

CHAPTER 10

94320-Q Avian Predation on Herring Spawn

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AVIAN PREDATION ON HERRING SPAWN
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EXECUTIVE SUMMARY

Avian predation on herring spawn was studied at northern Montague Island Alaska during spring 1994. We documented avian abundance and distribution by both date and location in relation to herring spawn. Three species of birds accounted for >90% of all observations on boat surveys (n= 204,630 birds): glaucous-winged gulls (57.7%), mew gulls (14.2%), and surfbirds (18.6%).

We tested the hypothesis that a particular species or groups of species (eg. sea ducks) were attracted to spawn using a Wilcoxon paired data test. We found that those birds with a positive response to spawn were generally the most numerous species: surfbirds, Bonaparte's, mew, and glaucous-winged gulls, harlequin and sea ducks ($P < 0.01$). Black turnstones showed a positive response but were only marginally significant ($0.05 < P < 0.10$). Generally, piscivorous birds showed a neutral (eg cormorants, mergansers, grebes) or negative response (pigeon guillemots) to spawn.

Prior to spawn initiation, aerial surveys (n=3) recorded gull numbers ranging between 15,600-25,700. Gulls responded immediately to the presence of spawning fish (19-25 April) with >97% of all gulls observed occurring in the 20 km of spawned shoreline on the remaining surveys. Gull numbers peaked during active spawn, with >55,000 observed on 24 April flight. From 28 April through 12 May, an average of 29,559 gulls occurred in spawn areas (SE= 2,669; range 20,200-36,800, n= 7 flights). Sea ducks, surfbirds, and mew gulls, are primarily spring migrants through Prince William Sound and did not occur in substantial numbers until after 27 April.

We used generalized linear models to test two hypotheses: a) that the distribution, timing, and abundance of gulls, sea ducks and shorebirds is positively correlated with the dispersion, timing, and abundance of herring spawn; and, b) avian consumption of herring spawn is a function of egg density and diminishes as spawn decreases.

We ran stepwise glm models to determine the relationship of total birds and total glaucous-winged gulls (dependent variables) and biomass variables at ADF&G spawn deposition transects. We included an additional suite of independent variables. For both models, the same two variables were significant: TOTAL EGGS ($P < 0.001$) and SPAWN DAYS (number of days spawn was laid) ($P < 0.02$ for GW gulls, and $P < 0.01$ for all birds). The models were both significant and explained 84.7% and 82.7% of the variation in GW gulls and all birds, respectively.

We tested the hypothesis that a threshold level of spawn was determining gull densities using two levels of spawn: <2,000 eggs, and >2,000 eggs. Mean number of gulls was significantly higher ($P < 0.05$) in areas with >2,000 eggs (10^3) than in areas with <2,000 eggs. Average number of glaucous-winged gulls on transects with <2,000 total eggs was 63 birds, whereas on transects with >2,000 eggs, the average was 370.

Using the results from the boat transects for northwestern Montague Island, we found a similar relationship between biomass (AVERAGE EGGS, TOTAL EGGS, SPAWN WIDTH) and total birds when we performed a simple regression on total bird abundances in grids where a spawn deposition survey had been previously completed. The TOTAL EGGS at the time of the deposition survey was always significant ($P < 0.05$). All three of the regressions outlined above then support the hypothesis that bird numbers are positively related to egg abundance, and that consumption (as indicated by total numbers present) is a function of egg density.

We used flock scans to test indirectly if herring spawn is a major component in the diet of bird species foraging in herring spawn areas. For both black turnstones and surfbirds, a significantly higher proportion fed 0-3m above the tideline than other zones and fed at low and mid tides than at high tide ($P < 0.01$). Both GW gulls and mew gulls fed by swimming below the tideline and fed standing in all tidal zones. For both species there was a highly significant difference in the proportion of gulls feeding by tidal zone. Based on this preference for feeding at or below the tideline, we tentatively conclude that these birds are most likely foraging on spawn.

INTRODUCTION

Pacific herring (*Clupea pallasii*) has been identified as a resource injured by the Exxon Valdez oil spill. Every April this species deposits their eggs on rocks and vegetative substrate in the intertidal and shallow subtidal zones of Prince William Sound (PWS). Since 1989, significant declines in spawner biomass have been documented. In both 1993 and 1994 low spawning populations have forced closure of the PWS herring fishery (J. Wilcock, Alaska Department Fish and Game (ADF&G), pers. comm.).

