from specific times and/or locations, and 3) not being biased by differential digestion rates. The disadvantages of this method were that 1) they required large amounts of time to collect; 2) some prey could not be identified; and 3) prey size could only be estimated. Pellet collections offered a quick and easy method of obtaining large samples such that dietary changes could easily be monitored over long periods. Prey could be identified and the size of some could be determined either by direct measurements or by using regressions of body size to size of some measurable body part. Pellet analysis had the disadvantage that pellets contained only prey that had large undigestible body parts. Other prey were biased against (e.g., seastars and sea cucumbers).

Data on diets that were obtained by observations and pellets taken during spring tides, and gut contents collected during spring and neap tides were compared (Fig. 10). The percent occurrence of

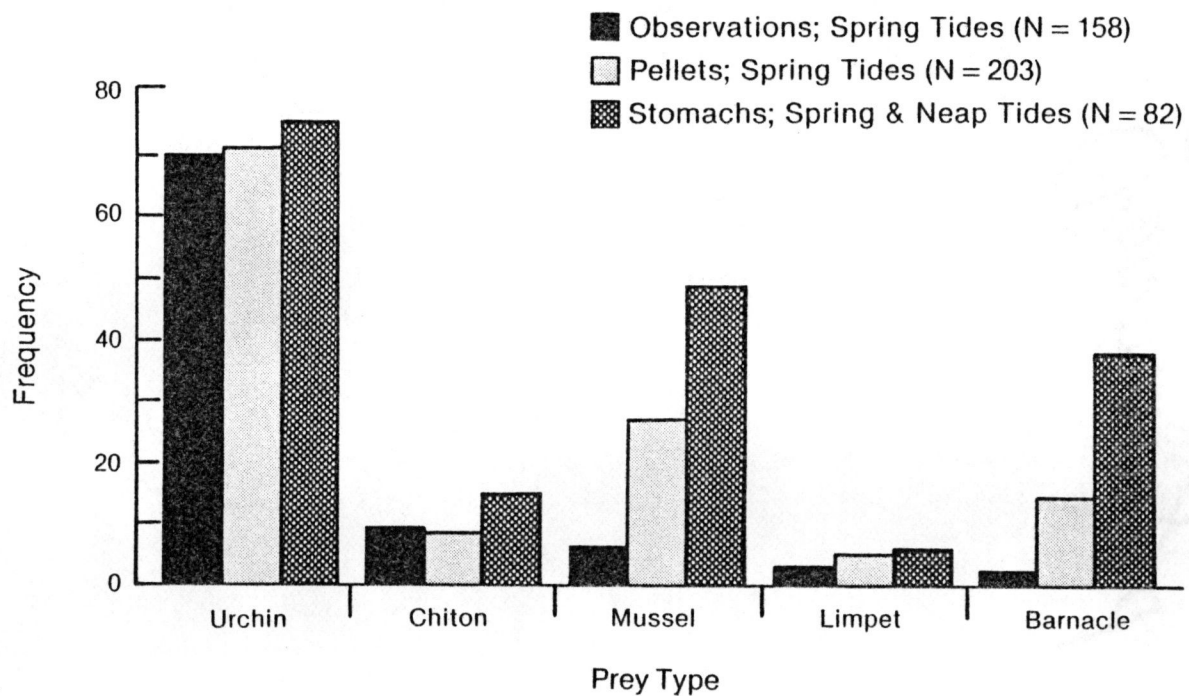


Figure 10. Frequency of selected prey (%) of Glaucous-winged Gulls, with data collected from observations, pellets, and stomachs from Chichagof Harbor, Attu Island, Alaska.



urchins, chitons, and limpets were similar for all methods, but, as suspected, the occurrence of mussels and barnacles were higher for data from pellets and stomachs. The reason for this was that the timing of collecting data by these three methods was different. The observational and pellet data were collected during spring tides, but pellet collections included days of intermediate tidal fluxes. The stomach data were collected during spring and neap tides. During neap tides more mussels and barnacles were eaten by gulls than during spring tides.

Four common methods are used to analyze diet data: number, weight, volume, and frequency of occurrence. The analysis that is least biased in any given case depends upon the foraging behavior of the predator and the type of prey species eaten. Analysis by number biases for small organisms and against large ones. Wet weight and volume possess biases for organisms that contain much fluid or have large parts that are undigestible (e.g. mussels, sea cucumbers, and sea urchins). Frequency of occurrence has biases against small organisms and for ones that have small parts that may get caught in the gizzard or stomach. Dry weight of digestible material is probably the best method of analysis but is difficult and time consuming.

Analysis by number, frequency of occurrence, and dry weight were compared for selected prey of gulls (Fig. 11). The three methods of analysis produced similar results, but analysis by number biased for small prey (mussels and limpets) and against large prey (chitons and urchins) and frequency of occurrence biased against small patchily distributed prey (limpets).

