

Exxon Valdez Oil Spill
Restoration Project Final Report

Sound Ecosystem Assessment (SEA):
Avian Predation on Herring Spawn in Prince William Sound

Restoration Project 95320Q
Final Report

Mary Anne Bishop

Pacific Northwest Research Station
Copper River Delta Institute
U.S. Forest Service
P.O. Box 1460
Cordova, Alaska 99574

S. Patrick Green¹

Center for Streamside Studies
University of Washington
Box 352100
Seattle, Washington 98195

¹deceased

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Study History: Restoration Project 95320Q began in 1994, and received funds for analysis and close-out in 1996. Project 95320Q was part of the Sound Ecosystem Assessment program. This is the final report on activities conducted by this project.

Abstract: Pacific herring (*Clupea pallasii*) has been identified as a resource injured by the spill. During spring 1994 and 1995 we assessed the effects of avian predators on herring spawn at northern Montague Island. We documented avian abundance and distribution by both date and location in relation to herring spawn. Glaucous-winged gull (*Larus glaucescens*) was the most abundant bird species in spawn surveys. There was a significant, positive relationship between glaucous-winged gull densities and the total eggs available above -1.2 m Mean Lower Low Water (MLLW). Coupling our surveys with spawn deposition survey data showed that in many areas glaucous-winged gulls probably removed all eggs above -1.2 m MLLW before spawn surveys were conducted. We estimated the daily herring spawn intake for the 5 most numerous predators based on estimated field metabolic rates, energy content of spawn, and proportion of energy acquired from herring spawn. In spring 1994 these 5 species removed an estimated 730 metric tons of spawn, or 27 % of total spawn available at Montague Island. These estimates are probably low due to energetic demands for migration and/or breeding for all 5 species. We provide a methodology to estimate losses to birds prior to spawn deposition surveys.

Key Words: Bioenergetics, black turnstone, fish consumption, foraging, glaucous-winged gull, herring spawn, intertidal, mew gull, predation, Prince William Sound, surf scoter, surfbird.

Project Data: *Description of data*—Bird abundance data were collected by the authors during aerial and boat surveys. Aerial surveys included video tapes. Herring spawn data were collected during underwater diver surveys by Alaska Department of Fish and Game. *Format*—The data were entered on Excel spreadsheets. *Custodian*—Contact Mary Anne Bishop, Pacific Northwest Research Station, US Forest Service, PO Box 1460, Cordova, Alaska 99574, (work phone: (907) 424-7212, fax: (907) 424-7214). *Availability*—Copies of the data can be provided on diskette or video cassettes (aerial data).

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EXECUTIVE SUMMARY

Avian predation on herring spawn was studied at northern Montague Island during spring 1994 and 1995. This project was designed to provide critical information to test the Sound Ecosystem Assessment's natal hypothesis #2: that recruitment success of Pacific herring (*Clupea pallasii*) populations in Prince William Sound (PWS) is related to physical processes and predation during early life stages. Results from this study were incorporated into a PWS-wide egg loss model (Rooper 1996) and embryo survival model (Norcross et al. unpubl. data). Our estimates of avian consumption of herring spawn also provide a management tool for Alaska Department of Fish and Game (ADF&G) whereby they can readjust their adult herring spawner biomass estimates.

The objectives of this study are to:

- (1) Determine the species composition, timing, and distribution of birds foraging in herring spawn areas in the rocky intertidal and subtidal habitats.
- (2) Estimate the amount of herring spawn consumed by avian predators.

Herring spawn deposition occurred from 18–25 April 1994 and from 27 April–1 May 1995 and hatched approximately 20–25 days after initial deposition. Prior to spawn initiation, 1994 aerial surveys ($n = 3$) recorded gull numbers ranging from 15,600–25,700, and 1995 boat surveys ($n = 2$) recorded 9,350–10,100 gulls in the vicinity of the herring schools. Of the gulls, >90% were glaucous-winged gulls (*Larus glaucescens*).

We documented avian abundance and distribution for all species by both date and location in relation to herring spawn. Glaucous-winged gull was the most abundant bird species in spawn surveys. Both years, the other principal species were mew gull (*Larus canus*), surfbird (*Aphriza virgata*), surf scoter (*Melanitta perspicillata*), harlequin duck (*Histrionicus histrionicus*) and black turnstone (*Arenaria melanocephala*).

Populations of mew gull and glaucous-winged gull in PWS consist of year-round residents and spring–summer residents. Surf scoters winter in small numbers in PWS, including Montague Island, however, the largest numbers are in migrant flocks in spring. Surfbird and black turnstone are transient spring migrants, occurring in large numbers almost exclusively at Montague Island in April and May. From 20–25 April both years, migrant flocks of surf scoter, surfbird, and black turnstone appeared at Montague Island. While in 1994 their arrival coincided shortly after spawn deposition, in 1995 their arrival occurred just prior to the 27 April spawn initiation. At the same time, despite a 9-day difference in spawn hatch date between years. Surfbird and black turnstone numbers decreased to negligible levels after 12 May both years as they moved on to their more northerly breeding areas.

We tested the hypothesis that birds were attracted to areas of spawn. We calculated the likelihood that a species would occur in a spawn area as opposed to a nonspawn area for an

18-km stretch of shoreline that included approximately even amounts of spawn and no spawn. We found that the birds more likely to occur in spawn areas were generally the most numerous: shorebirds, gulls, dabbling and offshore diving ducks, and bald eagles. Except for the bald eagle, all of these species are either known or suspected herring spawn consumers. Piscivorous birds (cormorants, mergansers, murrelets, grebes), along with inshore diving ducks and corvids (both omnivorous) and Canada geese (herbivorous) were equally likely to occur in spawn areas as nonspawn areas.

We documented foraging patterns in spawn areas for glaucous-winged gull, mew gull, surfbird, and black turnstone feeding in relation to a suite of variables: year, tide type, tide direction, tide stage, tide height, and tide zone. Our results suggested that because herring spawn is a superabundant food resource, resource partitioning among these 4 species in the intertidal zone is reduced. Glaucous-winged and mew gulls showed no significant relationship to any tide variables, with feeding occurring during all tide phases and tide heights. Surfbird and black turnstone exhibited a preference for feeding during low tide, however, foraging occurred at high levels throughout all tide cycles. Surfbird and black turnstone concentrated foraging efforts at the tideline and also foraged longer each day than gulls.

We tested hypotheses pertaining to egg loss. Egg loss can be estimated 2 ways: (1) by quantifying decreases in egg density throughout spawn incubation, and (2) by identifying sources of loss and estimating their impact (Haegele and Schweigert 1991). Using the second approach to egg loss, in spring 1995 we tested the hypothesis that herring spawn is a major component in the diet of bird species foraging in spawn areas. We collected and analyzed stomach contents of the 5 most abundant avian species foraging in spawn areas in northern Montague Island: glaucous-winged gull, mew gull, surf scoter, surfbird, and black turnstone. Based on the stomach contents, we estimated that these 5 species obtained from 93–100% of their total daily energy from spawn.

We applied a bioenergetics model to estimate the daily herring spawn consumption for each of these 5 species. Our model is based on field metabolic rates (FMRs), energy content of spawn, assimilation efficiency of spawn, and the proportion of daily energy acquired from herring spawn. Surf scoter had the highest daily consumption rate at 1.06 kg/day per individual, followed by glaucous-winged gull, the most numerous predator, at 0.73 kg/day. Mew gull consumed 0.32 kg/day, surfbird 0.19 kg/day, and black turnstone 0.16 kg/day. These estimates are probably low due to the seasonal energetic demands of migration and breeding for all 5 species.

We performed a sensitivity analysis for each of the 5 predator models to examine the implications of parameter uncertainty on their predicted herring spawn consumption. Four parameters (body mass, assimilation efficiency, proportion of energy acquired from herring spawn, and FMR) were evaluated for their effect on total herring spawn ingestion estimates. The sensitivity analysis showed that for all 5 species, a decrease in assimilation efficiency had the largest effect on the model's input. A 20% decrease in a bird's assimilation efficiency increased

total herring spawn consumption by 25%. Alternatively, a 10% increase in assimilation efficiency decreased total consumption by only 9%. Percent change in body mass had the least effect on spawn consumption. A 20% weight increase affected total herring spawn consumption by +18% whereas a 20% decrease lowered total consumption by -14%. There was a 1-to-1 direct correspondence between percent change in consumption and percent change in the other 2 parameters: proportion of energy acquired from herring spawn and FMR.

Based on our equation and population data, we determined that over 27 days in 1994 the 5 species removed 730.2 metric tons of herring spawn or 27% of estimated available herring spawn. Glaucous-winged gull is the major avian predator on spawn at Montague Island and its consumption far exceeded that of all other avian species combined. Within spawn areas, there was a significant, positive relationship between glaucous-winged gull densities and the total eggs available above -1.2 m Mean Lower Low Water (MLLW), the lowest tide during our study. Coupling our surveys with ADF&G spawn deposition survey data showed that in many areas glaucous-winged gulls probably removed all eggs above -1.2 m MLLW before spawn surveys were conducted.

A more accurate way to adjust ADF&G total biomass estimates could be achieved using the following methods. First, monitor glaucous-winged gull numbers in spawn areas from the air using aerial videography filmed from the side of the plane. Second, conduct spawn deposition surveys in a geographically sequential order whereby all surveys for one area are completed during a short time period. Third, calculate losses to gulls by area using our bioenergetics model.

Finally, we used ADF&G data on density of herring spawn at selected sites to test the hypothesis that egg loss to birds occurs at higher rates in years when eggs are scarce. Bird abundance in 1994 was positively related to egg loss rates; however, for 1995 bird abundance was negatively related to egg loss rates. Our egg consumption models suggest that egg loss rates do not necessarily vary with gull numbers. For example, small numbers of gulls may be taking the same proportion of eggs as large numbers of gulls. Egg loss rates instead appear to be effected by a synergistic relationship between gull abundance, total egg numbers, daily rate of consumption, and timing and location of herring spawn. We documented that avian spawn predators, including glaucous-winged gull, the largest consumer, respond positively to the abundance of spawn. At very low egg densities, we would predict low gull numbers, and up to a certain point, egg loss rates would decrease with increasing amounts of spawn and gulls. The relatively low gull densities at Montague Island in 1995 may not have been high enough to cause increased egg loss rates, thus explaining the negative relationship between egg loss rates and bird abundance.

CHAPTER 1. AVIAN RESPONSE TO PACIFIC HERRING (*Clupea pallasii*) SPAWN IN PRINCE WILLIAM SOUND, ALASKA

ABSTRACT: Pacific herring (*Clupea pallasii*) has been identified as a resource injured by the *Exxon Valdez* oil spill. During spring 1994 and 1995 we assessed and documented the timing, abundance, and distribution of potential or known avian herring spawn predators at northern Montague Island, Prince William Sound Alaska. Using aerial videography for gulls, and boat shoreline surveys for all other birds, we documented avian abundance and distribution by both date and location in relation to herring spawn. Glaucous-winged gull (*Larus glaucescens*) was the most abundant species. Both years, the principal nongull species were surfbird (*Aphriza virgata*), surf scoter (*Melanitta perspicillata*), harlequin duck (*Histrionicus histrionicus*) and black turnstone (*Arenaria melanocephala*). Within spawn areas, there was a significant, positive relationship between glaucous-winged gull densities and the total eggs available above -1.2 m Mean Lower Low Water (MLLW), the lowest tide during our study. Coupling our surveys with Alaska Department of Fish and Game spawn deposition survey data showed that in many areas glaucous-winged gulls probably removed all eggs above -1.2 m MLLW before spawn surveys were conducted.

INTRODUCTION

Pacific herring return to Prince William Sound (PWS), Alaska every April and deposit their eggs on rocks and vegetative substrate in the intertidal and shallow subtidal zones. Depending on seawater temperature, egg density and egg distribution, herring eggs hatch into drifting larvae at approximately 20–25 days. Along the northwest Pacific Coast, 18 bird species have been shown to feed on herring spawn (reviewed in Palsson 1984 and Haegele 1993a). Egg loss to these birds can be significant (Munro and Clemens 1931, Outram 1958, Palsson 1984, Haegele and Schweigert 1991, Haegele 1993a).

Breeding and migration of avian predators in PWS coincides spatially and/or temporally with herring spawn deposition and incubation. Surf scoters are abundant in the region (Isleib and Kessel 1973) with large numbers observed in migrant flocks during April and May. Glaucous-winged gulls are also an abundant resident. Although they are present in relatively high numbers during winter (Agler et al. 1994), an influx does occur in spring, mainly between mid-April and mid-May (Isleib and Kessel 1973). Glaucous-winged gulls nest in PWS, with >30 colonies ranging in size from 156–2,500 pairs scattered throughout (U.S. Fish and Wildlife Service (USFWS) 1997). Egg laying usually begins around the second week in May. Historically, large numbers of glaucous-winged gull have been observed during spring in areas with herring spawn. At Montague Island in PWS, in early May 1989 and 1992 approximately 30,000 and 50,000 gulls, respectively, were observed in areas with herring spawn (P. Martin, USFWS, unpubl. data).

PWS William Sound is also an important migratory stopover for shorebirds that prey on herring spawn. In 1989, northern Montague Island was discovered to be the most important spring staging area for 2 species of shorebirds: surfbird and black turnstone (Norton et al. 1990).

Total numbers using the area are not known, but in May 1992 a single day count of almost 56,000 surfbirds and 25,000 black turnstones was recorded (P. Martin, USFWS, unpubl. data). These numbers suggest that a high proportion of the world's population of these 2 species use northern Montague Island in spring (Norton et al. 1990, Martin 1994).

This study was undertaken during spring 1994 and 1995 to investigate bird response to herring spawn in PWS. Our objective was to determine the distribution, timing, numbers and species composition of birds foraging in herring spawn areas in the rocky intertidal and subtidal habitats. We tested the hypothesis that the distribution, timing, and abundance of gulls, sea ducks, and shorebirds is positively related to the dispersion, timing, and abundance of herring spawn.

STUDY AREA AND METHODS

Study Area

We studied avian response to herring spawn at northern Montague Island from immediately south of Port Chalmers to Zaikof Bay (Fig. 1-1). This 96-km section of shoreline primarily includes exposed wave-cut platforms and gravel beaches, as well as lesser amounts of sheltered tidal flats, and mixed sand and gravel beaches. Spawning has occurred in this area all but one year since 1980 (Alaska Department of Fish and Game (ADF&G), unpubl. data) with Rocky Bay, Montague Point, and Graveyard Point typically receiving high densities of spawn.

Herring Spawn Distribution and Abundance

We studied bird numbers and distribution from 7 April–15 May 1994 and 19 April–19 May 1995. First day of spawn (day 0) was 19 April 1994 and 27 April 1995. The extent and distribution of herring spawn (Fig. 1-1) was determined from visible milt observed during daily aerial herring surveys conducted as a regular part of ADF&G commercial fisheries management. Extent of spawn was corrected using direct observations of eggs during ADF&G spawn deposition surveys (Wilcock et al. 1995).

We obtained estimates of spawn biomass from ADF&G SCUBA diver spawn deposition surveys (Herring Natal Habitats, EVOS 94166 and 95166). In 1994 and 1995, ADF&G randomly sampled 56 and 33 sites, respectively, in our northern Montague Island study area. Biomass estimates were made 3–23 days after spawn deposition in 1994, and 9–16 days after deposition in 1995. Biomass estimates included: spawn width (defined by perpendicular distance from shoreline), average egg biomass (1,000's) per sampling station with eggs, and total eggs biomass (1,000's) in the 0.321-m wide transect. For 1994 surveys, calibrated biomass estimates enabled us to calculate egg biomass by depth.

Bird distribution and abundance

Aerial surveys. We used aerial and boat shoreline surveys to estimate the distribution, timing and abundance of birds on northern Montague Island. Low-altitude (95-m) surveys were attempted to document all species and numbers; however, high winds, a convoluted shoreline, and other safety consideration made this impractical. We used aerial surveys, therefore, to estimate numbers of only gull and offshore diving ducks.

Aerial surveys were conducted prior to spawn deposition ($n = 3$ in 1994, and $n = 1$ in 1995) and, weather permitting, every 2–3 days from spawn deposition through egg hatch ($n = 12$ in 1994, and $n = 8$ in 1995). In 1994, aerial surveys covered approximately 96 km of coastline from just south of Port Chalmers to (and including) Zaikof Bay. Spawned shoreline was estimated at approximately 22.6 km (Fig. 1-1; Wilcock et al. 1995). In 1995 we surveyed only spawn areas, which were estimated at 20.2 km (Fig. 1-1; Willette et al. 1996).

Surveys were conducted during the 1 ½ hr before or after low tide. Surveys were flown in a Cessna 185 float plane along a path approximately 100–150 m from shore at an altitude of 200–250 m. Multiple flight lines were flown in some areas for complete coverage. The shoreline was divided into sections based on recognizable landmarks and spawn distribution. In 1994, we used a combination of observers and videography to estimate numbers. Initially, 2 observers estimated the numbers of gulls and sea ducks on each side of the plane. For 9 of the 12 flights during spawn deposition and incubation, we used a hand-held Canon video camcorder to film gull numbers on spawn areas. Due to poor weather and/or lighting conditions, we substituted numbers from boat surveys (actual or interpolated) for the Graveyard point area for 5 flights. Later, we estimated gull numbers from 1994 videos by “freezing” frames on a video monitor and visually counting individual gulls. Flight lines were recorded on aerial photographs to prevent double counting.

In 1995 we used aerial videography exclusively to film gull numbers using methods devised by Anthony et al. (1995). A hi-8 video camcorder with composite video (RS-170) and S-video (Y/C) signal output was mounted over a floor port near the aft bulkhead of a Cessna 185 and linked to a GPS receiver via a time code generator. A video output on a color monitor was monitored by an observer. To estimate gull numbers in 1995 we first used National Institute of Health’s software program Duck-Hunt (Image 1.45, National Institute of Health, no date). Video images were “grabbed” using a Computer Eyes frame grabber on a Macintosh Iici computer with a high resolution video card. Images were transferred to a Power Macintosh 8100 for processing. Adobe PhotoShop was used to translate the analog video images to a pixel format with the deinterlace algorithm. Images were sharpened, converted to gray scale, and processed by Duck-Hunt. We also counted gulls from 1995 videos visually using the same freeze-frame method as in 1994.

Boat surveys. We conducted boat shoreline surveys prior to spawn deposition ($n = 2$ in 1994, and $n = 7$ in 1995), and every 2–3 days from spawn deposition through egg hatch ($n = 12$ in 1994, and $n = 10$ in 1995). In 1994, we surveyed all birds along 18.4 km of coastline from northern Stockdale Harbor to Montague Point that included approximately 6.4 km with spawn and 12 km without spawn. In 1995 we surveyed all nongull species, in spawn areas only (approximately 15.4 km total) from Rocky Bay to northern Stockdale Harbor. In 1995 we also randomly sampled gull flocks in spawn areas to determine species composition.

Survey protocols were adapted from USFWS marine birds and mammal surveys (USFWS 1991). The sampling area included all water within 120 m of shore plus shoreline (maximum shoreline width 50 m). A 5.2-m skiff was driven 20 m offshore, parallel to the coast at approximately 5 knots. One observer recorded all birds seen from the shore to the boat, while the other recorded all birds 100 m seaward. Surveys were conducted from 2 hr before to 2 hr after low tide, when the maximum amount of spawn is available for foraging. Data included number and species (or genus), location, habitat (land, water or air) and behavior (forage, rest, fly, other). For 1994, locations of observations were recorded on traced maps overlaid with a 250 x 250 m grid. In 1995, locations were marked on aerial photos with mylar overlays.

We determined gull and nongull abundance in relation to same-day biomass estimates at selected ADF&G spawn deposition survey sites at northern Montague Island during 1994. In conjunction with ADF&G, we recorded bird numbers and species as the dive boat approached the shoreline to begin spawn deposition surveys. Birds were recorded in a 100 x 300 m transect centered on the ADF&G survey site, and extending from the shore outward.

Data Analysis

Distribution of Birds. We first tested the effects of herring spawn distribution on bird distribution at northern Montague Island. Based on 1994 boat surveys ($n = 12$) conducted during spawn deposition and subsequent incubation, we calculated an odds ratio (Schafer and Ramsey 1996):

$$(pOb_{\text{spawn}}/1-pOb_{\text{spawn}}) / (pSur_{\text{spawn}}/1-pSur_{\text{spawn}}),$$

where pOb_{spawn} = proportion of a species observed in spawn, and $pSur_{\text{spawn}}$ = proportion of survey with spawn. For example, if 5 km of a 10-km survey had spawn, $pSur_{\text{spawn}} = 0.5$. An odds ratio of 1 indicated that a species was equally likely to occur in a spawn area as in a nonspawn area (e.g., a ratio of 30 indicates that a species is 30 times more likely to occur in a spawn area as in a nonspawn area). We log-transformed odds ratios and tested for equality using a Z-test.

Within spawn areas we investigated the distribution of gulls, the most numerous groups of birds. We used 1994 aerial data to examine gull densities (gulls/km of shoreline) across spawn in 4 broad geographic areas: Graveyard Point (6.0 km between northern Stockdale Harbor and Montague Point), Montague Point (5.4 km including spits on the northern shore of Rocky

Bay), East Rocky Bay (4.5 km) and West Rocky Bay (4.3 km; Fig. 1-1). First, a 1-way analysis of variance (ANOVA) was used to evaluate whether gull densities varied by geographic area. When significant differences were found, specific comparisons were examined using Bonferroni/Dunn's test.