Herring recruitment is dependent on the number of eggs produced by the spawning stock. There may be a critical threshold of spawning biomass below which embryo survival can significantly effect herring recruitment. The SEA Plan hypothesizes that the recruitment success of herring populations is related to both losses of eggs during the 20-25 day incubation and to losses during the larval stage. Sources of egg loss include predation and physical processes such as translocation through wave action and currents and temperature extremes (Palsson 1984; Haegele and Schweigert 1991).

Determining explicit causes of egg loss will allow for a better estimate of survival to the larval stage. Understanding egg loss is also important to fisheries management. Currently, ADF&G estimates the adult spawner biomass from total egg deposition, average fish size and sex ratio, and average fecundity at size measured. Egg deposition surveys take place 5-10 days after spawning. Losses to predation and physical processes between deposition and surveys are needed to accurately calculate spawning biomass estimates and improve fisheries management stock assessment models.

During a 2-year study in 1990 and 1991 in PWS, rates of egg loss as high as 91% have been measured, with an overall estimated egg loss rate of 50% throughout the incubation period, for a daily loss rate of 2% (Biggs et al in press). This study did not include collection of data to relate egg loss to habitat type, environmental conditions, or predation. During 1995, ADF&G's study EVOS 95166 will study egg loss with modifications to their sampling design to improve understanding of these mechanisms behind egg loss. Results will be used to model embryo survival as required by the SEA Plan.

Until now, only potential sources of predation have been identified in PWS. In Washington and British Columbia predators of herring spawn include invertebrates, marine mammals, fish (eg. salmonids, flatfishes, sculpins), and birds. Epibenthic invertebrates (crabs, snails, and starfish) and birds have been identified as the greatest sources of egg loss on these spawning areas (Palsson 1984; Haegele 1993a, 1993b).

Prince William Sound has a large resident population of potential herring spawn avian predators including surf scoters (Melanitta perspicillata) and glaucous-winged gulls (Larus glaucescens). Surf scoters are abundant and the most numerous sea duck. Migrant surf scoters are numerous in April and May. Historically, large numbers of glaucous-winged (GW) gulls have been observed in areas with herring spawn (P. Martin, US Fish Wildlife Service (USFWS), pers. comm.). While GW gulls are an abundant resident and are present in numbers throughout the year, an influx does occur in spring, mainly between mid-April and mid-May (Isleib and Kessel 1973). The primary nesting colony for GW gulls in PWS, estimated at approximately 10,000 pairs, is at Egg Island on the east end of Prince William Sound (Patten 1980). Egg laying usually begins around the second week in May.

Prince 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 two species of shorebirds: surfbirds (Aphriza virgata) and black turnstones (Arenaria melanocephala). Total numbers using the area are not known, however, in May 1992 a single day count of almost 56,000 surfbirds and 25,000 black turnstones was recorded (P. Martin, USFWS, pers. comm.). These numbers suggest that a high proportion of the world's population of these two species use northern Montague Island in spring (Norton et al. 1990; Martin in review).

Spatially and/or temporally then, herring spawn deposition in PWS coincides with breeding for a large resident population of glaucous-winged gulls, and with spring stopover areas for sea ducks and shorebirds. To date, however, we have no information on numbers and distribution, and how predictable or variable the use of herring spawn is by resident and migrant birds.

At the same time, from a fisheries management standpoint information on avian predation is important because if the avian predator population remains relatively constant or increases, then the lower herring stock levels that PWS is currently experiencing could experience higher rates of predation.

This project will assess and document the impact of avian predation on herring spawn in Prince William Sound. Results will eventually be integrated into a model relating sound-wide embryo survival to predation, habitat type, egg density, and meteorological conditions. As part of the SEA plan, it is designed to complement ongoing long-term studies on herring spawn deposition and survival (EVOS 95166) and juvenile herring growth and habitat partitioning (EVOS 95320-T).

RESEARCH HYPOTHESES & OBJECTIVES

Research hypotheses being tested include:

- 1) The distribution, timing, and abundance of gulls, sea ducks and shorebirds is positively correlated with the dispersion, timing, and abundance of herring spawn.
- 2) Avian consumption of herring spawn is a function of egg density, and diminishes as spawn decreases.
- 3) Egg loss resulting from avian predation occurs at higher rates in years when eggs are scarce.
- 4) Herring spawn is a major component in the diet of bird species foraging in herring spawn areas.
- 5) Viable herring spawn are preferred prey compared to dead and decaying spawn.

The objectives of this study are:

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

METHODS

Study Area

The study was conducted on northern Montague Island from just south of Port Chalmers to Zaikof Bay (Fig. 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. High densities of herring spawn have occurred in this area all but one year since 1980 (ADF&G, unpubl. data). Rocky Bay, Montague Point, and Graveyard Point typically receive high densities of spawn.