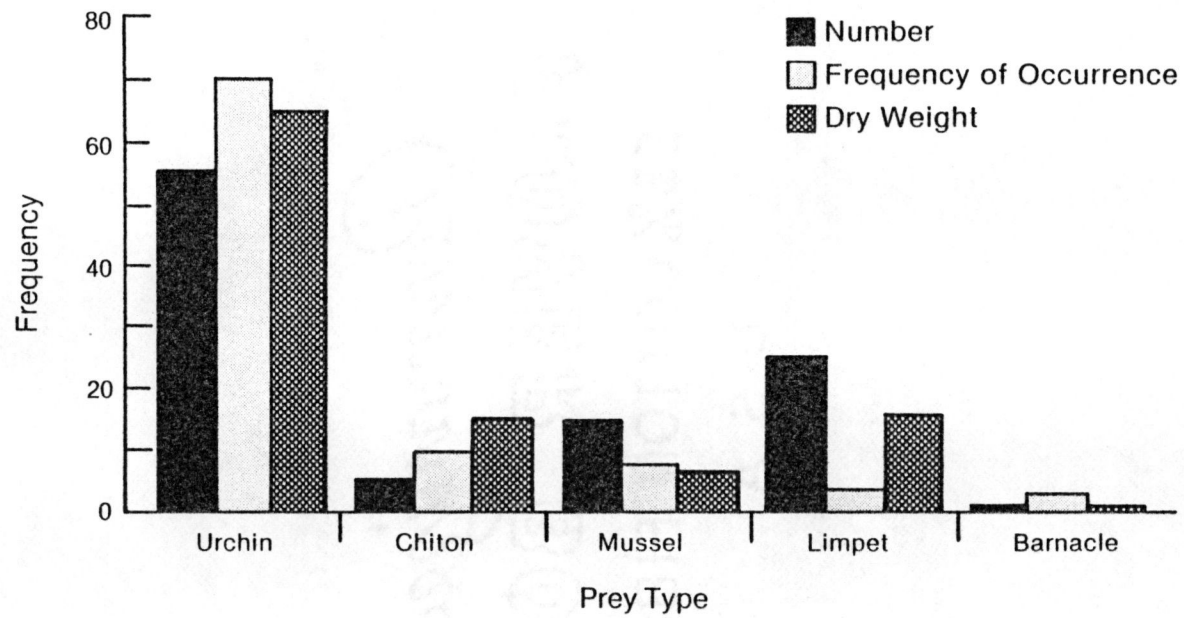


Figure 11. Frequency of selected prey (%) in diets of Glaucous-winged Gulls using observational data (n=158) collected during spring low tides at Chichagof Harbor, Attu Island, Alaska, and three methods of analysis: number of prey, occurrence, and dry weight.

## APPENDIX III

Percent occurrence of crop and gizzard contents from Glaucous-winged Gulls collected at Massacre Bay and Chichagof Harbor, Attu Island, Alaska, 1979 & 1980.

Prey item	Massacre Bay (n=69)	Chichagof Harbor (n=82)
Urchins ( <u>Strongylocentrotus polyacanthus</u> )	55	75
Fish <sup>a</sup>	49	17
Chitons ( <u>Katharina tunicata</u> )	25	15
Mussels ( <u>Mytilus edulis</u> )	24	49
Limpets <sup>b</sup>	10	7
<u>Nucella</u> spp.	10	28
<u>Littorina</u> spp.	7	4
Crabs <sup>c</sup>	16	14
Seastars ( <u>Leptasterias</u> spp.)	22	26
Sea cucumbers ( <u>Cucumaria</u> spp.)	12	5
Cephalopods	3	1
Fish eggs <sup>d</sup>	6	4
Amphipods	0	3
Isopods	1	1
Trematodes	7	2
Barnacles ( <u>Balanus glandula</u> & <u>B. cariosus</u> )	19	38
Algae	27	58
Grit	28	34
Mussels ( <u>Modiolus</u> spp.)	2	1
Bird feathers <sup>e</sup>	6	5
Crowberries ( <u>Empetrum nigrum</u> )	1	6
Blueberries ( <u>Vaccinium</u> spp.)	0	1
Clams ( <u>Hiatella</u> spp.)	0	3
unidentified larva	1	0

<sup>a</sup> Ammodytes hexapterus, Clupea harengus, and unidentified species

<sup>b</sup> Collisella pelta and Notoacmaea scutum

<sup>c</sup> Telmessus cheiragonus, Pugettia spp. and unidentified species

<sup>d</sup> Oncorhynchus spp. and Hexagrammos lagocephalus

<sup>e</sup> Larus glaucescens and Somateria mollissima

## APPENDIX IV

Kcalories per gram of dry body weight of selected invertebrates.

---



---

Species	N	Kcal/g dry wt
<u>Strongylocentrotus polyacanthus</u> (gonad)	4	5.5
<u>Strongylocentrotus polyacanthus</u> (viscera)	3	4.0
<u>Strongylocentrotus polyacanthus</u> (total)	3	4.3
<u>Katharina tunicata</u>	4	4.4
<u>Mytilus edulis</u>	4	4.8
<u>Notoacmaea scutum</u> <sup>a</sup>	11	4.9
<u>Collisella pelta</u> <sup>a</sup>	4	5.1
<u>Balanus glandula</u> <sup>a</sup>	22	3.3

---

<sup>a</sup>Data from Menge (1972).

APPENDIX V

Regression equations of digestible dry weight against length or diameter (mm) for selected invertebrates.

Species	N	Regression equation	R <sup>2</sup>
<u>Strongylocentrotus polyacanthus</u>	14	$y=ax^b$ a=5.1567x10 <sup>-6</sup> b=3.0523	0.9130
<u>Katharina tunicata</u> <sup>a</sup>	26	$y=ax^b$ a=2.1745x10 <sup>-6</sup> b=3.2555	0.8226
<u>Mytilus edulis</u> <sup>a</sup>	14	$y=ax^b$ a=3.8266x10 <sup>-6</sup> b=3.0362	0.9930
<u>Collisella pelta</u> <sup>a</sup>	10	$y=ax^b$ a=2.9774x10 <sup>-6</sup> b=3.5160	0.9885
<u>Notoacmaea scutum</u> <sup>a</sup>	15	$y=ax^b$ a=8.7860x10 <sup>-6</sup> b=2.9942	0.9772
<u>Balanus glandula</u> <sup>a</sup>	24	$y=ax^b$ a=5.1801x10 <sup>-6</sup> b=3.2624	0.5783

<sup>a</sup>Raw data from B.A. Menge (unpubl. data).