Bird Densities in Relation to Spawn Abundance. To describe the relationship between bird densities and spawn biomass we ran linear regressions. We used spawn deposition survey data provided by ADF&G. Biomass variables examined included spawn width, average eggs, total eggs, and for 1994 only, total and average eggs above -1.2 m Mean Lower Low Water (MLLW). We used eggs above -1.2 m MLLW eggs as an indication of the maximum amount of spawn exposed in the intertidal zone. Each biomass variable was evaluated individually. When the data indicated a curvilinear relationship, the quadratic term for that variable was added to the regression model. The relationship between bird densities and herring spawn biomass was evaluated using 1994 data collected at 3 spatial scales: all spawn areas (22.6 km spawn, 4 areas), spawn between Stockdale Harbor and Montague Point (6.4 km, 14 grid blocks), and 9, 100 x 300-m transects centered on ADF&G spawn deposition survey sites.

For gulls, we expanded our linear regression to also include the effects of date and other environmental factors. A best model for explaining variability in gull densities (dependent variable) was determined using a general linear model (GLM) with Systat (Systat, Inc. Evanston, IL) or SAS (SAS Institute, Cary, NC) computer software. A model was determined to be "best" when it explained the most variation in gull densities (as judged by adjusted R^2) with the fewest significant independent variables. The natural log or square root transformation of the dependent variable was used when appropriate to improve the fit of the model to the data (i.e., stabilize residual variance).

We first modeled gull densities across all spawn areas. Variables for date (Julian date and incubation stage—days since first spawn laid) and egg biomass (total eggs, average eggs, and spawn width) were highly correlated within their respective groups. To avoid multicollinearity, each variable within the date and egg biomass groups was evaluated in a simple linear regression. Mean square errors from these simple linear regressions were compared and the variable with the lowest mean square error was chosen from each group. The model with the highest adjusted R^2 and the fewest significant variables was selected as the final model. In evaluating the final model, both linear and quadratic variables and interactions were addressed.

Because more environmental variables were available on a finer scale, we used 1994 boat survey data ($n = 12$ surveys) to model densities mew gull (*Larus canus*) and glaucous-winged gull. Densities (gulls/m shoreline) were calculated for each grid block or combined grid blocks containing ADF&G spawn deposition survey sites ($n = 14$ blocks). We compared natural-log-transformed densities of glaucous-winged gull and mew gull (dependent variables) to date, spawn biomass, active spawn (presence or absence), and several habitat characteristics. We first modeled each species' density using an analysis of covariance (ANCOVA) that tested for the effects of all independent variables except spawn biomass variables. Using the best model from

this analysis, we then added spawn biomass variables one at a time and compared the adjusted R^2 to select a final model.

For species other than mew and glaucous-winged gull we used a logistic regression to analyze the effect of date, time of day, environment, and spawn biomass on the probability of a species (or species group) being present at an ADF&G spawn deposition survey sites. For 1994 boat surveys ($n = 12$), we compared species presence per block (or combined blocks) containing ADF&G spawn deposition survey sites ($n = 14$ blocks). For 1995 boat surveys ($n = 10$), we compared species presence per 200-m shoreline length centered on an ADF&G spawn deposition survey site ($n = 33$ blocks).

For both years we used stepwise and backward regression to arrive at a final model. We used likelihood-ratio tests to compare nested models. For all other models we used Akaike's Information Criterion (AIC) to determine the "best" model where models with lower AIC values represent the most appropriate model (Agresti 1990). When AIC statistics for alternative models differed by less than 3.0, we selected the model with the fewest estimable parameters.

The suite of independent variables analyzed for our logistic regressions included: date, egg biomass, time of day, active spawn (presence or absence during the days of spawn deposition), number of days spawn was laid (1–4), incubation stage (days since first spawn was laid), wave exposure (exposed, semi-protected, protected), low tide height, tide direction, tide stage, water height, and minutes since low tide. For 1994 data, shoreline distance in blocks was also used as a variable. Correlation matrices for date and egg biomass variables were examined and if variables were correlated, only one was selected based on model fit.

RESULTS

Herring spawned at northern Montague Island from 18–25 April 1994 along approximately 22.6 km of shoreline and from 27 April–1 May 1995 along 20.2 km of shoreline. Spawn deposition surveys were conducted by ADF&G divers from 28 April–14 May 1994, and 8–15 May 1995. (Wilcock et al. 1995, Willette et al. 1996). In 1994 and 1995, spawn deposition occurred from northern Stockdale Harbor to Rocky Bay. In 1995, spawn deposition also occurred at the Port Chalmers area, approximately 7.5 km south of all other spawn areas.

Species Composition and Phenology

Species Composition. Boat surveys provided the data base for species composition. We observed 63 bird species in spawn areas over both the 1994 and 1995 field seasons. For 1994, 3 bird species accounted for 90.5% of all observations in spawn areas ($n = 178,581$ birds in 12 surveys): glaucous-winged gull (57.7%), surfbird (18.6%), and mew gull (14.2%). In both 1994 and 1995, surfbird, offshore diving ducks, harlequin duck, and black turnstone comprised >93% of all nongull species in spawn areas. Offshore diving ducks were principally surf scoter, but also included oldsquaw (*Clangula hyemalis*), white-winged scoter (*Melanitta fusca*) and greater

scaup (*Aythya marila*). Gull composition (% of all gulls) in spawn areas varied from 1994–1995: 79.2–93.5% for glaucous-winged gull, 19.4–5.3% for mew gull, and 1.4–1.2% for Bonaparte's gull (*Larus philadelphia*).

Gulls. Prior to 19 April 1994 (day 0—first day of substantial spawn deposition), aerial survey data ($n = 3$) showed gull numbers ranging from 15,600–25,700. Some 89–95% of the gulls were concentrated between Stockdale Harbor and Zaikof Bay, where herring schools were located. From 21 April–15 May gull numbers averaged 35,221 in spawn areas ($SE = 5,400$, $n = 12$). Gull numbers more than tripled during spawn deposition (18–24 April), increasing from 15,100 to >55,000. Numbers peaked at approximately 84,000 on 30 April 1994, 5 days after all spawn deposition ended (day 11 of incubation). By the final flight on 15 May, gull numbers dropped to <7,700 (Fig. 1-2).

Prior to day 0 in 1995 (27 April), we estimated approximately 8,000 gulls between Zaikof Bay and Stockdale Harbor ($n = 2$ boat surveys). We were not able to accurately determine gull abundance from aerial videography surveys conducted during spawn deposition and incubation. Computer analysis of video was unsuccessful due to (1) insufficient resolution of standard s-video signal (600 lines per frame) for successful target discrimination, (2) flight line overlaps, and (3) insufficient coverage.

During both computer counting and freeze-frame counting, bird images that overlapped 2 or 3 video lines were not always resolved as 1 target. In addition noise from sun reflections on the ocean surface and confusion of birds with beach cobble made accurate counts difficult. Due to the irregular shoreline, flight lines were overlapped for complete coverage. Because of difference in recording time, this created problems with combining data from overlapped images. At other times, the irregular coastline and the belly-mounted camera's narrow field of view resulted in incomplete coverage. As a result, our spring gull estimate for 1995 should be considered minimal ($\bar{x} = 13,738$ $SE = 1,465$, range = 8,724–19,543, $n = 8$).

Boat surveys along northwest Montague Island indicated a difference in the phenology of glaucous-winged and mew gull in both 1994 and 1995. Both years prior to 20 April, glaucous-winged gulls numbered in the thousands, whereas mew gulls did not appear in significant numbers (>1,000 per survey) until 22 April 1994 and 21 April 1995.

Other Species. Flocks of offshore diving ducks up to 3,500 birds per flock were observed both years on or after 24 April, and peaking around 8–10 May. In 1994 a flock of 3,500 remained until at least 15 May, whereas the following year <500 ducks remained at northern Montague Island on 15 May. Both years, neither surfbirds nor black turnstones were observed on boat surveys before 21 April and both species were gone by 13 May. Peak surfbird numbers occurred from 27–29 April in both years, with numbers remaining relatively high until 8 May. Black turnstones peaked from 3–7 May, and both years declined rapidly after peak (Fig. 1-2).

Distribution of Birds

Testing the hypothesis that the distribution of birds is related to the distribution of spawn, we found that birds more likely to occur in spawn areas were generally the most numerous: gulls, shorebirds, dabbling and offshore diving ducks as well as bald eagles (*Haliaeetus leucocephalus*). Except for the bald eagle, these species are either known or suspected herring spawn consumers. Piscivorous birds (cormorants, mergansers, murrelets, grebes, inshore diving ducks) along with corvids (omnivorous) and Canada geese (*Branta canadensis*; herbivorous) were equally likely to occur in spawn and nonspawn areas (Table 1-1).

There was a significant difference (1-way ANOVA, $n = 48$, $P = 0.003$) in gull distribution among all spawn areas in 1994. On all but 1 flight, highest densities of gulls were recorded at Montague Point ($\bar{x} = 3,080$, $SE = 399$, $n = 12$, range = 1,038–6,433 gulls/km). Montague Point had a higher gull density than both Rocky Bay East and Graveyard Point ($P < 0.001$; Table 1-2).

Bird Densities in Relation to Spawn Abundance

We hypothesized that bird abundance was positively related to the abundance of herring spawn. A significant relationship was found for all gulls, glaucous-winged gull, mew gull, and black turnstone (Table 1-3). Of the 3 spatial scales (i.e., overall spawn areas, boat survey areas, and 100 x 300-m plots), total eggs above –1.2 m MLLW and spawn width were found to be the best predictors of bird densities. Across the 4 spawn areas (largest spatial scale), total eggs above –1.2 m MLLW was the best predictor for gull abundance ($R^2 = 0.211$, $P < 0.001$, $n = 48$). At the smallest spatial scale (100 x 300 m transects surveyed just prior to ADF&G spawn deposition) total eggs was the best predictor in describing glaucous-winged gull abundance ($R^2 = 0.95$, $P < 0.001$, $n = 9$; Fig. 1-3). At midscale (boat shoreline surveys), mew gull and black turnstone each showed a significant ($P < 0.05$) increase with spawn width. No biomass variables were significant in explaining variation in harlequin duck and surfbird numbers (P s > 0.13 ; Table 1-3).

We modeled the effects of geographic area, spawn biomass, and date on 1994 gull densities across all spawn areas using multiple regression. Our final model included incubation stage (normal and quadratic) and total eggs above –1.2 m MLLW. These 3 variables were highly significant and explained 60% of the variation in gull densities (Table 1-4). The quadratic term for incubation stage indicated that gull densities increased up to a point and then decreased as the incubation of herring spawn progressed (see Fig. 1-2).

The importance of total eggs above –1.2 m MLLW indicates that spawn in intertidal areas attracts gulls. Further analysis showed that the proportion of total eggs occurring above –1.2 m MLLW differed among the 4 geographic areas in 1994 (Kruskal-Wallis ANOVA = 9.124, 3 df, $P = 0.028$), with the highest proportion occurring at Rocky Bay West (Table 1-2). At a finer scale we used 1994 boat data to compare patterns of glaucous-winged gull abundance around ADF&G spawn deposition survey sites with ($n = 7$) and without ($n = 8$) eggs above –1.2 m MLLW. We

found a clear pattern of glaucous-winged gull absence at spawn deposition survey sites without eggs above -1.2 m MLLW (Fig. 1-4).

Using boat survey data, we examined the effects of a suite of environmental variables on glaucous-winged gull and mew gull densities. For glaucous-winged gull, the final model included total eggs above -1.2 m MLLW ($P < 0.001$) as well as 6 other variables (Table 1-5). This model explained 58% of the variation in glaucous-winged gull densities. For mew gull, the final model consisted of 5 variables, including 2 biomass variables: number of days spawn was laid down, and the interaction of spawn width x exposure. This model explained 41% of the variation in mew gull densities (Table 1-6).

Using logistic regression, we modeled the effects of environmental variables on the presence of 7 species and species groups: black turnstone, surfbird, harlequin duck, offshore diving ducks, inshore diving ducks, dabbling ducks, and corvids. For all these species combined, spawn width, number of days spawn was laid down, incubation stage (quadratic term) and site exposure were significant. Except for offshore divers, however, there was no consistent pattern in variable effects from year to year (Table 1-7).

DISCUSSION

Surf scoter and gulls, primarily glaucous-winged, were the most numerous birds at herring spawn areas in British Columbia (Outram 1958, Vermeer 1981, Haegele and Schweigert 1989, Haegele 1993a). In our study area, glaucous-winged gull was the most numerous birds throughout incubation followed by surfbird, mew gull, surf scoter, harlequin duck, and black turnstone, respectively. Our 1994 estimates of surfbird, black turnstone, and harlequin duck should be considered a minimum for spawn areas since we were able to census these species only for 6.4 km of the 22.6 km of spawn. At the same time, 1994 mew gull numbers are probably overestimated, and glaucous-winged gull numbers are probably underestimated. Numbers were calculated by multiplying each species' flock composition percentage (as determined by boat surveys) by total gull estimates (as determined from aerial surveys). Our 1994 boat surveys did not include Montague Point area, the area with the highest numbers of gulls, or Rocky Bay areas. When we sampled gull flocks at Montague Point during 1995 boat surveys, it contained almost exclusively glaucous-winged gulls.

From mid-April through late May, PWS is on the main Pacific Flyway for northern latitude breeders (Isleib and Kessel 1973). Part of the build-up of glaucous-winged gulls prior to deposition and during spawn incubation is a result of resident birds shifting their distribution within PWS and part is the result of arriving migrants. The mean March (winter resident) and July (breeding) population estimates of glaucous-winged gulls in PWS are 21,862 birds and 32,755 respectively (Agler et al. 1994, S. Kendall, USFWS, pers. comm.). We observed >25,700 gulls at Montague Island just prior to deposition when herring schools began moving into shallower areas. Our highest count of >64,000 glaucous-winged gulls on 30 April 1994 suggested that immigration of nonresident birds into the area occurred. These nonresidents

probably include birds breeding in large colonies just outside of PWS on the western Copper River Delta, as well as gulls migrating through to more westerly breeding grounds.

Mew gulls do not exhibit the same distribution shift as glaucous-winged gulls prior to spawn deposition. Average March population of mew gull in PWS is >6,700 birds (Agler et al. 1994), yet in both years we found <1,000 mew gulls at Montague Island prior to spawn deposition. While mew gulls can forage successfully on herring spawn, due to their size, they cannot effectively forage on adult herring. This would explain why mew gulls do not move into the area until after spawn deposition has occurred. Glaucous-winged gulls, on the other hand, forage regularly on adult herring schools prior to and during active spawn deposition (Haegele 1993a, this study). While we believe our 1994 peak estimate of 18,909 mew gulls is high (see above), a comparison with the average July population (6,224; Agler et al. 1994) indicated that some immigration by transient migrants probably occurred during spawn incubation.

Wintering surf scoters in PWS, estimated at 12,655 each winter (Agler et al. 1994) appear to have migrated by mid-April (this study). The summer population in PWS averages 2,742 birds (op. cit.). Based on the influx observed both years after 23 April and peak numbers occurring 8–10 May, we believe the scoters observed on spawn areas represent transient migrants en route to their interior breeding grounds or nonbreeding birds that summer in PWS.

Surfbird and black turnstone both winter south of Alaska and are transient migrants through PWS. While these birds were numerous in spawn areas, large flocks (1,000–7,000 birds) of both species were observed both years in nonspawn areas both from the ground and air. However, we never observed numbers as high as the 56,000 surfbirds and 25,000 black turnstones observed in 1992 (P. Martin, USFWS pers. comm.), even for spawn and nonspawn areas combined. Compared with mew gull, glaucous-winged gull, and surf scoter, migration through PWS by these 2 shorebird species is relatively fast (approximately 23 April–10 May). While length of stay is not known, weather conditions in some years could cause a build-up of numbers similar to those reported by Martin.

Depending on the year, timing of surfbird and black turnstone migration with herring spawn deposition and incubation may not be synchronous. At Montague Island, average first and last day of spawn deposition from 1976–1995 was 18 April and 1 May, respectively. First day of spawn has occurred after 9 May twice since 1973 (ADF&G unpubl. data). Stomach contents of surfbird and turnstone collected in spawn areas have included abundant invertebrate prey items such as blue mussels (*Mytilus trossulus*), *Littorina*, and *Balanus* as well as herring spawn (Martin 1994, and this study Chapter 2). With large flocks of both species foraging outside of spawn areas (Norton et al. 1990; P. Martin, USFWS, unpubl. data; this study) we suggest that the use of Montague Island by these 2 migrant shorebird species could be better explained by the geographic location and physiography of Montague Island. The Gulf of Alaska has an arc-shaped shoreline with PWS forming an embayment in the center (Isleib and Kessel 1973). For rocky, intertidal species such as surfbird and black turnstone, Montague Island is the first large area of suitable habitat after several hundred kilometers of sandy beach and mudflat shorelines.

As a seasonal and abundant resource, herring spawn provides an important source of energy for migration and breeding. Shortly after leaving Montague Island, all 5 species begin breeding. For surfbird and black turnstone, Montague Island may be especially important for fat deposition. Early breeding activities in both male and female sandpipers in arctic Alaska are at least partially supported by stored fat reserves (MacLean 1969). For surfbirds, as with other arctic and alpine breeding birds, a limited amount of food is available early in the breeding season. This suggests that breeding displays and egg production are supported by nutritional reserves gained in migration (Senner and McCaffery 1997). By arriving on the breeding grounds with good body condition (i.e., large fat reserves), birds can more readily withstand adverse weather conditions and more rapidly produce eggs. This ensures that chicks hatch when food is still abundant, increasing the probability of survival.

Our study showed that species such as glaucous-winged gull, mew gull, harlequin duck and surfbird are more likely to be found in spawn areas than nonspawn areas (Table 1-1). However, we could find no single biomass variable common to all species. Total eggs and total eggs above -1.2 m MLLW were significant for glaucous-winged gull, and spawn width for mew gull and black turnstone. However, no biomass variable was significant for harlequin duck or surfbird. In our general linear model for mew gull and our logistic regressions for nongull species, both spawn width and the number of days spawn was laid down (an indirect measure of biomass) were most likely to be significant in explaining the presence of these species; and in the case of mew gull its abundance.

The distribution of herring eggs is dependent on the type of vegetation on which eggs are laid, and on the slope of the beach (Haegele et al. 1981). Our work showed that total herring eggs and the vertical distribution of eggs affects glaucous-winged gull distribution. The strong relationship between glaucous-winged gulls and total eggs above -1.2 m MLLW indicates that gulls select areas with high numbers of eggs in the intertidal zone, even though they can forage on spawn in subtidal areas by swimming and surface dipping (see Chapter III this report). When we counted gulls immediately prior to a spawn survey, there was a very significant, positive relationship between glaucous-winged gull numbers and total eggs. At spawn deposition survey sites with few eggs, fewer or no glaucous-winged gulls were present. Palsson (1984) suggested that the attractiveness of a foraging area to birds depended upon some threshold egg density. Our glaucous-winged gull data support this idea.

In testing for relationships between spawn biomass and gull densities or the presence of nongull species over time, we had to rely on 1-time ADF&G spawn deposition biomass estimates. Median date for ADF&G spawn deposition surveys was 4 May 1994 (day 15 of incubation) and 10 May 1995 (day 13 of incubation, $n = 33$ surveys). In 1994, peak gull numbers occurred on 30 April, before 45 of the 56 spawn deposition surveys had been completed. Coupling our surveys with ADF&G spawn deposition survey data showed that in many areas glaucous-winged gulls probably removed all eggs above -1.2 m MLLW before ADF&G conducted their surveys. At the 8 survey sites with no eggs above -1.2 m MLLW, gulls had been present in high numbers prior to ADF&G's spawn deposition survey. At the 7 transects

with eggs above -1.2 m MLLW, gulls were present both before and after the spawn deposition survey.

Implications of Future Commercial Herring Fisheries

Until recently, herring spawn was commercially harvested in 2 ways in PWS. The first, closed pounding, consists of catching, then placing, herring into a temporary impoundment supplied with kelp to spawn on. This commercial harvest is relatively new to PWS. It began in the early 1980's and has been geographically limited to northeastern PWS. The second commercial harvest method, the wild spawn kelp, consists of divers (scuba or snorkel) and beach walkers harvesting spawn in the intertidal and subtidal areas. This harvest lasts <7 days with areas open for harvest varying by year, depending on spawn locations and the commercial market for kelp types (J. Wilcock, ADF&G, pers. comm.).

In the past, human disturbance at Montague Island during spawn deposition and incubation has been minimal, and limited to the short wild spawn kelp harvest. In spring 1997, commercial harvest of spawn resumed after being closed for 3 years due to low adult herring stocks. A new harvest method using open impoundments was allowed in the Montague Island area (J. Wilcock, ADF&G, pers. comm.).

On herring spawn areas in Oregon, Bayer (1980) observed that repeated disturbance by fisherman at 2 of his study sites affected flock formation, with few large flocks occurring in these areas. He reported that birds moved frequently between areas where fisherman were absent. The introduction of impoundments for commercial spawn harvest at Montague could affect bird distribution. To avoid human presence, birds may concentrate in shallow and rocky areas where boats cannot safely moor. Effects of human disturbance on abundance and distribution at Montague are unclear and warrant further study.

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Table 1-1. Ratios, total numbers, and significance of species and species groups observed on boat shoreline surveys in spawn versus nonspawn areas. Ratios indicate the relative odds of being observed in a spawn area as opposed to a nonspawn area. Significance levels refer to results from an odds ratio test.