Data Collection

Distribution and Abundance of Herring Spawn

The extent and distribution of herring spawn was documented from daily aerial flights conducted as a regular part of ADF&G commercial fisheries management. Using SCUBA diver transects, spawn biomass and egg loss was estimated by a concurrent ADF&G Herring Natal Habitats study, EVOS 94166. Egg loss sites ($n=10$) were sampled every 3-4 days between 21 April and 19 May, and spawn deposition transects ($n=73$) once each between 20 April and 9 May 1994. Locations of spawn and ADF&G spawn sampling sites were recorded on aerial photograph tracings with a 250m x 250m grid overlay.

Aerial Surveys

Aerial surveys were considered the most accurate and efficient means of estimating the distribution, timing and abundance of gulls and sea ducks on northern Montague Island. Aerial surveys were conducted prior to spawn deposition (7, 12, and 18 April) and every 2-3 days during and post spawn deposition from 21 April - 15 May. Surveys covered approximately 96km of coastline from just south of Port Chalmers to Zaikof Point (Fig. 1), and included all spawn areas (approximately 20 km).

Surveys were conducted during the 1 1/2h before or after low tide. Surveys were flown in a Cessna 185 float plane along a path approximately 100m from shore. Initially, surveys were to be conducted at low altitude (95m) in order to document all species and numbers. However, a combination of high winds, convoluted shoreline, and large numbers of gulls in spawn areas made a higher survey altitude (200m) a better methodology for the Rocky Bay and Montague Point areas. The shoreline was divided into sections based on recognizable landmarks and spawn distribution. For each section, two observers, one in the front with the pilot and the other in the back seat directly behind the pilot, estimated the numbers of gulls and sea ducks on their respective sides of the plane.