Species	Ratio	Total Observed	P-value
Positive Association			
Bonaparte's gull	85.1	1,880	$P < 0.001$
Offshore diving ducks ^a	43.3	6,700	$P < 0.001$
Mew gull	32.1	26,211	$P < 0.001$
Glaucous-winged gull	15.5	110,736	$P < 0.001$
Dabbling ducks ^b	12.3	187	$P < 0.001$
Harlequin duck	11.9	4,698	$P < 0.001$
Surfbird	5.6	40,006	$P < 0.001$
<i>Calidris</i> shorebirds	7.7	617	$P < 0.001$
Bald eagle	3.7	222	$P < 0.001$
Black turnstone	2.8	3,331	$P < 0.001$
Black oystercatcher	1.4	73	$P < 0.025$
Neutral			
Corvids	1.1	401	$0.1 < P < 0.25$
Cormorants	1.0	648	$0.1 < P < 0.25$
Canada goose	0.9	354	$0.1 < P < 0.25$
Mergansers	0.6	480	$0.1 < P < 0.25$
Murrelets	0.4	234	$P > 0.25$
Inshore diving ducks ^c	0.3	234	$P > 0.25$
Grebes	0.1	30	$P > 0.25$
Negative Association			
Pigeon guillemot	0.0	15	$P > 0.5$

^a Offshore diving ducks include surf scoter, white-winged scoter, black scoter, oldsquaw, and greater scaup.

^b Dabbling ducks include mallard, northern pintail, American widgeon, green-winged teal, northern shoveler, and gadwall.

^c Inshore diving ducks include Barrow's goldeneye, common goldeneye, and bufflehead.

Table 1-2. Mean density of gulls (gulls/km) and spawn biomass by area. Data from aerial surveys ($n = 12$). Montague Island, spring 1994.

Area	Mean Density ^a Gulls/km $\bar{x} \pm SE$	Spawn Biomass/0.1 m ²			
		ADF&G Spawn Transects (n)	Mean Total Eggs (1000's)	Mean Total Eggs (1000's) Above -1.2 m MLLW	Proportion Above -1.2 m MLLW
Graveyard Point	1,359 \pm 281.3	11	6,628	428	0.065
Montague Point	3,080 \pm 398.8	13	32,328	3,041	0.087
Rocky Bay East	1,324 \pm 294.8	19	12,276	948	0.077
Rocky Bay West	2,239 \pm 421.5	11	9,655	2,812	0.291

^a Bonferroni Dunn's: Montague Point = Rocky Bay West > Graveyard Point = Rocky Bay East

Table 1-3. Results of simple and multiple regressions of spawn biomass on bird abundance. Montague Island, spring 1994. Best biomass variable indicates significant variable(s) with the highest adjusted R^2 . n = number of observations.

Species	Survey Method ^a	n	Best Biomass Variable	Adj. R^2	P	Dependent Variable
All Gulls	Aerial survey	48	Total Eggs above -1.2 m MLLW	0.211	0.001*	square root (gulls/km)
Glaucous-winged gull	Boat survey	148	Total Eggs above -1.2 m MLLW (Total Eggs above -1.2 m MLLW) ²	0.279	<0.001*	ln(glaucous-winged gulls/m)
Glaucous-winged gull	Spawn transect boat survey	9	Total Eggs	0.95	0.001*	glaucous-winged gulls
Mew gull	Boat survey	148	Spawn Width	0.69	0.001*	ln(mew gulls/m)
Harlequin duck	Boat survey	148	Total Eggs	0.000	0.32	ln(harlequins/m)
Surfbird	Boat survey	148	Spawn Width	0.009	0.13	ln(surfbirds/m)
Black turnstone	Boat survey	148	Spawn Width	0.24	0.034*	ln(turnstones/m)

^a Aerial surveys were of entire 22.6 km of spawn (4 areas) on Montague Island. Boat surveys covered 6.4 km of spawn (14 blocks) from Montague Point south to Stockdale Harbor. Nine spawn transect boat surveys (100 x 300 m) were conducted concurrent with ADF&G spawn deposition surveys.

Table 1-4. Results of regression of gull densities on date, biomass, and area. Data from aerial surveys ($n = 12$). Montague Island, spring 1994.

Regression

Dependent Variable: square root of gull density

N: 48

Adjusted R^2 : 0.600

Source	Sum of Squares	df	Mean Square	F Ratio	P
Regression	7680.0	3	2556.0	24.48	0.000
Error	4600.9	44	104.6		

Variable	Coefficient	SE	T	P(2 Tail)
Constant	23.77	5.08	4.67	<0.00
Total Eggs above -1.2 m MLLW	0.007	0.001	5.13	<0.001
Incubation Stage	3.08	0.82	3.75	0.001
(Incubation Stage) ²	-0.15	0.03	-4.98	<0.001

Table 1-5. Results of general linear model to determine the effects of date (incubation stage), spawn biomass (total eggs above -1.2 m MLLW), and environmental variables on the density of glaucous-winged gull. Montague Island, spring 1994.

Dependent Variable: natural log of glaucous-winged gull density

N: 148

Adjusted R^2 : 0.579

Source	Sum of Squares	df	Mean Square	F Ratio	<i>P</i>
Substrate	6.88	4	1.72	8.24	0.000
Wave Exposure	1.33	1	1.33	6.38	0.013
Incubation Stage	10.71	1	10.71	51.34	0.000
No. Days Spawn Laid Down	3.01	1	3.01	14.42	0.000
Low Tide Height	0.84	1	0.84	4.04	0.047
Total Eggs > -1.2 m MLLW	10.98	1	10.98	52.65	0.000
Incubation Stage x Substrate	5.16	4	1.29	6.19	0.000
Error	27.95	134	0.21		

Table 1-6. Results of general linear model to determine the effects of date (incubation stage), spawn biomass (spawn width), and environmental variables on the density of mew gull. Montague Island, spring 1994.

Dependent Variable: natural log of mew gull density

N: 148

Adjusted R^2 : 0.413

Source	Sum of Squares	df	Mean Square	F Ratio	<i>P</i>
Tide Direction	1.46	1	1.46	20.98	0.000
No. Days Spawn Laid Down	3.33	1	3.33	47.71	0.000
(Incubation Stage) ²	1.79	1	1.79	25.73	0.000
Minutes Since Low Tide	0.84	1	0.84	12.10	0.001
Spawn Width x Exposure	1.45	1	1.45	20.81	0.000
Error	9.90	142	0.07		

Table 1-7. Best models for predicting the presence of species based on logistic regression. Legend: *0.01 < P < 0.05; ** P < 0.01, NS = no significant model.

Variable	Species																
	Black Turnstone		Harlequin Duck		Surfbird		Corvids		Offshore Divers		Inshore Divers		Dabbling Ducks		All		
	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	
total eggs				*													
spawn width		*		**					*	**	*	*					**
incubation stage		**				*				**							
incubation stage ²		**		**		**											**
exposed (y or n)		**							*	**		**		**			**
time of day	**				**												
no. days spawn laid down	**				**	*			**	**	**		**			**	
water height						*		*	**								
low tide height	*			*													
tide direction						**		**									
overall P value	**	**	NS	**	**	**	NS	**	**	**	**	**	**	**	**	0.0002	**

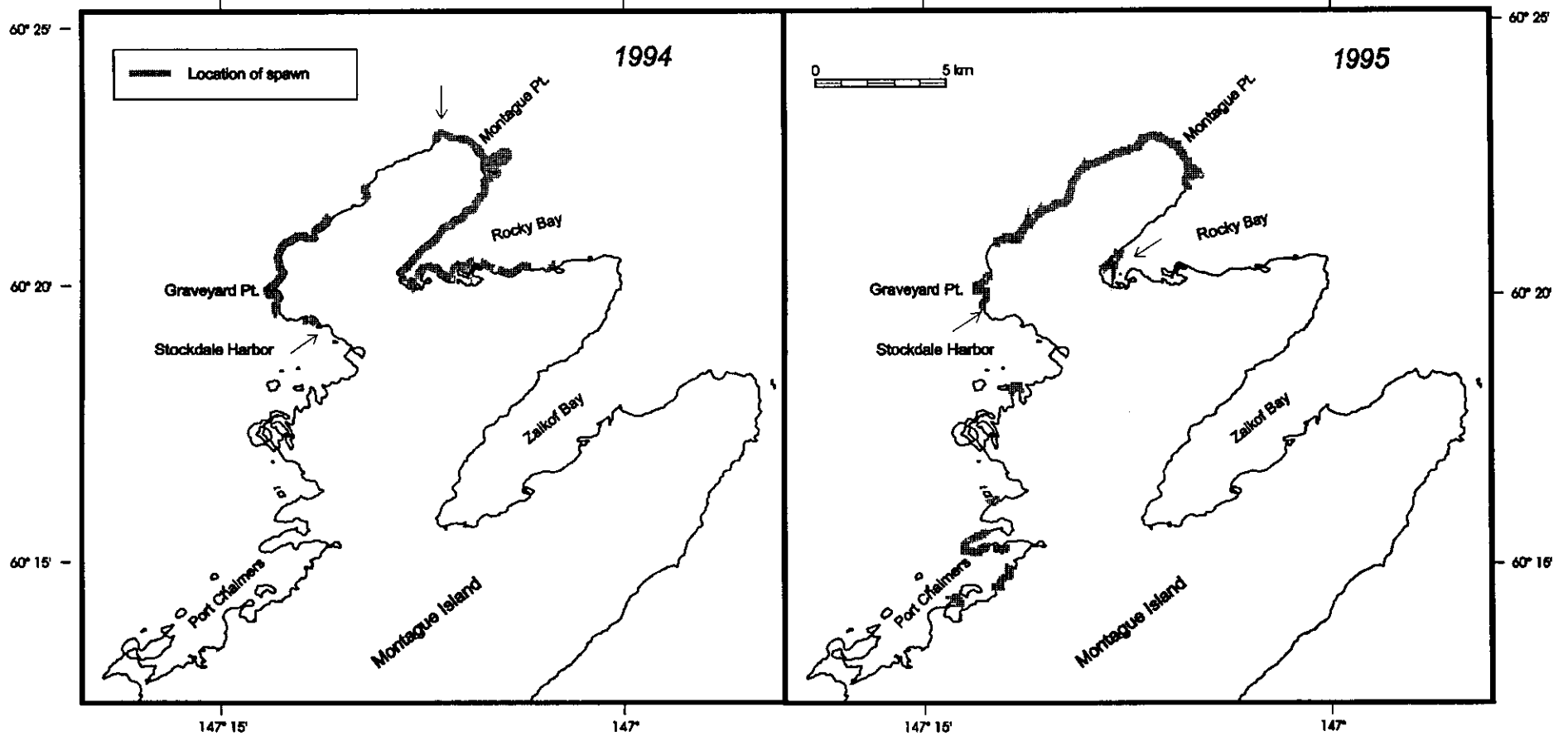


Fig 1-1. ADF&G spawn deposition surveys at northern Montague Island, spring 1994 and 1995. Sites approximate spawn distribution. Arrows indicate extent of boat shoreline surveys.

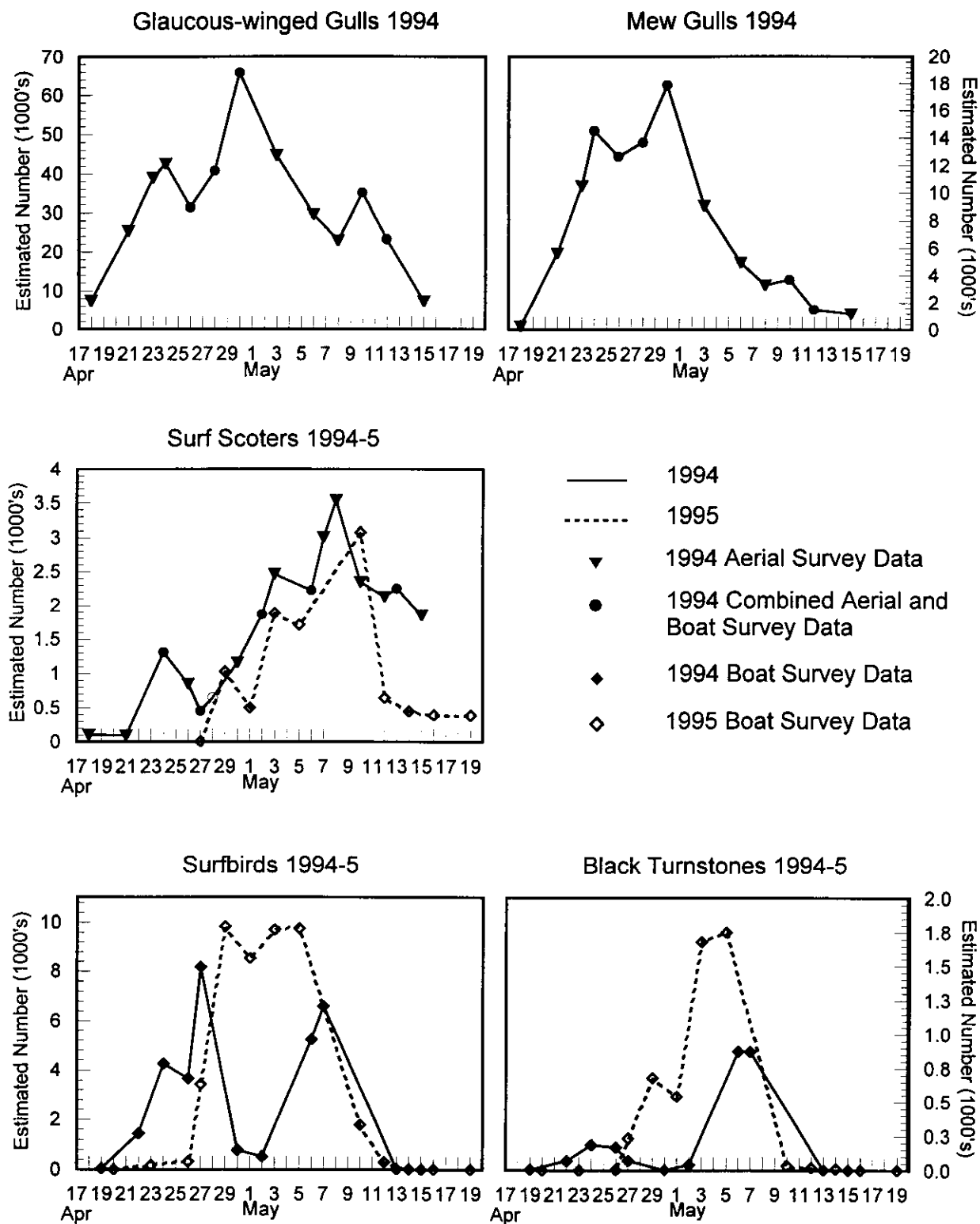


Fig. 1-2. Phenology and abundance of the 5 most numerous avian predators in herring spawn areas. Montague Island, springs 1994-95.

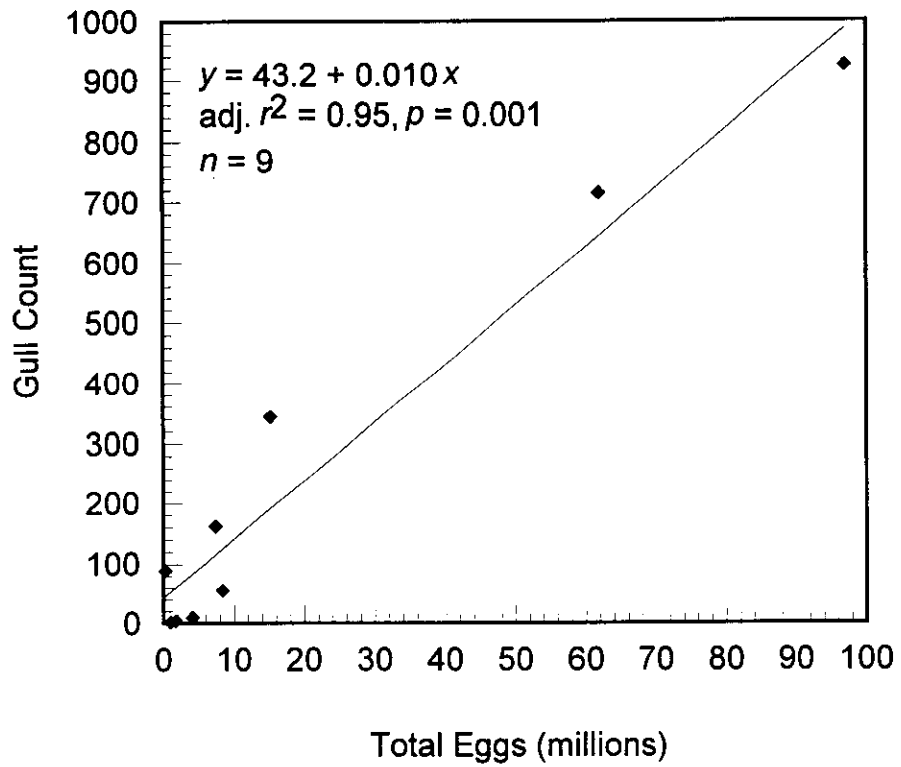


Fig. 1-3. Total glaucous-winged gulls recorded concurrent with spawn deposition surveys regressed against total eggs recorded at survey sites. Montague Island, spring 1994.

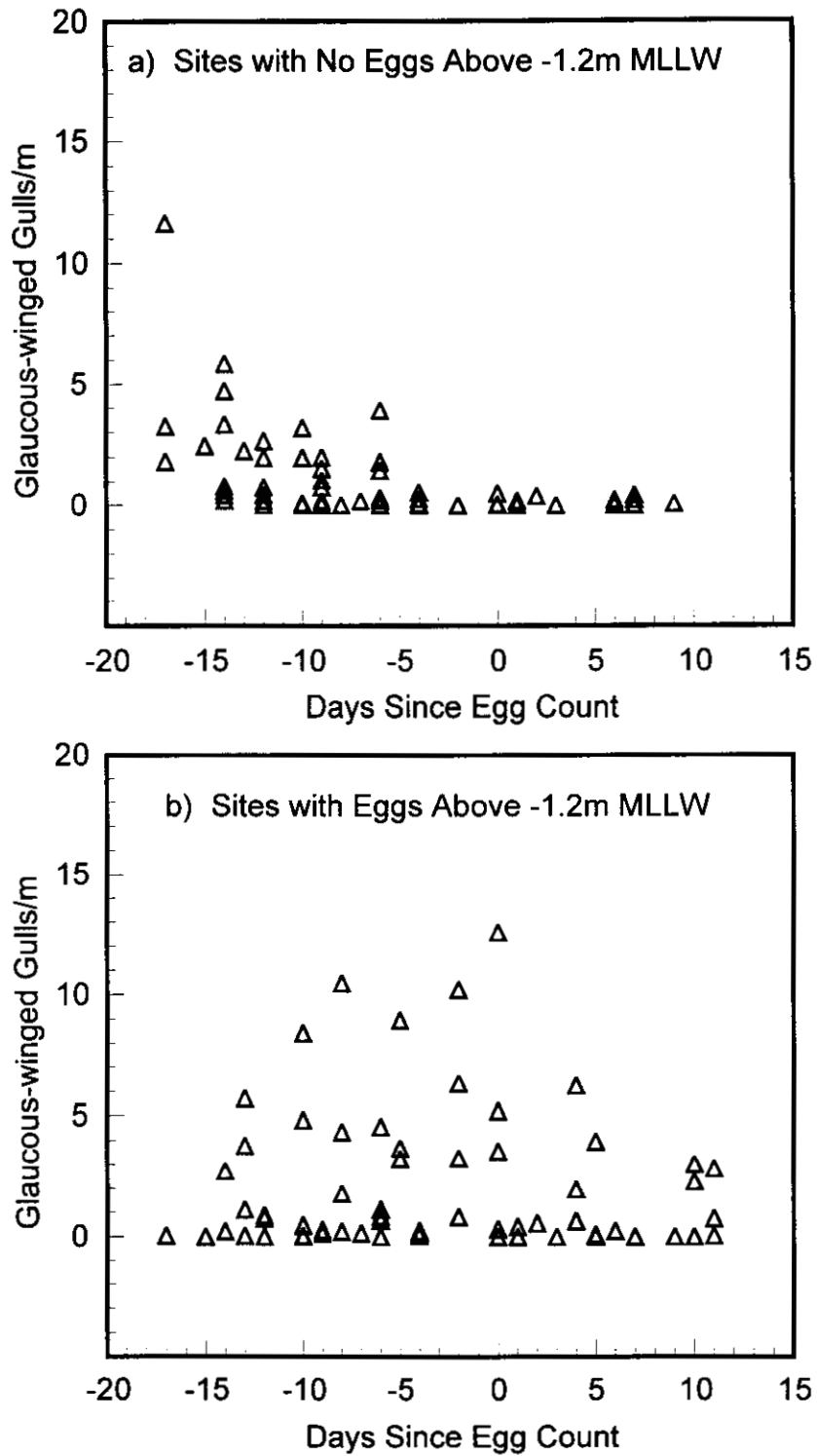


Fig. 1-4. Glaucous-winged gull densities in relationship to days since spawn surveys at ADF&G spawn deposition sites: (a) without eggs above -1.2 m MLLW ($n = 8$), and (b) with eggs above -1.2 m MLLW ($n = 7$). Graveyard Point area. Montague Island, spring 1994.

CHAPTER 2. AVIAN PREDATION ON PACIFIC HERRING SPAWN (*Clupea pallasii*) IN PRINCE WILLIAM SOUND, ALASKA.

ABSTRACT: In spring 1995 we collected and analyzed stomach contents of the 5 most abundant avian species foraging in Pacific herring spawn areas at northern Montague Island. Herring spawn occurred in 100% of the glaucous-winged gull (*Larus glaucescens*), mew gull (*Larus canus*), and surf scoter (*Melanitta perspicillata*) stomachs with aggregate percent wet weights of 100%, 96%, and 100% respectively. Surfbird (*Aphriza virgata*) and black turnstone (*Arenaria melanocephala*) stomachs contained relatively less spawn with aggregate percent wet weights of 71% and 74% respectively. We estimated the daily herring spawn intake for each of these 5 species based on estimated field metabolic rates, energy content of spawn, and proportion of energy acquired from herring spawn. Estimated herring spawn ingested was 0.73 kg/day per individual glaucous-winged gull, 1.06 kg/day per surf scoter, 0.32 kg/day per mew gull, 0.19 kg/day per surfbird, and 0.16 kg/day per black turnstone. These estimates are probably low due to energetic demands for migration and/or breeding for all 5 species. Based on 1994 aerial and boat surveys, we calculated that these 5 species removed an estimated 730 metric tons of spawn, or 27% of the estimated total spawn available at Montague Island during spring 1994. We provide a methodology to estimate losses to birds prior to spawn deposition surveys.

INTRODUCTION

Pacific herring (*Clupea pallasii*) spawn in Prince William Sound (PWS) Alaska every April, depositing their eggs on rocks and vegetation in intertidal and shallow subtidal zones. Depending on water temperature, egg density, and egg distribution, herring eggs hatch into drifting larvae at approximately 20–25 days. Studies in Washington showed that throughout incubation, egg loss or removal from the original incubation environment can be significant (Palsson 1984). In PWS, the percentage of eggs lost during incubation has ranged from 50–100% (Biggs-Brown and Baker 1993, Rooper 1996).

Herring egg loss is caused by several processes: predation, physical displacement by wave action, anoxia, and desiccation (Palsson 1984, Haegele and Schweigert 1991, Rooper 1996). Predators of herring spawn include birds, invertebrates, marine mammals, and fish. In Washington and British Columbia epibenthic invertebrates (crabs, snails, and starfish) and birds have been identified as the greatest sources of egg loss on spawning areas (Munro and Clemens 1931, Outram 1958, Palsson 1984, Haegele and Schweigert 1991, Haegele 1993a, 1993b). In those studies, maximum estimates of localized egg losses was 4% to invertebrates (Haegele 1993b) and 55% to birds (Outram 1958). Prior to this study, no studies had investigated herring spawn predation in PWS, Alaska. In spring 1995 Rooper (1996) documented herring egg predation at Montague Island by greenling (*Hexagrammidae*) and Dolly Varden char (*Salvelinus malma*). He estimated that greenling removed 2–9% of the herring eggs.

Egg loss has important implications to herring fisheries management in PWS. From 1994 through 1996, commercial herring fishing in PWS was closed because the adult herring biomass

was estimated to be below minimal harvest levels (Sharp et al. 1996). From 1989–1997, the Alaska Department of Fish and Game (ADF&G) calculated adult herring biomass for PWS using total spawn estimates, average fish size, sex ratio, and average fecundity. Total spawn biomass was determined from underwater diver transect surveys. At the time of this study, total spawn biomass was adjusted by +10% to correct for egg losses occurring before the diver transect surveys (Wilcock et al. 1995). Egg loss varies over time and area. Because spawn transect surveys are conducted from 4–20 days after the initiation of spawning activity, we hypothesized that egg loss could be significantly greater than +10%, with herring stocks underestimated as a result.

Egg loss can be estimated in 2 ways: (1) by quantifying decreases in egg abundance throughout the incubation period, and (2) by identifying sources of loss and estimating their magnitude (Haegeler and Schweigert 1991). We used the second approach to estimate herring egg loss to avian populations at Montague Island in PWS. We determined the diet composition of the most numerous bird species foraging in herring spawn areas. We then used a bioenergetics model to estimate egg consumption by these species. Previously, bioenergetics simulation models have been applied to coastal and freshwater bird populations to estimate fish consumption (Wiens and Scott 1975, Cairns et al. 1991, Madenjian and Gabrey 1995).

STUDY AREA AND METHODS

We conducted our study at Montague Island, located in PWS, Alaska from 7 April–15 May 1994 and 19 April–19 May 1995. Our study area included all shoreline areas with herring spawn. In both years, spawn occurred at the northern end of Montague Island from Rocky Bay to Stockdale Harbor. In 1995, spawn also occurred in the Port Chalmers area. See Chapter 1 for a more detailed description of the study area.

Bird Abundance

We estimated abundance of the 5 most numerous birds in spawn areas: glaucous-winged gull, mew gull, surf scoter, black turnstone, and surfbird. Location of spawn was determined from visible milt observed during ADF&G aerial herring surveys, and corrected using direct observations of eggs during ADF&G diver surveys (Wilcock et al. 1995).

We used aerial videography to estimate gull abundance. Offshore diving duck populations were estimated from aerial and boat surveys in 1994 and boat surveys in 1995. We extrapolated numbers of glaucous-winged gull, mew gull, and surf scoter from flock compositions observed during boat shoreline surveys. Black turnstone and surfbird numbers were determined from boat surveys of selected spawn areas: 6.4 km and 15.5 km of spawned shoreline for 1994 and 1995, respectively. For days without aerial or boat surveys, we interpolated bird numbers. See Chapter 1 for a more detailed description of aerial videography and boat shoreline surveys.

Diet

From 28 April–17 May 1995 we collected glaucous-winged gulls, mew gulls, surf scoters, surfbirds and black turnstones on northern Montague Island. Birds were collected from foraging flocks in spawn areas using either a 12-gauge shotgun or 0.22 caliber pellet rifle (Federal Permit PRT-789411, Alaska Permit 95-53). Surfbirds and black turnstones were collected as part of a separate study at Montague Island spawn areas on 3–4 May and 11–13 May 1994 (R. Gill, U.S. Geological Survey—Biological Resources Division).

All specimens were weighed, measured, and dissected in the field. We removed contents of the mouth, esophagus, and proventriculus (combined and hereafter referred to as esophagus), and gizzard, and stored them separately in Gilson's solution. For specimens collected from 4–17 May 1995, we examined spawn in the esophagus to estimate percent viable spawn. Clear eggs indicated viability, whereas partially to totally milky-colored eggs indicated nonviable eggs (Palsson 1984). Pearson's correlation coefficient (R) was used to evaluate the strength of the relationship between percent viable spawn and date of collection.

In the laboratory, samples were identified to lowest possible taxon and weighed (wet mass, including shells). For mew gull, glaucous-winged gull, and surf scoter, diet analysis did not include gizzard contents due to biases toward hard bodied prey and dissimilar digestion rates. Gizzard contents of surfbird and black turnstone were included due to a lack of prey in their esophagi. For each prey type, we determined percent occurrence and aggregate wet weight including shells (Korschgen 1980). The number and size of individual prey items were noted, and herring eggs numbers were estimated by counting eggs in subsamples. The number of hard shell individuals could often be determined by identifiable shell fragments (e.g., hinges). When no unique shell fragments occurred, we assumed the fragments represented 1 individual with a length equal to the average length found in stomach contents from this or similar studies (Navarro et al. 1989; P. Martin, U.S. Fish and Wildlife Service, unpubl. data).

We calculated the total energy ingested (kJ) per individual bird based on number, size, estimated dry weight of soft tissue (predigested), and the caloric density (kJ/g) of each prey type. Aggregate percent energy for each prey type was calculated for each bird and averaged for all individual birds (Korschgen 1980). We determined caloric density for herring spawn and blue mussels (*Mytilus trossulus*, soft tissue only) collected from northern Montague Island using a Parr model 1241 adiabatic bomb calorimeter (American Society for Testing and Materials 1972). We estimated caloric densities for other prey items based on similar species reported in the literature (Cummins and Wuycheck 1971). Dry weights of edible body parts of mussels were estimated using values obtained from a length-weight regression of *Mytilus trossulus*.

Consumption Model

We calculated daily herring spawn consumption for glaucous-winged gull, mew gull, surf scoter, surfbird, and black turnstone. Our bioenergetics model is similar to that used by Castro and Myers (1993) and Madenjian and Gabrey (1995). We used the following equation to calculate C , the daily herring spawn consumption (total eggs):

$$C = (FMR/AE) \times P \times 196.411$$

where FMR = field metabolic rate (kJ/day), AE = assimilation efficiency of digestible food, P = proportion of energy acquired from herring spawn as determined from stomach contents of collected birds (aggregate energy), and 196.411 = number of herring eggs needed to produce 1 kJ of energy (this study).

Based on the daily spawn consumption (C), total herring egg consumption (TC) for each species was then computed as:

$$TC = C \times BD$$

where BD = bird days, and 1 bird = 1 bird day. Bird days per species were calculated from the first day of spawn for each geographic area, 19 or 20 April–15 May 1994, and 27–28 April 1995. We observed glaucous-winged gulls feeding on adult herring only during active spawning. We therefore excluded glaucous-winged gull bird days by geographic area during days of active spawn. This included Graveyard Point on 19 and 21 April, Rocky Bay East from 19–22 and 24 April, and Rocky Bay West and Montague Point on 20 and 21 April 1994 (see Fig. 1-1).

For our model, we assumed an assimilation efficiency of 0.75 for all species, as recommended by Castro et al. (1989b). FMR for mew gull, glaucous-winged gull, and surf scoter were calculated from the allometric equation for FMR of nonflapping flight seabirds (Birt-Friesen et al. 1989):

$$FMR = 10^{(3.00 + 0.726 \log(M))}$$

where M = average body mass (kg) based on specimens collected at Montague Island. FMR s for black turnstone and surfbird were derived from the basal metabolic rate (BMR) equation for shorebirds (Kersten and Piersma 1987) and multiplied by 2.5, the standard BMR to FMR conversion for shorebirds (Drent and Piersma 1990):

$$FMR = 2.5 \times (437M^{0.729})$$

where M = average body mass (kg) for surfbird ($n = 32$) and black turnstone ($n = 28$) collected on spawn areas during 1989, 1994 and 1995. FMRs for surf scoter were estimated using Feltham's (1995) FMR for common mergansers (*Mergus merganser*; FMR = 1867 kJ/day) scaled to the mean weight of surf scoters in this study.

For comparative purposes, we calculated daily spawn consumption by species using an equation previously used to estimate avian spawn consumption in Georgia Strait, British Columbia (Haegele and Schweigert 1991, Haegele 1993a):

$$C = 0.51M^{0.85}$$

where C = daily food consumption (g) and M = average body mass (kg), (Nilsson and Nilsson 1976). For our comparison, we assumed that C represented 100% herring spawn, and 1 g = 441 eggs (wet weight; this study).

Sensitivity Analysis

A sensitivity analysis was performed on our herring spawn consumption model using the individual parameter perturbation method (Bartell et al. 1986). Four parameters: average body mass, assimilation efficiency, proportion of energy acquired from herring spawn, and FMR were evaluated by species for their effect on total herring spawn ingestion estimates. Each parameter was increased and decreased by a percentage of its nominal value while all other variables were held constant. Average body mass was adjusted by 20% on either side of its nominal value, and FMR was adjusted by 15%. Depending on the species, nominal values for the proportion of energy acquired from spawn were decreased by 20% and increased by 0–7%, resulting in a maximum value of 100%. Assimilation efficiency was increased by 10% and decreased by 20%.

Estimated values for total herring spawn ingested were calculated for all perturbations in 1% increments using S-Plus software (Mathsoft 1994). For each parameter perturbation, a simple linear regression was calculated using percent change in the parameter's nominal value as the independent variable and total spawn ingested as the dependent variable. Within each species, the absolute value of regression slopes for each parameter were compared to determine which parameter had the greatest effect on herring spawn consumption.

Rate of Egg Loss

We estimated total herring egg loss to the 5 avian predators at northern Montague Island for 1994. We calculated percent spawn loss to birds by dividing total consumption (TC) by total eggs (TE). Available herring egg estimates from underwater diver transects conducted from 28 April–14 May 1994 for all Montague Island spawn areas were provided by ADF&G (J. Wilcock and E. Brown, ADF&G, Cordova, AK, unpubl. data). For an area, we calculated TE in billions of eggs as:

$$TE = (N \times \hat{y} \times 10^{-6}) / (1 - R)$$

where N = total number of possible transects (e.g., 100 m of shoreline spawn = 316.227 transects), \hat{y} = average estimated total number of eggs (thousands) per transect, and R = estimated proportion of eggs disappearing from the study area before the survey (Wilcock et al. 1995). Since we were concerned only with consumption on or after the spawn deposition survey, R is considered to be zero. Based on laboratory measurements, we converted billions of eggs to metric tons using a wet weight of 2.27×10^{-3} per individual egg (this study).

A 1-day egg consumption rate was determined at selected spawn transects in northeast PWS and at northern Montague Island. In conjunction with underwater diver transect surveys, we recorded bird numbers and species as the dive boat approached the shoreline to begin spawn surveys. Birds were recorded for a 100 x 300 m transect centered on the spawn deposition transect, and extending from the shore outward. An egg consumption rate for that day only was then calculated for the 100 x 300 m area.

We used a similar technique to estimate the number of eggs removed from 2 areas in 1994: 4.5 km shoreline on the east side of Rocky Bay, and 5.5 km shoreline at Graveyard Point. Bird days for these areas were determined from aerial videography surveys for gulls and diving ducks at Rocky Bay, and from boat shoreline surveys at Graveyard Point (see Chapter 1 for descriptions of survey designs). Herring egg biomass for these shorelines had been estimated on diver surveys conducted from 28 April–1 May at Rocky Bay (\bar{x} = 29 April, n = 17 transects) and 2–6 May at Graveyard Point (\bar{x} = 4.7 May, n = 14 transects). For all consumption estimates, means are presented \pm SE.

RESULTS

Herring spawned at northern Montague Island from 18–25 April 1994 along approximately 22.6 km of shoreline and from 27 April–1 May 1995 along 20.2 km of shoreline. Spawn deposition transects were conducted by ADF&G divers from 28 April–14 May 1994, and 8–15 May 1995 (Wilcock et al. 1995, Willette et al. 1996).

Diet

We analyzed diets for 13 glaucous-winged gulls, 9 mew gulls, 8 surf scoters, 20 surfbirds and 14 black turnstones (Table 2-1). Diet analysis showed that herring spawn occurred in 100% of the esophagi of glaucous-winged gull, mew gull, and surf scoter and accounted for aggregate wet weights of 96–100%. Quantity of eggs found in the esophagus ranged from 0.04 g (16 eggs) in a mew gull to 145.8 g (64,513 eggs) in a glaucous-winged gull. Compared to gulls and surf scoter, food habits of surfbird and black turnstone in spawn areas were more varied and included herring spawn, *Mytilus trossulus*, gastropods, and crustaceans. No herring spawn was present in the guts of 5 surfbirds and 3 black turnstones.

We examined esophageal contents for viable spawn. Percent viable spawn for glaucous-winged gull ranged from 0–50% ($\bar{x} = 18\%$, SE = 9%, $n = 7$), and from 0–100% for both mew gull ($\bar{x} = 66\%$, SE = 16%, $n = 8$) and surf scoter ($\bar{x} = 56\%$, SE = 20%, $n = 6$). No viable spawn was observed for black turnstone ($n = 2$; Fig 2-1). We tested a relationship between percent viable spawn in the esophagus and date of collection. Percent viable spawn in the esophagus was strongly negatively correlated with date of collection for surf scoter ($R = -0.73$, $P = 0.04$, $n = 6$) and glaucous-winged gull ($R = -0.73$, $P = 0.03$, $n = 7$), but not in mew gull ($R = 0.06$, $P = 0.45$, $n = 8$).

Consumption Model

Average caloric density (kJ/g dry weight) of herring spawn and *Mytilus trossulus*, the 2 most numerous prey items were 18.7 ($n = 2$) and 19.9 ($n = 4$), respectively. The proportion of daily energy acquired from herring spawn ranged from 93–100% per species. Based on our consumption model, we estimated that black turnstone, the smallest (kg mass) predator, and surf scoter, had the lowest and highest daily herring spawn consumption rates at 0.16 and 1.06 $\text{kg}\cdot\text{d}^{-1}$ per individual, respectively (Table 2-2). By comparison, Nilsson and Nilsson's (1976) consumption equation estimates daily herring spawn consumption for the 5 species at 0.03–0.22 $\text{kg}\cdot\text{d}^{-1}$ per bird (Table 2-2).

In a sensitivity analysis of our consumption model, a decrease in assimilation efficiency had the greatest effect on herring spawn consumption for all 5 species (Table 2-3). A decrease of 20% in assimilation efficiency increased consumption by +25%. Alternatively, a 10% increase in assimilation efficiency decreased consumption by only –9%. There was a 1:1 direct relationship between herring spawn consumption and percent changes in the proportion of spawn in the diet and FMR. Percent change in body mass had the least effect on consumption. A 20% mass increase affected total herring spawn consumption by +18%, whereas a 20% mass decrease lowered total consumption by –14% (Fig. 2-2).

Egg Losses to Avian Predators

We estimated total losses to the 5 avian predators for 1994, but not for gulls in 1995. Based on aerial and nearshore boat surveys, we estimated 729.1 t of herring spawn were consumed by the 5 major avian predators over 27 days in 1994 (Table 2-4, Fig. 2-3). Over 63% of egg consumption occurred before 4 May, day 16 of incubation and the average date for herring biomass estimates. Using average fecundity and average weight to determine eggs to female herring spawners in 1994 (21,881 eggs/female; Wilcock et al. 1995), bird consumption represents spawn from 4,211 t of adult herring. Glaucous-winged gull was the most numerous spawn consumers with an estimated 825,156 bird days from 20 April–15 May. These gulls were also the largest consumers, accounting for 82% of estimated eggs removed by the 5 species (Fig. 2-4). For 1995, we were unable to calculate egg consumption by gulls because aerial video coverage was insufficient and prevented an accurate determination of gull numbers (see Chapter 1). In

1995 surf scoters, surfbirds, and black turnstones removed an estimated 47.7 metric tons of eggs over 23 days, compared with 60.2 metric tons during 27 days in 1994.

To determine daily percent loss to birds, we conducted sixteen, 100 x 300 m bird transects in conjunction with diver transect surveys at Montague Island from 28 April–8 May 1994 and at northeast PWS on 20 April and 9–10 May 1994. All 5 predators except surf scoter were observed on these transects. The 1-day egg consumption rate ranged from 0.2–17.3% at Montague Island ($\bar{x} = 2.8 \pm 1.8\%$, $n = 9$), and 0–14% at northeast PWS ($\bar{x} = 2.1 \pm 2.0\%$, $n = 7$).

On the east side of Rocky Bay, based on underwater diver transect survey results we estimated 424.1 t of available spawn on 29 April 1994. From 30 April–15 May, daily percent loss to gulls and surf scoters combined ranged from 0.14–1.4% ($\bar{x} = 0.64 \pm 0.08\%$, $n = 16$). Estimated total consumption by these 3 species was 43.5 t over 16 days, or 10.3% of available eggs. At Graveyard Point from 5–15 May 1994 the daily percent egg consumption rate ranged from 0.4–2.7% ($\bar{x} = 1.4 \pm 0.23\%$, $n = 11$). Assuming that 288.9 t were available as of the evening of 4 May, average date for transect biomass estimates, the 5 major predators consumed 44.9 t over 11 days or 15.5% of available eggs. For Graveyard Point, our estimate of total eggs available, and consequently the total percent loss is probably low because 6 transects incorporated into the total available eggs calculation were conducted on 2 May ($n = 3$ transects) and 4 May ($n = 3$ transects). From 2–4 May large glaucous-winged gull numbers were in the area (range = 8,930–11,105 glaucous-winged gulls per day), however their consumption is not taken into account in our estimate of available eggs.

DISCUSSION

At Montague Island in PWS, herring spawn is a superabundant, ephemeral resource for approximately 25–30 days each spring. We documented herring spawn consumption by the 5 most numerous avian species: glaucous-winged gull, mew gull, surf scoter, surfbird, and black turnstone. All 5 of these species are more likely to occur in spawn areas than nonspawn areas (see Chapter 1). Diet results show that when in spawn areas, glaucous-winged gull, mew gull, and surf scoter forage almost exclusively on herring spawn. During other times of the year, the 2 gull species are omnivorous (Götmark 1984, Verbeek 1993), and surf scoters are primarily bivalve consumers (Vermeer 1981).

Herring spawn at Montague Island is deposited largely in the lower intertidal and shallow subtidal zone (approximately +1.0 m to –4.5 m tide height, where –1.2 m = maximum extent of the intertidal zone; J. Wilcock, ADF&G, pers. commun.). Surf scoters can access subtidal herring spawn regardless of tide stage and height because of their ability to dive. Mew and glaucous-winged gulls can forage while swimming, standing above the tideline, and to a lesser extent, standing below the tideline. Black turnstones and surfbirds can only access spawn by standing within the exposed intertidal zone. This may explain their more varied diet, even while in spawn areas.

Consumption Model

Based on our bioenergetics model, daily consumption for each of the 5 species ranged from 3–5 times the consumption estimated using the daily ration equation (Haegele 1993a) applied to herring spawn predators in British Columbia. The daily ration equation was developed from a regression of estimated fish consumption (taken from the literature) on body mass of 4 species of avian piscivores (Nilsson and Nilsson 1976). This equation underestimates daily consumption because it does not take into account (1) differences in the relative FMRs between species groups (for example shorebirds and seabirds), and (2) different caloric values and digestibility of prey items. Because this equation was developed for a food source with relatively high energetic values, it may not be completely suitable for use with herring eggs.

Martin (1994) studied surfbirds and black turnstones at Montague Island in 1999. Using focal animal sampling, he estimated that surfbirds and black turnstones peck for food at rates of 72 and 77 pecks per minute, respectively. To achieve the daily consumption rate that we calculated, black turnstones and surfbirds would have consume an average of 2 eggs per peck and feed for about 8 and 10 hours, respectively. Herring eggs are small and occur in gelatinous clumps, and most likely more than 2 eggs are consumed per peck. In addition, our behavioral observations showed that while surfbirds and black turnstones exhibit a preference for feeding during low tide, foraging occurs at high levels throughout all tide cycles (see Chapter 3). Given these peck rates and the prolonged feeding bouts of these shorebirds, our consumption estimates appear to be realistic.

Nevertheless, there are several possible sources of error in our bioenergetics model. To date, FMR has not been directly measured for any *Larus* gull. We used an allometric equation for nonflapping flight seabirds derived from double-labeled water studies of free-living seabirds (Birt-Friesen et al. 1989). The nonflapping flight seabird equation produces a conservative FMR and, in turn, a conservative daily consumption estimate (0.73 kg/day for glaucous-winged gull) when compared with consumption estimates derived from allometric equations for cold water seabirds (0.96 kg/day) and flapping flight for cold water seabirds (1.3 kg/day).

Our sensitivity analysis showed that assimilation efficiency had the greatest effect on consumption. Assimilation efficiency was estimated at 75% in our model. Foods with higher lipid contents have higher assimilation efficiencies (Brekke and Gabrielson 1994). However, lipid content of herring spawn is low, ranging from 1.6–3.5% of wet weight and 11.3–14.6% of dry weight (Kaitaranta and Ackman 1981, Sidwell 1981, Tocher and Sargent 1984), and spawn maturation causes no noticeable variation in lipid content (Kaitaranta and Ackman 1981). Given this low lipid content, we believe that the assimilation efficiency estimate of 75% is conservative (i.e., the estimate is high).

A lower assimilation efficiency would increase the amount of spawn consumed. For example, shorebirds stopping at Delaware Bay each spring primarily consume horseshoe crab

(*Limulus polyphemus*) spawn. In a study of spawn consumption by sanderlings (*Calidris alba*), Castro et al. (1989a) found extremely low ($\bar{x} = 38.6\% \pm 1.0\%$) assimilation efficiencies and high gut passage rates for horseshoe crab spawn. They attributed the shorebirds' low assimilation efficiency to the egg cuticle's resistance to digestion as well as its rapid passage rate. Piersma et al. (1993) later proposed that horseshoe crab eggs were small enough (1 mm) to pass through the pylorus without being ground in the gizzard. Once in the lower gastrointestinal tract, where no mechanical digestion takes place, the eggs could pass through relatively unaffected. This could explain the large proportion of unbroken eggs in feces.

Pacific herring eggs are only slightly larger than horseshoe crab eggs. During our collections, we often found intact herring eggs in gizzard contents. For species with a larger gizzard and pylorus such as glaucous-winged gull, herring eggs may be passing through the pylorus before the gizzard can grind them. If bypass is occurring, assimilation efficiency would decrease, and in order to meet the bird's energy requirements, the number of eggs ingested would need to increase proportionately.

Finally, caloric density of herring eggs may change throughout the incubation stage. Paul et al. (1996) estimated that the ovarian energy content per gram (wet weight) of ripe whole herring ovaries was 5–7 kJ/g, whereas energy content per gram of herring spawn (wet weight) is estimated between 2.24 kJ/g (this study) and 2.66 kJ/g (D. Roby, U.S. Geological Survey, Biological Resources Division, Corvallis, OR). Herring eggs may lose 50% of their dry mass between laying and hatching (Hay 1984), which may cause a decline in caloric density. If this is true, birds would need to consume more eggs as the season progressed to obtain the same amount of energy. Because we collected eggs early in the season, our energy estimates are probably higher than true mean values for the season, and true consumption may be somewhat greater than our consumption estimates.

Although body mass had the smallest effect on herring spawn consumption, it still produced noticeable changes in our estimates. The mean weights of our collected birds were, in all cases, higher than those reported in the literature (Vermeer 1981, Dunning 1992, Verbeek 1993). It is likely that while at Montague Island, the birds foraging on spawn are laying down endogenous reserves, primarily fat. All 5 species showed high fat indices with maximums ranging from 0.73 to 1.81 (total body fat /lean dry mass; Bishop and Green, unpubl. data). Endogenous reserves are needed for both migration and breeding. This is particularly true for the 2 migrant shorebird species. As long distance migrants, surfbirds and black turnstones theoretically arrive at Montague Island at the end of April with their nutrient stores depleted. Not only do they have to replenish their reserves to continue migration but once they reach the breeding ground they may need to draw on those reserves to withstand inclement weather or for clutch formation and territory defense.

Egg Loss

Total eggs available at Montague Island in 1994 were initially estimated at 2,685 t (1.183×10^{12} eggs; Wilcock et al. 1995) using a formula that included a constant 10% egg loss rate. Later, the 1994 estimate was revised upwards by 57% to 4,673 t (2.061×10^{12} eggs, Willette et al. 1998) using a formula that modeled egg loss as a function of the cumulative time of air exposure between the peak day of spawn and the dive surveys. Based on our consumption model we determined that over 27 days in 1994, the 5 bird species removed 730.2 t of herring spawn, representing 27% of the initial estimate of spawn biomass at Montague Island or 16% of the revised spawn biomass estimate.

Previous research determined that 10–15% of all eggs were lost prior to spawn surveys; however, losses in very shallow depths were excluded from those calculations (Biggs-Brown and Baker 1993). More recently, Rooper (1996) modeled egg loss in PWS for 4 seasons (1990–91, 1994–95) using analysis of variance (ANOVA) based on environmental measurements taken at transects with egg loss quadrats. Depth of spawn was the primary factor determining egg loss, and air exposure could be substituted for depth. Using egg counts from 1995 spawn deposition transects (diver surveys) located adjacent to egg loss quadrats, Rooper calculated an egg loss rate for each depth based on air exposure. He estimated a daily percent egg loss rate at 6.7% and average percent egg lost over incubation at 76%.

Our estimated egg loss to birds is much higher than reported losses to vertebrate and invertebrate predators in British Columbia. Over an average incubation time of 14 d, 3–18% of total spawn was consumed including 3–4% to birds (Haegele and Schweigert 1989, 1991; Haegele 1993a, 1993b). While herring stocks and spawn were abundant during these studies (Haegele 1993a), calculated losses were based on a daily ration equation that underestimated daily consumption (see previous discussion).

Our estimated losses are lower than those recorded in exclosure experiments. Estimated losses to avian predators using exclosures ranged from 34–97% (Cleaver and Franett 1946, Outram 1958, Steinfeld 1971). However, methodology is often a problem: at least 2 studies have recorded higher losses inside exclosures, resulting from invertebrate predators (Palsson 1984) or intra- and inter-variability in diver counts (Rooper 1996). At the same time, exclosure studies primarily have measured losses in the intertidal zone, whereas our estimate is for both intertidal and subtidal areas.

A more accurate way to adjust total biomass estimate for losses to birds could be achieved using the following methods. First, monitor glaucous-winged gull numbers in spawn areas from the air using videography filmed from the side of the plane (instead of from a belly mount, see Chapter 1). Second, conduct spawn deposition surveys in a geographically sequential order whereby all surveys for 1 area are completed during a short time period. Third, calculate losses to gulls by area using our bioenergetic model.

One factor influencing the high proportion of spawn removed in 1994 is the low amount of spawn relative to other years. Comparing herring biomass indices between 1974 and 1994 in PWS, the lowest length of shoreline with spawn and the lowest spawn deposition estimate both occurred in 1994. In contrast, peak spawn deposition biomass for this 20 year period was 7 times the 1994 estimate (Sharp et al. 1996). While we were not able to address interannual variation in bird numbers in this study, we do not believe that bird numbers would increase proportionally to the amount of spawn available. Glaucous-winged gull, the largest spawn consumer, is both an abundant year-round resident and migrant breeder in PWS, arriving in large numbers between mid-April and mid-May (Isleib and Kessel 1973). With their migration and breeding coinciding both spatially and temporally with herring spawn deposition and incubation, overall glaucous-winged gull abundance throughout spawn areas is probably similar among years.

Conclusions

While the herring spawn consumption rates for the 5 avian predators are approximations, our model suggests that these 5 predators are a significant component in herring spawn egg loss. Currently herring spawn deposition biomass is used in determining herring stock assessment for commercial fisheries in PWS and other Pacific coast areas. Methods to calculate egg loss for stock assessment vary across areas, and often change. Nevertheless, our bioenergetics model provides management an improved method to estimate egg losses to birds prior to spawn biomass surveys.

Glaucous-winged gull is the dominant consumer of spawn at Montague Island. In years with low spawn deposition and high avian consumption, the number of herring larvae produced could be significantly affected. At the same time, the high consumption by gulls, shorebirds, and surf scoters underscores the importance of herring spawn in the annual cycle of these species. Herring spawn contributes to both breeding and migratory needs. Future investigations into the ecological significance of herring spawn in the life history of these avian species are warranted.

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Table 2-1. Percent occurrence and aggregate percent weight of prey items contained in gut samples of birds collected from spawn areas on northern Montague Island, April–May 1994, 1995.

Species	Glaucous-winged gull (n = 13) ^a		Mew gull (n = 9) ^a		Surf scoter (n = 8) ^a		Surfbird (n = 20)		Black turnstone (n = 14)	
	% Occ. ^b	Agg.%Wt. ^c	% Occ.	Agg.%Wt	% Occ.	Agg.%Wt	% Occ.	Agg.%Wt	% Occ.	Agg.%Wt
Fish										
Herring egg	100	100	100	96	100	100	75	70.5	69	74.0
Bivalves										
<i>Mytilus trossulus</i>	-	-	-	-	-	-	80	27.7	19	1.6
Crustaceans										
<i>Balanus</i> spp.	-	-	-	-	-	-	5	0.2	19	23.6
<i>Amphipod</i> spp.	-	-	-	-	-	-	-	-	6	0.9
<i>Amphithoe</i> spp.	-	-	-	-	-	-	5	<0.1	-	-
Hermit crab	-	-	-	-	-	-	10	0.3	-	-
Gastropods										
<i>Alia</i> spp.	-	-	-	-	-	-	10	0.7	-	-
<i>Lirularia</i> spp.	-	-	-	-	-	-	5	<0.1	-	-
<i>Littorina secana</i>	-	-	-	-	-	-	10	0.1	-	-
<i>Margarites</i> spp.	-	-	-	-	-	-	10	0.4	-	-
Unid. gastropod	-	-	-	-	-	-	5	<0.1	-	-
Insects										
Diptera Larvae	-	-	11	4.2	-	-	-	-	-	-
Nemetodes										
Nemetode	8	<0.1	-	-	-	-	-	-	-	-
Unid. organic material	8	<0.1	-	-	-	-	-	-	-	-

^a Aggregate weight based on 12 glaucous-winged gulls, 8 mew gulls, 7 surf scoters.

^b Percent occurrence: number of individuals with prey item / total number of individuals.

^c Aggregate weight: total weight of prey item for all individuals / total weight of all prey items for all individuals.

Table 2-2. Daily herring spawn consumption for the 5 main avian predators based on (a) energetic equations and proportion of spawn in diet (this study) and (b) Nilsson and Nilsson's (1976) results as used by Haegele (1993a).

Species	Mean Mass (kg)/bird	FMR (kJ/d)	Agg. Energy (%)Eggs	Eggs/day	Eggs kg(wet)/day	
					This Study	Nilsson & Nilsson (1976)
Glaucous-winged gull	1.33	1,227	100	321,328	0.73	0.22
Mew gull	0.45	563	95	140,067	0.32	0.09
Surf scoter	1.16	1,783	100	466,934	1.06	0.20
Surfbird	0.21	349	93	85,165	0.19	0.05
Black turnstone	0.14	266	99	68,981	0.16	0.03

Table 2-3. Slopes of parameters analyzed in sensitivity analysis. Slopes represent the estimated change in egg consumption (metric tons) for each percent increase in parameter value.

Species	Weight	Assimilation Efficiency	Proportion of Herring Spawn	FMR
Glaucous-winged gull	1.14	-1.76	1.56	1.56
Mew gull	0.12	-0.18	0.16	0.16
Surf scoter	0.24	-0.27	0.24	0.24
Surfbird	0.10	-0.16	0.14	0.14
Black turnstone	0.007	-0.01	0.01	0.01

Table 2-4. Estimated bird days and spawn consumed on northern Montague Island from 19 April–15 May 1994 and 27 April–19 May 1995. Bird numbers taken from aerial videography, aerial surveys, and boat surveys.

Species	Spawn Consumed					
	Total Bird-Days		Eggs (billions)		Metric Tons	
	1994	1995	1994	1995	1994	1995
Glaucous-winged gull	825,156		265.1		601.1	
Mew gull	213,755		29.9		67.8	
Surf scoter	42,392	24,558	19.8	11.5	44.9	26.0
Surfbird	73,742	102,248	6.3	8.7	14.3	19.8
Black turnstone	6,297	12,432	0.4	0.9	1.0	1.9

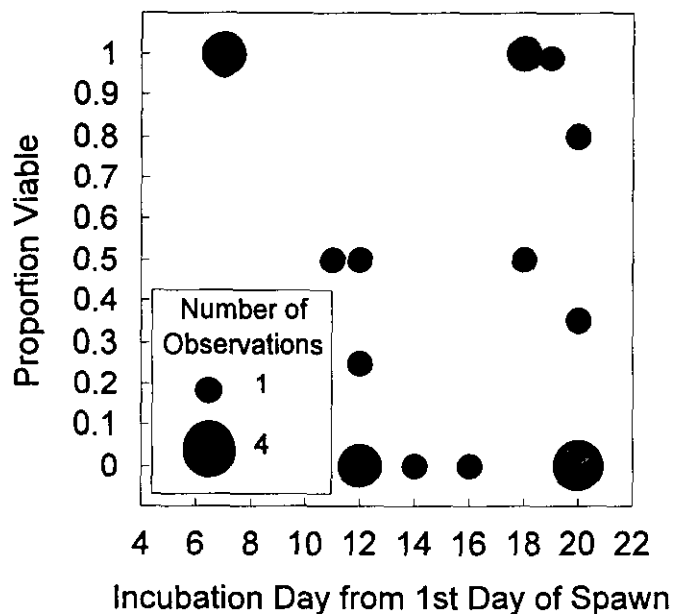


Fig. 2-1. Percent viable spawn contained in esophagi of 4 species of birds collected from within spawn areas on northern Montague Island, May 1995. Data taken from glaucous-winged gulls ($n = 7$), mew gulls ($n = 8$), surf scoters ($n = 6$), and black turnstones ($n = 2$).

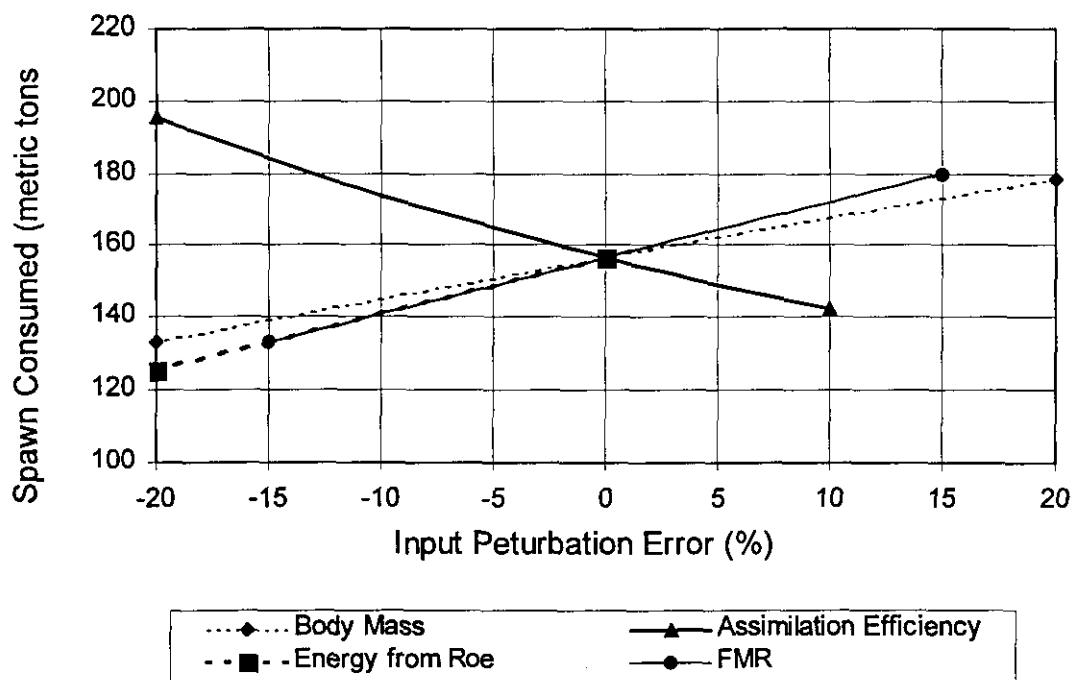


Fig. 2-2. Sensitivity analysis of spawn consumption model for glaucous-winged gull. Spawn consumed plotted as a function of possible errors (%) in estimates of body mass, assimilation efficiency, proportion of energy derived from spawn, and FMR.

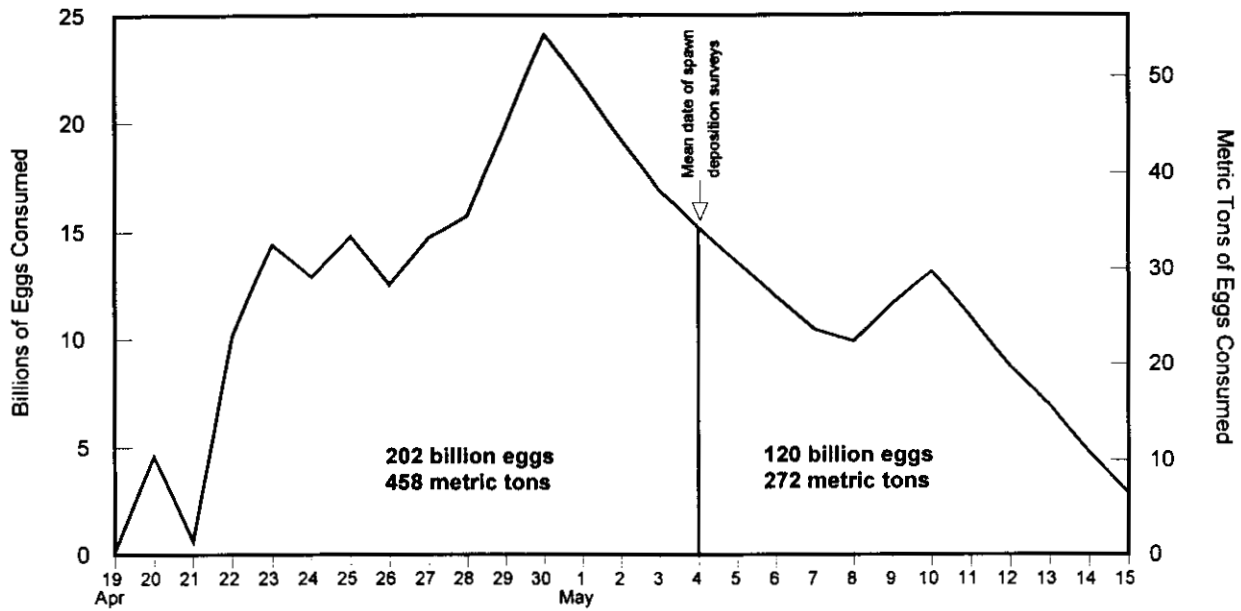


Fig. 2-3. Total spawn consumption by glaucous-winged gull, mew gull, and surf scoter over 22.6 km of spawn, and by surfbird and black turnstone over 6.4 km of spawn. Northern Montague Island, spring 1994.

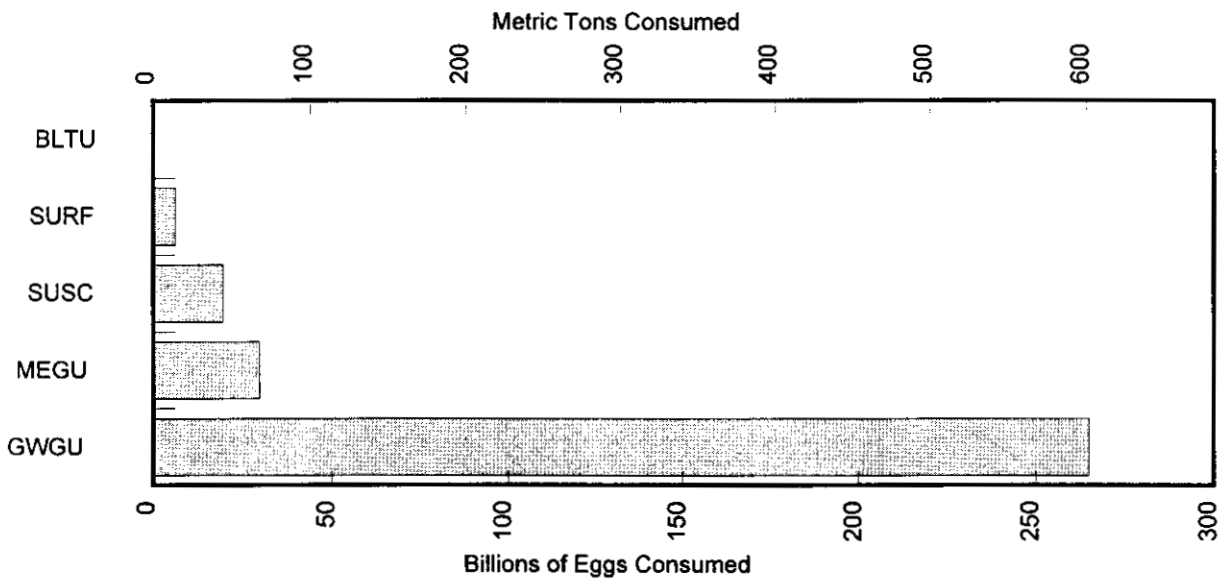


Fig. 2-4. Total spawn consumption by species. Montague Island, spring 1994. BLTU = black turnstone, SURF = surfbird, S USC = surf scoter, MEGU = mew gull, and GWGU = glaucous-winged gull.

CHAPTER 3. EFFECTS OF TIDE CYCLES ON AVIAN FORAGING PATTERNS IN RESPONSE TO THE AVAILABILITY OF PACIFIC HERRING (*Clupea pallasii*) SPAWN

ABSTRACT: We observed gulls, shorebirds, and sea ducks aggregated on Pacific herring (*Clupea pallasii*) spawn at Montague Island during spring 1994 and 1995. We examined the proportion of birds feeding in relation to a suite of variables: year, tide type, tide direction, tide stage, tide height, and tide zone. Glaucous-winged gull (*Larus glaucescens*) and mew gull (*Larus canus*) showed no significant relationship to any tide variables, with feeding occurring during all tide phases and tide heights. Surfbird (*Aphriza virgata*) and black turnstone (*Arenaria melanocephala*) exhibited a preference for feeding during low tide, though foraging occurred at high levels throughout all tide cycles. Surfbird and black turnstone concentrated foraging efforts at the tideline and in general did not feed on spawn found in windrows high in the intertidal zone. Both shorebird species feed on spawn only by walking, which would explain why shorebirds were affected by tide height. In contrast, glaucous-winged and mew gulls are able to forage by walking, wading, and swimming, and are able to access the intertidal region while flooded and exposed. Black turnstones and surfbirds foraged longer each day than the gulls. This might be because surfbirds and black turnstones are migrating through the area while the gulls are mostly summer residents of Prince William Sound. Results strongly suggest that the presence of a superabundant food resource, such as herring spawn, reduces resource partitioning among these species in intertidal zone.

INTRODUCTION

Foraging time and location of birds feeding in the intertidal zone is restricted by the extent of the tide range and the distribution of suitable prey. Many invertebrate species are common only below midtide and may, therefore, only be exposed for a short time during each tide cycle. Prey species with highest densities toward the subtidal zone may only be exposed at very low spring tides (Ricketts et al. 1985).

At northern Montague Island in Prince William Sound (PWS) Alaska, from mid-April to mid-May, 2 species of gull and 2 species of shorebird are the most common birds in the intertidal and shallow subtidal areas. The gull species, glaucous-winged gull (*Larus glaucescens*) and mew gull (*Larus canus*), are omnivorous and opportunistic feeders. Both species feed on a wide variety of fish and marine invertebrates (Götmark 1984, Verbeek 1993). Their foraging methods include surface dipping, surface seizing, jump plunging, aerial dipping (mew gull only) and picking up items from the ground (Ashmole and Ashmole 1967, Burger 1988, Verbeek 1993). In spite of these similarities, mew and glaucous-winged gulls have been shown to partition the intertidal habitat (Tangren 1982).

The 2 shorebird species, black turnstone (*Arenaria melanocephala*) and surfbird (*Aphriza virgata*), feed on barnacles, mussels, snails and other mollusks and crustaceans (Ehrlich et al. 1988, Senner and McCaffery 1997) in the rocky intertidal zone. Although often observed feeding together, each species exhibits distinct food preferences, feeding zones, and foraging

methods on wintering grounds (Connors 1977, Marsh 1984). For feeding, the surfbird uses its stout bill to tug firmly attached prey from the substrate. The black turnstone has a chisel-shaped bill and uses a hammering method to dislodge firmly attached prey (Marsh 1984).

Distinct differences in foraging patterns between gulls and shorebirds can partially be explained by differences in their morphology (e.g., leg length, bill size) and foraging methods (Recher 1966, Tangren 1982). These differences enable multiple species to partition available food resources, thereby reducing potential interspecific competition. While this is the case for much of the year, during spring migration there can be an extensive overlap in food choice and foraging habitat because of the transitory character of migratory assemblages and the relative abundance of food along the migratory route (Recher 1966).

In this chapter we describe the foraging patterns of 4 avian species and offshore diving ducks during spring migration in areas of Pacific herring spawn. Birds foraging in spawn areas consume primarily herring spawn (see Chapter 2). Therefore, we assume that the proportion of birds observed foraging is an indirect measure of spawn consumption. We hypothesized that avian consumption of spawn should (1) be greatest in the intertidal zone, and (2) vary with tide height.

STUDY AREA

We conducted our study at Montague Island, PWS, Alaska from 7 April–15 May 1994 and 19 April–19 May 1995. Our study area included all areas with herring spawn. Both years, spawn occurred at the northern end of Montague Island from Rocky Bay to Stockdale Harbor. In 1995, spawn also occurred in the Port Chalmers area (Fig. 1-1). Herring spawned at northern Montague Island from 18–25 April 1994 along approximately 22.6 km of shoreline (Wilcock et al. 1995), and from 27 April–2 May 1995 along 20.2 km of shoreline (Willette et al. 1996). See Chapter 1 for a more detailed description of the study area.

METHODS

Scan Observations

Behavior by the 5 most numerous avian species or species group in herring spawn areas was determined from scan sampling of flocks and focal animal observations (Altmann 1974). These included glaucous-winged gull, mew gull, surfbird, black turnstone, surf scoter (*Melanitta perspicillata*), white-wing scoter (*Melanitta fusca*), oldsquaw (*Clangula hyemalis*), and greater scaup (*Aythya marila*). Data were collected at 5 sites coinciding with transects monitored by Alaska Department of Fish and Game (ADF&G) for herring egg loss ($n = 2$ sites in 1994 and $n = 4$ sites in 1995, Fig. 1-1), and in addition, 1 site with spawn found in windrows in 1994.

We made 116 scans on 10 days from 28 April–11 May 1994. Two sites with permanent blinds were sampled for 6 days each, and a site with spawn found in windrows was sampled

once. In 1995, we made 296 scans over 16 days from 1–19 May. Two of the 4 sites in 1995 had very few birds and were sampled twice each. We concentrated our efforts at the other 2 sites ($n = 8$ and 9 days each).

For 1994 scan samples, we observed all birds within a 100 x 100-m plot, extending seaward from the upper boundary of the intertidal zone. In 1995 sampling areas were extended to 100 m x 300 m to include diving ducks. We made scan observations from a blind on the half hour for 6-hr periods. Each scan varied in length depending on the number of bird in the plot. For each scan we recorded time and total number of birds by species, activity, and location (for foraging birds only). Activity classes included foraging, foraging while swimming (1994 only), swimming, walking, flying, comfort, rest, and unknown. For 1995, comfort, rest, and unknown were recorded only as nonforaging. Locations of foraging birds were recorded as >3 m below tideline, 0–3 m below tideline, 0–3 m above tideline, or >3 m above tideline. In all cases distance refers to horizontal distance measured perpendicular to the tideline.

To evaluate scan data, we used Kruskal-Wallis tests to assess the effects of year on the proportion of birds foraging by species (or species group). Proportional data were arcsine square root transformed before analysis to meet the assumptions of normality and homogeneity of variance (Sokal and Rolf 1981). Based on this analysis, separate Kruskal-Wallis tests were used to test the effects of tide type (high, mid, or low), tide direction (incoming or outgoing), and tide stage (incoming low, incoming mid, incoming high, outgoing high, outgoing mid, and outgoing low) on the proportion of foraging birds.

We assessed the strength and significance of the relationship between tide height and the proportion of birds foraging. Tide height (cm) was defined as the height of the water above the level of mean low tide. None of these continuous variables were normally distributed ($P < 0.05$) based on the W test for normality (PROC UNIVARIATE, SAS Institute, Cary, NC). Therefore, Spearman's rank correlation coefficient (R_s) was used to test for relationships. Because of the large difference in sample size between years ($n = 52$ in 1994, and $n = 204$ in 1995), all data were analyzed by year.

To evaluate the relationship between the distribution of foraging birds and tideline, we used a multinomial model (PROC GENMOD, SAS Institute, Cary, NC). Changes in the proportion of birds foraging in each of 4 locations (>3 m below tideline, 0–3 m below tideline, 0–3 m above tideline, or >3 m above tideline), were assessed in relation to tide type and tide direction. The two years were evaluated separately due to unbalanced data sets.

Significance level for tests was $P = 0.05$. For simultaneous statistical tests, we used the Bonferroni probability value of 0.01 ($P = 0.05/4$ comparisons; Kuehl 1994). Nonsignificant values are reported for comparison.

Focal Animal Observations

In 1994 we also conducted focal animal observations (Altmann 1974) between scan samples. We randomly selected a foraging black turnstone, surfbird, glaucous-winged gull or mew gull and recorded all behavior for 10 min or until the bird was lost. We used *Pision* LZ64 dataloggers and *The Observer* (ver. 2.0, Noldus Information Technology, Wageningen Netherlands), a behavior recording computer program. We recorded foraging intensity (high, low, none), activity (see above), and location. Other data collected included species, age (gulls only), weather, prey species, flock size, and foraging habitat (water, exposed intertidal, egg windrow, high tide wrack line, wave wash zone). High intensity foraging was characterized by continuous foraging behavior.

Focal animal data were analyzed using a stepwise general linear model. First we tested for the effect of tide zone location on the time spent foraging. Our dependent variable was the proportion of time spent feeding, and the independent variables were location, foraging intensity, and the interaction of these 2 effects. Next we tested for the effect of environmental variables on the time spent foraging. Environmental variables included site, tide type, tide direction, tide stage, bird, age of bird, flock size, foraging habitat, weather, wind speed, wind direction, and sea state. We also compared high intensity and low intensity feeding behaviors by species using a paired *t*-test.

RESULTS

Glaucous-winged Gull

Mean proportion of glaucous-winged gulls foraging was greater in 1994 (0.56, $n = 52$) than in 1995 (0.23, $n = 204$; Kruskal-Wallis: $\chi^2 = 23.50$, 1 df, $P = 0.0001$). There was no difference either year in the proportion of birds foraging by tide type, tide direction, and tide stage (all P 's > 0.07 ; Table 3-1). There was a trend, however, for a greater proportion of glaucous-winged gulls to forage at low tide than mid and high tides (Fig. 3-1). There was no significant relationship in either year between the proportion of birds foraging and tide height (Spearman Correlation: both P 's > 0.09).

Tide type influenced foraging location in 1994 ($\chi^2 = 18.01$, 2 df, $P < 0.001$) but not in 1995. In 1994, $>95\%$ of the gulls foraged >3 m below the tideline at high tide. At mid and low tides, however, foraging birds were more evenly split among all locations, with $<28\%$ of the birds foraging >3 m below tideline. While foraging below the tideline, swimming was the primary means of locomotion. Tide direction had no influence on distribution of foraging glaucous-winged gull either year.

Mew Gull

Mean proportion of mew gulls foraging differed (Kruskall-Wallis: $\chi^2 = 27.47$, 1 df, $P = 0.0001$) between 1994 (0.69, $n = 71$) and 1995 (0.40, $n = 111$). Tide type had no effect on the proportion of foraging mew gulls in either year (both P 's > 0.56). Tide direction ($\chi^2 = 14.45$, 1 df, $P = 0.0001$) and tide stage ($\chi^2 = 15.85$, 5 df, $P = 0.007$) affected the proportion of mew gulls foraging in 1995 (Table 3-1). More birds foraged on the incoming and around high tides (Fig. 3-1). There were no significant effects of tide direction and tide stage during 1994 (both P 's > 0.36), and trends were not consistent with 1995. Both years, there were no significant relationships between the proportion of mew gulls foraging and tide height (Spearman Correlation: $P > 0.14$).

Location of foraging mew gulls differed by tide direction in both 1994 ($\chi^2 = 282.3$, 1 df, $P < 0.001$) and 1995 ($\chi^2 = 79.1$, 1 df, $P < 0.001$). On incoming tides, a large proportion of the birds foraged 0–3 m above the tideline, whereas on outgoing tides, most birds ($>74\%$) foraged below the tideline. Tide type influenced foraging location in both 1994 ($\chi^2 = 32.0$, 2 df, $P < 0.001$) and 1995 ($\chi^2 = 47.4$, 2 df, $P < 0.001$). In both years, the greatest proportion ($>81\%$) of foraging birds were below tideline during high tides. No consistent patterns were observed for low and midtides.

Black Turnstone

Mean proportion of black turnstones foraging differed (Kruskall-Wallis: $\chi^2 = 5.68$, 1 df, $P = 0.017$) between 1994 (0.86, $n = 59$) and 1995 (0.77, $n = 41$). There was no relationship between tide direction or tide stage and the proportion of foraging turnstones for either year (all P 's > 0.03). Tide type was significant in 1994 ($P = 0.01$), but not in 1995 ($P = 0.04$; Table 3-1). Trends were not consistent between years: in 1994 foraging was inversely related to tide type (L $>$ M $>$ H), and in 1995 highest foraging proportions were again during low tides, but mid and high tides were reversed (L $>$ H $>$ M; Fig. 3-1). Tide height was consistently negatively correlated with proportions of foraging turnstones in both 1994 ($R_s = -0.453$, $P = 0.0003$) and 1995 ($R_s = -0.301$, $P = 0.056$). Location of foraging black turnstones was not influenced by tide type or tide direction either year (all P s = 1.0). Black turnstones were observed foraging most frequently ($>82\%$) 0–3 m above tideline regardless of tide type or direction.

Surfbird

The mean proportion of foraging surfbirds foraging differed (Kruskall-Wallis: $\chi^2 = 10.04$, 1 df, $P = 0.002$) between 1994 (0.83, $n = 44$) and 1995 (0.76, $n = 41$). Tide type ($\chi^2 = 13.2$, 5 df, $P = 0.001$) and tide stage ($\chi^2 = 15.11$, 5 df, $P = 0.01$) both influenced the proportion of foraging surfbirds in 1994 but not in 1995 ($P > 0.12$) (Table 3-1). The influence of tide direction on foraging was nearly significant in 1995 ($P = 0.06$), with more birds foraging on incoming tides. Generally the proportion of surfbirds foraging was inversely related to the tide type, with more surfbirds foraging at low tides than at mid and high tides (Fig. 3-1). Tide height was negatively

related to the proportion of birds foraging in 1994 ($R_s = -0.601$, $P = 0.0001$) and 1995 ($R_s = -0.319$, $P = 0.042$).

Surfbird foraging locations were similar to black turnstone (Fig. 3-2), with the majority (>79%) of observations 0–3 m above the tideline. Neither tide type nor tide direction affected foraging location either year. Surfbirds foraged 0–3 m below the tideline on 10 occasions, all during incoming mid and low tides.

Offshore Diving Ducks

There were sufficient data for analysis of diving ducks in 1995 but not 1994. No significant relationships (Kruskal-Wallis: $P > 0.23$) were found between the proportion of foraging offshore diving ducks and tide type, tide direction, and tide stage. Similarly, there were no significant relationships between the proportion of birds foraging and tide height.

Focal Animals

We made 93 focal animal observations ($\bar{x} = 350.2$ s per observation period) on 4 species: black turnstone, surfbird, glaucous-winged gull, and mew gull. Prey type was identified on 47 occasions and included herring spawn, mussels, barnacles, and vegetation (e.g., eelgrass, kelp) (Table 3-2). While vegetation was the prey item observed, typically herring spawn was attached to most vegetation in that area. Across all 4 species, birds spent more time feeding intensively ($\bar{x} = 18,427.8$) than non-intensively ($\bar{x} = 5,586.6$; $t = 4.43$, 3 df, $P = 0.01$). Black turnstones spent the least time foraging intensively ($\bar{x} = 112.2$ s, $n = 25$), followed by surfbird ($\bar{x} = 128.6$ s, $n = 19$), glaucous-winged gull ($\bar{x} = 184.2$ s, $n = 28$), and mew gull ($\bar{x} = 201.1$ s, $n = 21$).

When we modeled the proportion of foraging time for black turnstone, location (0–3 m above, >3 m above, >0–3 m below) and foraging intensity (high intensity > low-intensity = not foraging) were highly significant (ANCOVA: $R^2 = 0.58$, $n = 25$, $P = 0.0001$). For surfbirds, only location was highly significant (0–3 m above >0–3 m below; $R^2 = 0.30$, $n = 19$, $P = 0.0001$) in explaining the variability in time spent foraging. For mew gull, the interaction of location x foraging intensity was significant in explaining the variability in foraging time ($R^2 = 0.32$, $n = 21$, $P < 0.02$). For glaucous-winged gull, only foraging intensity (high intensity = low intensity > not foraging) was significant ($R^2 = 0.86$, $n = 28$, $P < 0.02$). For all 4 species, we found no significant effects when we modeled the proportion of time foraging with the suite of environmental variables (all P 's > 0.05).

DISCUSSION

Many bird species alter their foraging location or method of searching to feed where the density of available prey is highest, while others shift their diet or migrate to alternative habitats (Evans 1978). On the Oregon coast, both western gull (*Larus occidentalis*) and glaucous-winged gull regularly prey on intertidal organisms, but rarely foraged in the high intertidal zone (i.e., the

zone above *Mytilus* beds; Marsh 1986). Similarly, in the Aleutian Islands, glaucous-winged gulls were selective in their choice of the intertidal zone for foraging, prey species, and prey size (Irons et al. 1986). Daily foraging activity was most intense at maximum low tide and was concentrated at the lowest intertidal zones available. Prey in the lowest intertidal zones had the highest net rate of energy gain (average energy value of a prey item divided by average combined search and handling times for that prey item). By being selective, glaucous-winged gulls maximized their net energy gain.

Invertebrate prey in the intertidal zone is typically patchy. At Montague Island, herring spawn is a superabundant, albeit ephemeral resource available at all levels of the intertidal zone and shallow subtidal zone along extensive amounts of shoreline. For both gulls and shorebirds, search and handling time is minimal for herring spawn. In addition, energy value of herring spawn is similar, if not higher than for other intertidal prey. For example, black turnstones and surfbirds were observed during focal observations feeding on barnacles and blue mussels (*Mytilus trossulus*) respectively. A comparison of energy content shows that herring spawn (4.5 Kcal/g; see chapter II) is only slightly lower than blue mussels (4.7 Kcal/g without shell; this study) and is higher than barnacles (3.3 Kcal/g; Irons 1982). Therefore, with similar energy content but lower search and handling time, net energy gain for herring spawn is high relative to other intertidal invertebrate prey.

For black turnstone and surfbird, this study found that in herring spawn areas, the only apparent trend was for a higher proportion of birds to forage on the low tide when a greater amount of intertidal habitat was available (Fig. 3-1). Although shorebirds exhibited a preference for foraging at low tide, feeding occurred during all tide cycles. Since both shorebird species can feed on spawn only by walking, this would explain the effect of tide height on foraging.

We suggest that the superabundance of herring spawn overshadows any normal intertidal foraging pattern for these 2 shorebird species. A superabundant food resource may explain why we also were not able to discern any consistent foraging patterns for gulls in relation to the tide variables. With spawn available in both the intertidal and subtidal zones, and both on the surface and below the surface, mew and glaucous-winged gulls could feed on spawn in the intertidal zone by walking and wading, or in the subtidal zone by swimming and surface dipping.

We did find a difference between years in foraging locations. For all species, there was an increased proportion of birds in the zone from 0–3 m below the tideline in 1995. For gulls, the shift was from >3 m below the tideline to 0–3 m below the tideline. For surfbird and black turnstone, the shift was from 0–3 m above the tideline to 0–3 m below the tideline. This shift may relate to differences in spawn distribution or in the slope of the intertidal zone between scan sites. During 1995, heavy winds and surf resulted in greater amounts of loose floating spawn that may have influenced the location of foraging birds, particularly of gulls.

Similarities in foraging patterns of the 2 gull species and of black turnstone and surfbird in our study suggests that the potential for interspecific competition might be high within these

pairs of species if prey abundance was limiting. In our study area, black turnstones and surfbirds typically fed together in mixed flocks in the rocky intertidal, suggesting a lack of interspecific competition. Mew gulls were typically observed feeding on the edge of gull flocks, indicating that the large and abundant glaucous-winged gulls may displace mew gulls and other species from preferred foraging areas. In Puget Sound, Tangren (1982) found that glaucous-winged gulls foraged below the tideline, even at low tide levels, while mew gulls fed predominantly above the water line on outgoing tides. He suggested this was due to a dominance hierarchy, with the larger species excluding the smaller ones.

At Montague Island, however, some areas having abundant herring spawn were not exploited, suggesting that prey abundance was not limiting during our study. We did not observe interspecific competition nor resource partitioning, which often occurs during time of limited food. Similarly, Götmark (1984) found that 5 species of sympatric *Larus* gulls that were separated in foraging ecology during the breeding season exhibited extensive overlap in food choice and foraging habitat when there was a superabundance of prey.

A phenomenon similar to the deposition of herring spawn in PWS occurs for red knots (*Calidris canutus rufa*) and ruddy turnstones (*Arenaria interpres*) at Delaware Bay where the spring shorebird migration coincides with egg deposition by horseshoe crabs (*Limulus polyphemus*). Similar to our study, Burger et al. (1997) found no pattern with the numbers of foraging birds and tide cycle during spring. She suggested that in spring, shorebirds in Delaware Bay feed nearly all the time, and rest only minimally, even during high tide. This strategy allowed birds to obtain maximum energy reserves in a short time, before migrating on to their breeding grounds.

In Prince William Sound, the timing of herring spawn deposition is immediately prior to the onset of breeding in mew and glaucous-winged gulls, with egg-laying beginning the second week of May for glaucous-winged gulls (Patten 1980). Feeding on this abundant resource may help to bring breeding gulls into peak body condition. As long-distance migrants, surfbirds and black turnstones may arrive at Montague Island with their nutrient stores depleted. Their passage through PWS usually coincides with herring spawn deposition (Norton et al. 1990; see chapter I). Energy gained from herring spawn at Montague Island is probably used by both these shorebird species for migration as well as early breeding activities. Based on records from the Yukon-Kuskokwim Delta (Handel 1982), it appears that black turnstones fly directly from Montague Island to their breeding grounds. Less is known about the migration and breeding biology of surfbirds. Senner and McCaffery (1997) speculated that surfbirds also fly directly from Montague Island to their breeding grounds.

Our study shows that in the presence of a superabundant resource such as herring spawn, the locations of foraging glaucous-winged gulls and mew gulls are qualitatively similar. Glaucous-winged gulls and mew gulls were almost evenly distributed either below or 0–3 m above the tideline. Foraging patterns and locations of foraging black turnstones and surfbirds are also similar. During both years, black turnstones and surfbirds foraged predominantly 0–3 m

above the tideline. Black turnstones and surfbirds foraged longer each tidal cycle than either gull species. Compared with the energetic needs of the resident gulls, we suggest that surfbirds and black turnstones need to forage longer and lay down greater endogenous reserves, primarily fat, in order to continue migration and arrive with enough reserves to begin breeding activities. Further studies of surfbird and black turnstone energetic needs during migration would be especially valuable in understanding their ecology.

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Table 3-1. Probability values resulting from Kruskal-Wallis tests on effects of tide type, tide direction, and tide stage on the proportion of foraging birds ($P \leq 0.01$). Montague Island, Alaska, April and May 1994 and 1995. n = number of scans. Asterisk indicates a significant difference at $P = 0.05$.

Species-Year	Kruskall-Wallis Probability		
	Tide Type	Tide Direction	Tide Stage
<i>Glaucous-winged gull</i>			
1994 ($n = 52$)	0.7	0.99	0.28
1995 ($n = 204$)	0.07	0.08	0.23
<i>Mew gull</i>			
1994 ($n = 71$)	0.76	0.98	0.36
1995 ($n = 111$)	0.56	<0.001**	0.006*
<i>Surfbird</i>			
1994 ($n = 44$)	0.001*	0.58	0.01*
1995 ($n = 41$)	0.12	0.06	0.15
<i>Black turnstone</i>			
1994 ($n = 59$)	0.01*		0.083
1995 ($n = 41$)	0.041*		0.036*
<i>Offshore diving ducks</i>			
1995 ($n = 76$)	0.37	1.23	0.35

Table 3-2. Percent frequency of prey items observed during focal observations in spawn areas. Northern Montague Island, Alaska, spring 1994. Vegetation may often include attached herring eggs.

Species	<i>n</i>	Herring Spawn	Vegetation	Mussels	Barnacles
Glaucous-winged gull	28	21	64	0	0
Mew gull	21	5	52	0	0
Surfbird	19	11	16	11	0
Black turnstone	25	12	4	0	8

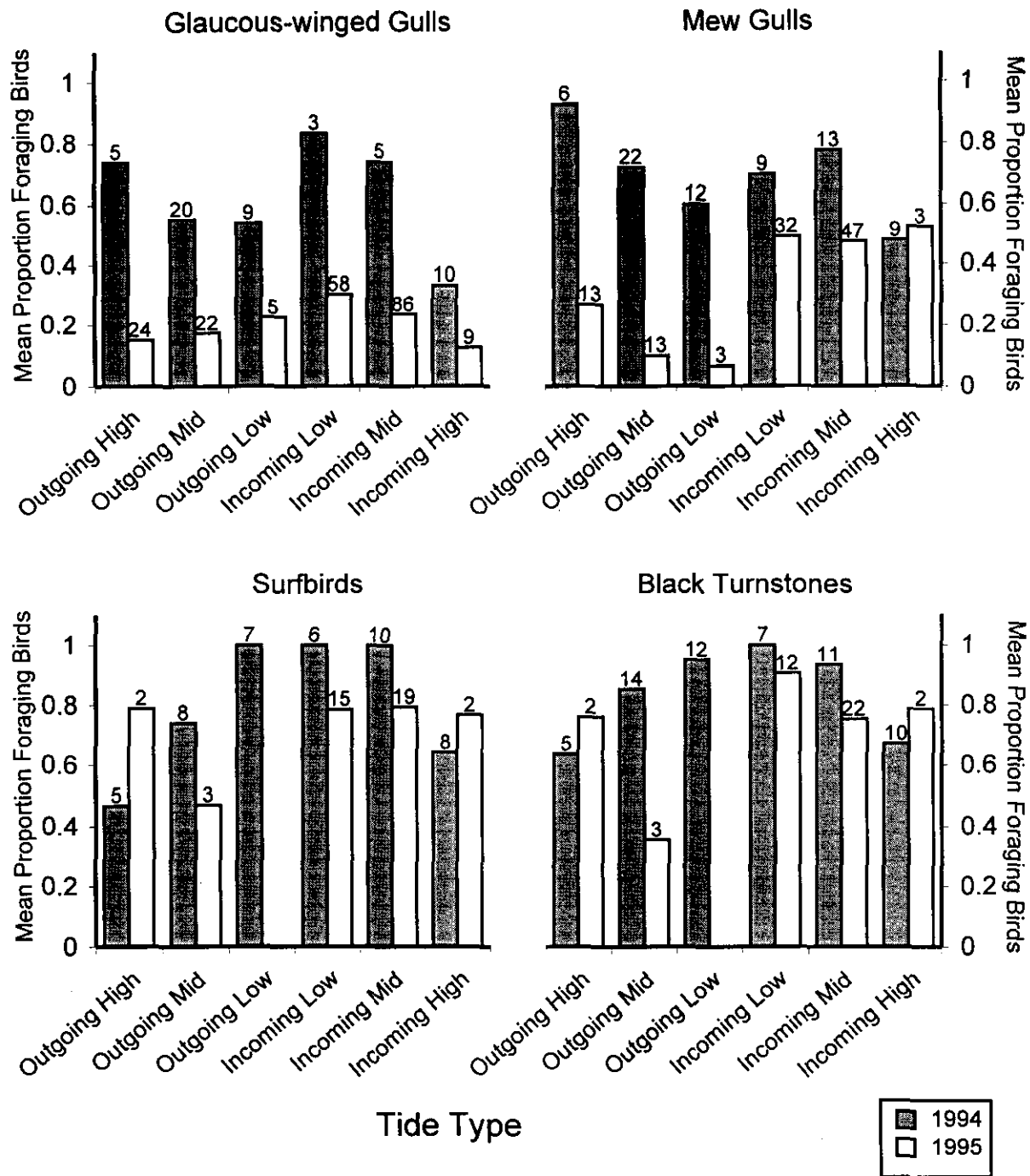


Fig. 3-1. Mean proportion glaucous-winged gulls, mew gulls, surfbirds, and black turnstones foraging in Pacific herring (*Clupea pallasii*) spawn by tidal stage. Montague Island, Alaska, April-May 1994 and 1995. Numbers above bars represent the number of scan samples.

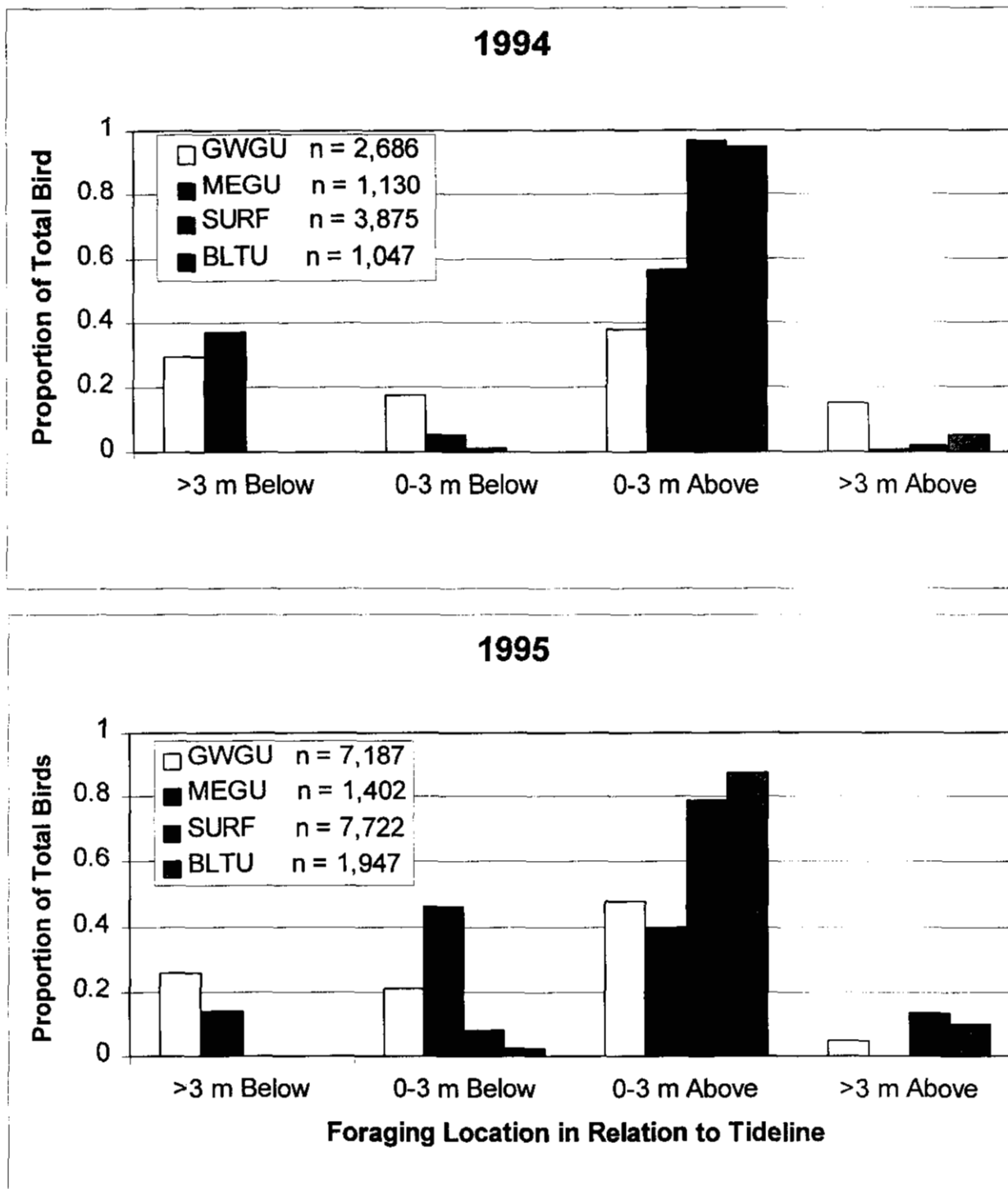


Fig. 3-2. Proportion of foraging birds within 4 distance classes from the tideline at Montague Island, spring 1994–95. GWGU = glaucous-winged gull, MEGU = mew gull, SURF = surfbird, and BLTU = black turnstone.

CHAPTER 4. EFFECTS OF BIRD PREDATION ON PACIFIC HERRING (*Clupea pallasii*) EGG LOSS

ABSTRACT: We tested the hypothesis that egg loss to birds occurs at higher rates in years when eggs are scarce using ADF&G data on density of herring spawn at selected sites. Bird abundance in 1994 was positively related to egg loss rates; however, for 1995 bird abundance was negatively related to egg loss rates. Our 1994 and hypothetical models of egg consumption suggest an explanation for these contrasting results by demonstrating that egg loss rates do not necessarily vary with the number of gulls. For example, small numbers of gulls may be taking the same proportion of eggs as large numbers of gulls. Egg loss rates instead appear to be effected by a synergistic relationship between gull abundance, total egg numbers, daily rate of consumption, and timing and location of herring spawn. We documented that avian spawn predators, including glaucous-winged gull, the largest consumer, respond positively to the abundance of spawn. At very low egg densities, we would predict low gull numbers and up to a certain point egg loss rates would decrease with increasing amounts of spawn and gulls. The relatively low gull densities at Montague Island in 1995 may not have been high enough to cause increased egg loss rates, thus explaining the negative relationship between egg loss rates and bird abundance.

INTRODUCTION

Throughout the range where Pacific herring (*Clupea pallasii*) spawn, egg loss or the removal of eggs from their original incubation environment (Palsson 1984) can be significant. For Prince William Sound (PWS), Alaska Department of Fish and Game (ADF&G) corrects their total spawn estimate +10% to account for egg losses. The 10% loss rate is based on values recommended in the literature (Haegele et al. 1981, Blankenbeckler and Larson 1982).

Understanding egg loss is important to fisheries management. Currently, estimated adult spawner biomass is used to guide herring fisheries management. Spawner biomass is calculated using the total spawn estimate (incorporating the 10% egg loss rate), as well as average fish size, sex ratio, and average fecundity (Wilcock et al. 1995).

Egg loss can be estimated 2 ways: (1) by quantifying decreases in egg density throughout spawn incubation, and (2) by identifying sources of loss and estimating their impact (Haegele and Schweigert 1991). In 1994 and 1995, ADF&G collected data on density of herring spawn at selected sites in PWS over time to determine what factors influence egg loss. Initially these data were analyzed by Rooper (1996) with respect to all the physical and biological variables collected. He built models to best explain the variation in egg abundance and in the rate of egg loss.

In this chapter we test the hypothesis that avian predators affect egg loss. Our hypothesis predicts that egg loss to birds occurs at higher rates in years when eggs are scarce. Although these data have been previously analyzed to assess the effects of avian predators on egg loss rates

(Rooper 1996), we use different statistical and model building approaches to expand upon Rooper's findings. We propose alternative explanations to Rooper's conclusions regarding the effects of bird abundance on herring spawn.

STUDY AREA & METHODS

During April and May of 1994 and 1995, we conducted our study at northern Montague Island, located in PWS, Alaska. The study area included all shoreline areas with herring spawn from northern Stockdale Harbor to Rocky Bay (Fig. 1-1). Spawn deposition occurred in this area from 19–25 April 1994, and 27–30 April 1995.

Egg Loss Monitoring

Egg loss transects were established from 21–25 April 1994 ($n = 10$ sites) and 30 April–2 May 1995 ($n = 6$ sites in our study area; Fig. 1-1). Sites were monitored by ADF&G 8–11 times each in 1994 and 9–12 times each in 1995. Egg loss was estimated using decaquads (5 x 2-m quadrats). Decaquads were permanently positioned parallel to shore, at various depths along a perpendicular transect from shoreline. Divers estimated egg density within the 5, 0.1-m² quadrats along the bottom row of the fixed decaquad, with the top row reserved in case of destruction of any quadrats in the bottom row (Wilcock et al. 1995, Willette et al. 1996).

In both years, experimental predator exclosures and controls were placed at 3 depths along the egg loss transect. In 1994, each experimental block consisted of 3 treatments: (1) a control stake, (2) a shrimp trap (0.6325 m³) with mesh size small enough to retain eggs and exclude all large predators, and (3) a shrimp trap (0.6325 m³) with mesh size that allowed egg removal by wave action, but excluded avian predators. Placement of treatments were side by side. In 1995, a rectangular 0.316 x 0.6325 x 0.316-m frame was staked into the substrate. This frame had gill netting on all sides except the bottom. A stake within close proximity served as the control.

In 1995, herring spawn deposition surveys were conducted at each egg loss monitoring site and replicated 3 times from 2–16 May. ADF&G divers used 0.1 m² quadrats to estimate abundance along a perpendicular transect from shoreline to where spawn ended. Methods were identical to standard protocol for spawn deposition surveys (see Willette et al. 1996).

Bird Abundance at Egg Loss Sites

Concurrent with egg loss data collection, we collected information on avian abundance at egg loss monitoring sites. From 22 April–7 May 1994, avian surveys were conducted 3–6 times ($\bar{x} = 4.3$ visits) along transects at each egg loss site. In conjunction with ADF&G egg loss transects, we recorded bird numbers and species as the dive boat approached the shoreline to begin their transect. Birds were recorded within a 100 x 300-m belt transect centered on the spawn deposition transect, and extending from the shore outward.

In 1995 we surveyed bird abundance at 5 of 6 egg loss monitoring sites in our study area (see Fig. 1-1). Data collection on bird abundance was not possible at egg loss transect 11 due to site access difficulties. Abundance was estimated from (1) scan samples (Altmann 1974) in a 100 x 300 m area, and (2) data collected during the nearshore boat surveys (100 x 120 m, see chapter 1). Scan observations were conducted from a blind every 30 min for 6-hr periods and covered all stages of the tide cycle. (see Chapter 3 for details on methodology). Nearshore observations were conducted only around low tides (see Chapter 1 for details on methodology)

Data Analysis

Table 4-1 provides a list of similarities and differences between the analysis in Rooper (1996) and this study. We used Rooper's (1996) linear regression of ln(egg abundance) versus days:

$$\ln N(t) = \ln N_0 - Zt + \mathcal{E}$$

where $N(t)$ = total eggs at day t (days since spawn initiation), N_0 = total eggs at spawn initiation (day 0), Zt = instantaneous rate of egg loss at day t , \mathcal{E} = random error term with $\bar{x} = 0$ and constant variance. The intercept of the regression represents initial egg abundance and the slope estimate Z , the instantaneous egg loss rate. We calculated Z for 10 egg loss transects in 1994 and 5 transects in 1995.

We calculated gull densities at each egg loss site. Bird densities were calculated from boat transects centered on the egg loss site (100 x 300 m in 1994, and 100 x 120 m in 1995) or from scan samples (average number of birds/scan) centered on the egg loss site. We used the mean bird density from the boat transects and scan samples that were closest in time to the date of each egg loss survey. We log transformed all bird densities as $\ln(\text{bird density} + 1)$. Adding 1 to bird densities avoids the possibility of taking the log of zero.

Tests and Models. In order to determine whether different egg abundance survey methods give similar estimates and variance, we used 1995 data to calculate Z values for average and total eggs from spawn deposition surveys and decaquad transects, and compared coefficients of variation (CV). Based on those results, we used 1-way analysis of variance (ANOVA) to test for differences in rate of egg loss and initial egg numbers across decaquad transects and depths in 1994. For both years we used stepwise analysis of covariance (ANCOVA) to build models that best explain the variation in egg loss. Covariates included depth, average gull abundance, wave exposure (protected, exposed), and initial number of eggs. Bonferroni adjustments were made for multiple pairwise comparisons of least square means.

Previous analysis of bird abundance (see Chapter 1) indicated a significant effect of total eggs above -1.2 m mean lower low water (MLLW) on glaucous-winged gull (*Larus glaucescens*) abundance ($P < 0.001$, $R^2 = 0.288$). We regressed total eggs above -1.2 m MLLW on $\ln(\text{glaucous-winged gull densities})$. For 1994, we estimated total eggs lost to glaucous-

winged gull flocks, by dividing gull egg consumption (321,328 eggs per glaucous-winged gull; see Chapter 2) by total eggs above -1.2 m MLLW. A hypothetical model was then produced to assess egg consumption when glaucous-winged gull density is reduced 3-fold. For this model we used 1994 gull densities, divided by 3. All other variables in the hypothetical model were the same as in the 1994 model.

1995 Exclosure Experiment. Assuming the paired exclosure and control plots are acted upon equally by the same factors, we calculated $Z_{\text{dif}} = Z_{\text{control}} - Z_{\text{excl}}$. This calculation eliminates variation between sites and increase the power of the test for significant effects. For each transect, Z_{dif} was assessed for differences across depths using Kruskal-Wallis and 1-way ANOVA.

Power Analysis. To further elaborate on the effects of avian predation on herring spawn, we estimated the sample size of bird numbers required to detect differences of varying sizes given the variance calculated in estimates of egg loss rates. It was assumed that a simple 2-sample *t*-test would be conducted to test for significant differences. The plot of 31 *Z* values resulting from 1995 egg loss data revealed a skewed distribution due to 3 outliers. The outliers were removed and a normal distribution was approximated. Setting variance = 0.007 and alpha = 0.05, sample sizes required to detect a difference in the mean *Z* values of 0.01, 0.02, 0.04, 0.05, and 0.10 were derived for a range of powers.

RESULTS

Tests and Models

Estimates of *Z* (egg loss rate) from spawn deposition surveys (SDS) were more variable than those from decaquad transects (DT) ($CV = -3.045, -2.028$ for SDS, and $CV = -0.267, -0.204, -0.388, -0.758, -0.703, -1.775$ for DT). Therefore, we used *Z* values calculated only from decaquad transects for our tests and egg loss model building. In 1994, no significant differences were detected in initial number of eggs or rate of egg loss at different depths and across transects (ANOVA, $P > 0.05$). Stepwise ANCOVA suggested that only the average number of gulls significantly effected the variation in rate of egg loss ($P = 0.009, R^2 = 0.22$). The associated rate of increased egg loss per individual gull was 0.01% (Fig. 4-1).

For 1995, depth and habitat (exposed or protected) both significantly effected rate of egg loss (ANCOVA, $P < 0.01, R^2 = 0.75$). A Bonferroni-adjusted pairwise comparison of probabilities for egg loss rates indicated that shallow depths had higher egg loss rates. Losses ranged from -11% to -18% for depths 0 to +1.5 m MLLW and -4% to -5% for depths -0.3 m to -1.5 m MLLW. Moreover, protected transects had higher egg loss rates, than exposed transects (-12% versus -7%, respectively).

Stepwise ANCOVA on combined 1994 and 1995 egg loss rates indicated that both depth and the interaction of year x average gull numbers was highly significant ($P < 0.01, R^2 = 0.27$).

As in Rooper 1996, we found that egg loss rate increased with increasing bird abundance in 1994. However, the inverse relationship occurred in 1995 when egg loss rate decreased with increasing bird abundance.

Average gull abundance was significantly higher in 1994 (290 gulls) than in 1995 (43 gulls; Kruskal-Wallis, $P < 0.001$). In order to understand the impact of gull abundance on the rate of egg loss, we modeled for 1994 the rate of egg consumption by glaucous-winged gull flock size. When glaucous-winged gulls and total eggs were low, egg loss occurred at a very high rate. However, egg loss rate dropped off dramatically with increasing total eggs, with increasing loss rates occurring only at relatively high gull densities (Fig. 4-2a). Our hypothetical model, based on 3x fewer gulls than in 1994, suggests a similar pattern at low flock sizes and low total eggs. However, when flock size remains relatively low as total eggs increase, the relative egg loss rate does not increase as fast as when flock size and total egg numbers are high (Fig. 4-2b).

Predator Exclosures

Calculation of Z_{dif} (i.e., $Z_{control} - Z_{excl}$) indicated that the rate of egg loss was greater in the exclosure than in the control ($\bar{x} = -0.01\%$, $SE = 0.027$, $n = 14$). There was no significant effect of depth on Z_{dif} (Kruskal-Wallis = 2.691, $P = 0.26$). In some cases, egg numbers increased in the controls, causing a positive Z_{dif} . Sample size was also a problem with this data set. Many of the quadrats had only 2 data points, making their estimates very inaccurate.

Power Analysis

As inadequate sample size may have been responsible for the failure to find a significant effect in the exclosure experiment, we attempted to estimate the number of paired control exclosure plots required to detect a difference between treatments of various sizes given the amount of variance in estimates of Z . The power analysis (Fig. 4-3) suggests that there was too much variance in the estimate of rate of egg loss to detect a difference between control and exclosure less than 2% without very high sample sizes. For differences <4% a sample size of 20 should detect a treatment effect 68% of the time. For differences >10% a sample size of 20 plots should be adequate.

DISCUSSION

Both Rooper's and our analysis found a significant effect of birds on egg loss rates (Table 4-2). For both analyses, bird abundance in 1994 was positively related to egg loss rates. However, in 1995 bird abundance was negatively related to egg loss rates. Our 1994 and hypothetical models of egg consumption suggest an explanation for these contrasting results by demonstrating that egg loss rates do not necessarily vary with the number of gulls. For example, small numbers of gulls may be taking the same proportion of eggs as large numbers of gulls.

Our data suggest that our hypothesis—that egg loss to birds does not occur at higher rates in years when eggs are scarce—should be rejected. Egg loss rates instead appear to be effected by a synergistic relationship between gull abundance, total egg numbers, daily rate of consumption, and timing and location of herring spawn. Analysis of our boat and aerial surveys documented that avian spawn predators, including glaucous-winged gull, the largest consumer of spawn, respond positively to the abundance of spawn (see Chapter I). Thus, at very low egg densities, we would predict no gulls or low gull numbers. Under this scenario, up to a certain point, egg loss rates would decrease with increasing amounts of spawn and gulls. The relatively low gull densities at Montague Island in 1995 may not have been high enough to cause increased egg loss rates, thus explaining the negative relationship between egg loss rates and bird abundance.

Palsson (1984) suggested the attractiveness of a foraging area to birds depended upon some threshold egg density. Initial egg numbers at egg loss sites were similar between years however gull densities at egg loss sites were significantly lower in 1995. Attractiveness of foraging areas to gulls may also be affected by timing of spawn initiation and location of spawn. Spawn initiation at Montague Island occurred 8 days later in 1995 (27 April) than in 1994 (19 April). And in 1995, initial spawn deposition occurred at Northeast and Southeast herring management areas in PWS almost 1 week earlier than at Montague Island. While <1 km of spawn was observed in these Northeast and Southeast herring areas during 1994 (Wilcock et al. 1995), in 1995 these 2 areas received >12 km of spawn (Willette et al. 1996). Perhaps these 2 areas attracted gulls that otherwise would have gone to Montague Island. Or, perhaps migrant gulls had already moved through or breeding gulls had moved to their breeding colonies before the 28 April spawn initiation at Montague Island in 1995.

We found no difference in egg loss rates across transects or depths between exclosures and controls. Palsson (1984) used exclosures and found that in only 3 of 6 experiments did exclosures reduce egg loss rates and that egg loss within exclosures was at least 96.2%. Palsson attributed egg losses within exclosure to snail and amphipod predators, drawn into the cages as a refuge response from their predators. In PWS, however, invertebrate predators do not appear to be a factor in egg loss (J. Wilcock, ADF&G, pers. comm.).

Our power analysis suggests that (1) with our sample size of 14, we were not able to detect a difference between controls and exclosures because avian predation was not responsible for a $\geq 10\%$ difference; (2) the exclosures did not work properly; or (3) the birds avoided the controls. Because exclosures lost more eggs than controls, we conclude that the problem was not one of sample size but a failure of the treatments.

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Table 4-1. Comparison of methods between the present study and Rooper 1996.

WHAT WE DID	WHAT ROOPER DID
<ul style="list-style-type: none"> • Egg loss rate was calculated using egg abundance data from the decaquad transects in 1994 and 1995, and the formula in Rooper 1996. Gives 1 estimate of egg loss per depth per transect. • Used ANOVA to test for significant effects in egg loss rate, and stepwise ANCOVA to build models that best describe the variance in egg loss rate. • 1995 data set did not include transect 11 ($n = 5$ sites). • Covariates used in 1994, 1995 ANOVA included: depth, mean gull abundance, habitat, and initial number of eggs. • Due to the unbalanced nature of the 1994 egg loss estimate at different depths, each depth at each transect was used as a separate Z estimate in the 1994-1995 combined ANCOVA (i.e., depth was treated as a continuous variable). • Data not subsetted. Substrate was not included as an effect in ANCOVA. • Compared Z values and variance between measures of egg abundance collected from the spawn deposition survey vs the decaquad transect. • Control-exclosure data were examined using the difference in Z values for paired control-exclosure plots. 	<ul style="list-style-type: none"> • Egg loss rate was calculated using egg abundance data from the decaquad transects in 1994 and 1995, and the formula $\ln N(t) = \ln N_0 - Zt + E$. • Used ANCOVA to test for significant effects in $\ln(\text{egg abundance})$, and factorial analysis to build models that best describe the variance in egg loss rate. • 1995 data set included transect 11 ($n = 6$ sites). • Covariates used in 1994, 1995 ANOVA included: days since first spawn, depth, air, wave exposure, substrate type, kelp type, loose eggs, fish predation, mean bird and mean gull abundance, habitat, and initial number of eggs. • Due to the unbalanced nature of the 1994 egg loss estimate at different depths, Z estimates from 6 depths were combined by 2s, grouping egg loss rates by 2 closest depths. Z estimates for 3 depths were used in factorial analysis. • Data subsetted by substrate (rocky or boulder) for 1994 and 1995 combined ANCOVA. Data for 1994 and 1995 combined factorial analysis used estimates from rocky substrate only). • Did not compare the 2 methods. • Z values were calculated for every control and exclosure and analysed separately. Treatment was used as an effect.

Table 4-2. Comparison of results between present study and Rooper 1996.

WHAT WE FOUND	WHAT ROOPER FOUND
<p style="text-align: center;"><i>1994</i></p> <ul style="list-style-type: none"> • No significant differences in rate of egg loss or initial egg numbers across transects or across depths (ANOVA). • Average number of gulls per transect was significant in explaining the rate of egg loss (ANCOVA). • The associated rate of increase in egg loss per individual gull was 0.01 % (regression). 	<p style="text-align: center;"><i>1994</i></p> <ul style="list-style-type: none"> • Days since spawn accounted for most of the variability in of ln(egg abundance) (ANCOVA) • All of the effects included in the model were significant (ANCOVA). • Depth, depth*bird abundance, and wave action*kelp abundance significantly effected rate of egg loss (factorial model). • Increasing bird abundance leads to higher egg loss rates (regression).
<p style="text-align: center;"><i>1995</i></p> <ul style="list-style-type: none"> • Depth and habitat were significant variables effecting the rate of egg loss (ANCOVA). Egg loss is significantly greater at more shallow depths (Bonferroni-adjusted pairwise comparison). • Protected transects had a higher egg loss rate than exposed transects (Bonferroni-adjusted pairwise comparison). 	<p style="text-align: center;"><i>1995</i></p> <ul style="list-style-type: none"> • Most factors and interaction terms including depth, habitat, and bird abundance were significant (ANCOVA). • Depth and average bird abundance significantly effected egg loss rates (factorial model). • Increasing bird abundance is associated with decreased egg loss rates (regression). • Egg loss rate appeared greater at more shallow depths (regression).
<p style="text-align: center;"><i>1994 and 1995 combined</i></p> <ul style="list-style-type: none"> • Depth and year*average number of gulls significantly effected egg loss rate (ANCOVA). 	<p style="text-align: center;"><i>1994 and 1995 combined</i></p> <ul style="list-style-type: none"> • Depth*days, kelp type, wave exposure, and depth were significantly effected ln(egg abundance) (ANCOVA). • Depth significantly effected egg loss rate (factorial model).

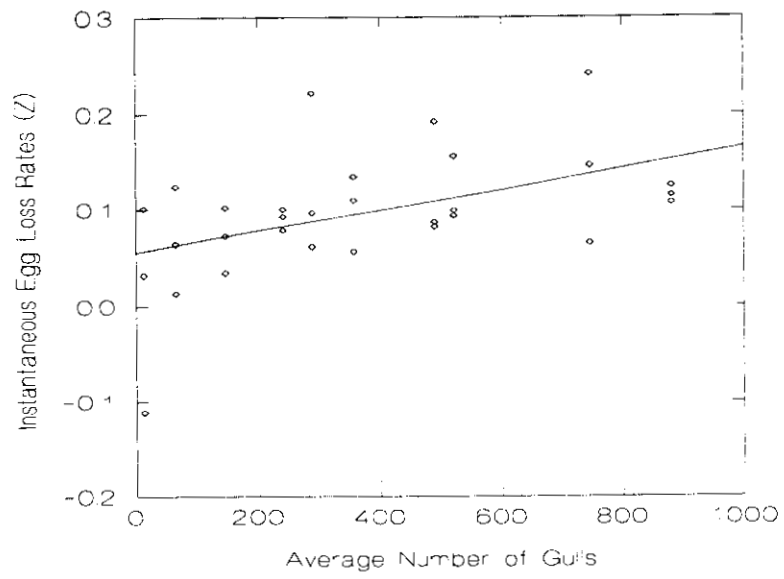


Fig. 4-1. The relationship between average number of gulls and the instantaneous egg loss rate (Z) in 1994.

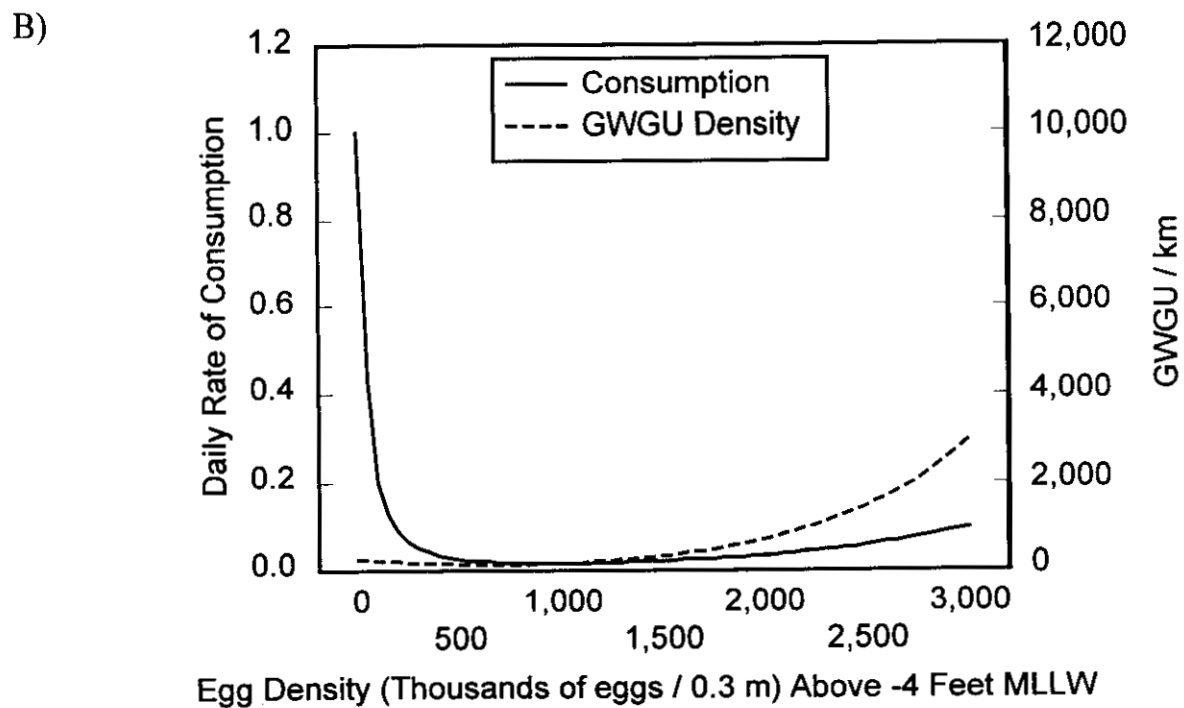
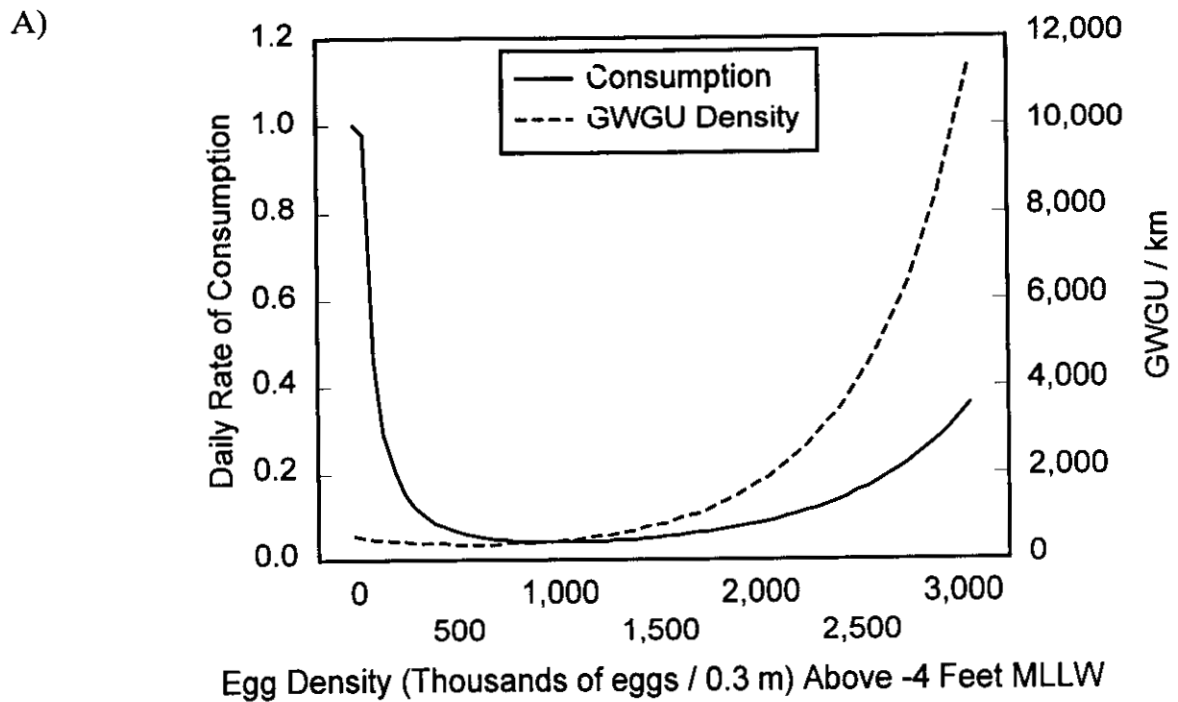


Fig. 4-2. (a) Model of 1994 egg consumption by glaucous-winged gull at northern Montague Island, and (b) Hypothetical model of egg consumption when glaucous-winged gull density is 3 times lower than in 1994.

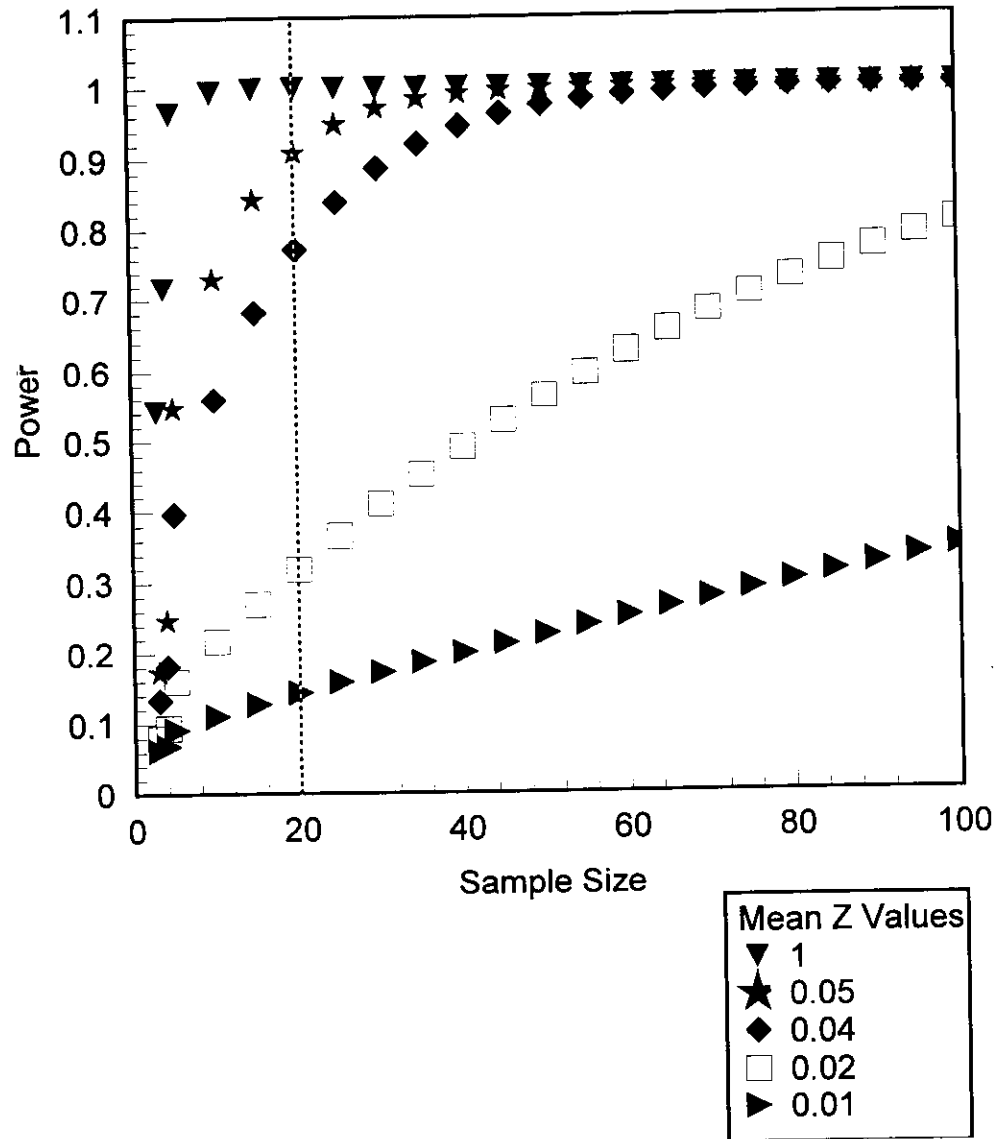


Fig. 4-3. Power analysis of avian predation exclosure sample size. Montague Island, spring 1994.

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