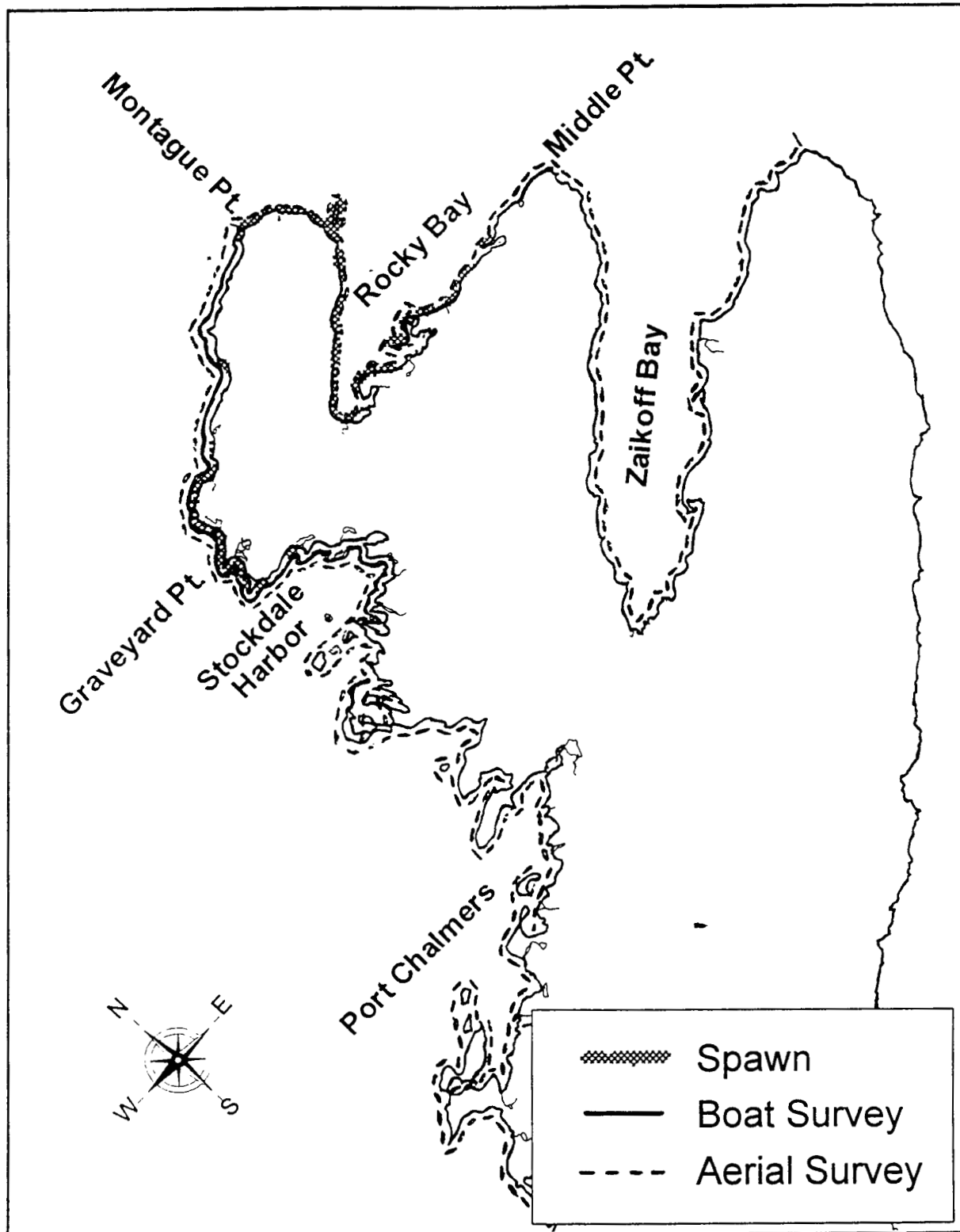


Figure 1. Map of Northern Montague Island with place names and locations of spawn and avian survey, spring 1994.

Boat Shoreline Surveys

Shoreline surveys documented the distribution, timing, and abundance of all avian species for 18.4km of coastline from northern Stockdale Harbor to Montague Point. Thirteen surveys were conducted every 2-3 days between 13 April and 13 May, including two prior to spawn deposition (13 and 15 April). Based on 250m x 250m blocks, the shoreline was divided up into 87 blocks, including 38 blocks with spawn (7,573m of shoreline) and 49 blocks without spawn (10,836m of shoreline). Due to the convoluted shoreline, shoreline length per block in nonspawn areas ranged from 20m-506m and from 100-517m for spawn areas.

The sampling area included all water within 120m of shore, as well as shoreline (maximum shoreline width 50m). A 5.2m skiff travelled 20m 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 between 20-120m offshore. Surveys were conducted between the 2 hr before and after low tide, when the maximum amount of spawn is available for foraging. Surveys were not conducted or were suspended when seas were >1m or when the observers' optics could not be adequately cleared due to persistent precipitation.

Survey protocols were adapted from USFWS marine birds and mammal surveys (USFWS 1991). While the boat moved along the survey route, all birds were counted within a "window" that extended 100m on the seaward side, 20m+ on the shoreward side, 50m ahead, and 100m above the boat. Birds moving into the survey window from behind were ignored. One observer recorded birds from the boat to shore, and the other from the boat seaward 100m. Data collected included: number and species (or genus), location, habitat (land, water or air) and behavior (forage, rest, fly, unknown). Locations of observations were recorded on aerial photograph tracings with a 250m x 250m grid overlay. Other data collected included precipitation, wind speed and direction, temperature and wave height.

100x 300m Spawn Deposition & Egg Loss Transects

In order to document changes in avian abundance, species composition, and foraging behavior as they relate to egg loss and spawn density, avian transects were conducted at EVOS 94166 (ADF&G Herring Natal Habitats) egg loss and spawn deposition sampling sites. Avian transects were 100m x 300m long and perpendicular to the shoreline. As the ADF&G dive boat approached the shoreline to begin their spawn sampling, our on board observer surveyed the transect. Data collected included: number and species (or genus), habitat (land, water or air) and behavior (forage, rest, fly). Other data collected included precipitation, wind speed and direction, temperature and wave height.

Intensive Behavioral Observations

Behavior and microhabitat use by avian species in relation to herring spawn abundance and the tidal cycle was determined from scan sampling of flocks and focal animal observations (Altmann 1974) collected at two ADF&G egg loss transects (north shore of Stockdale Harbor and near Graveyard Point) and one windrow site (1.5km north of Graveyard Point). The scan sample plots were 100m x 100m, extending seaward from the upper boundary of the intertidal zone. Scan observations were collected from a blind every 30 minutes over a six hour period (one tidal cycle) at three locations: 1) low egg density, protected shoreline, and gravel/cobble substrate; 2) high egg density, exposed shoreline, rocky substrate; and, 3) egg windrow, exposed shoreline, rocky substrate.

For each scan sample, the following information was recorded: time, number and species of birds by activity and location. Activity classes included: foraging, foraging while swimming, swimming, walking, flying, comfort, rest and unknown. Tidal zone of foraging birds was recorded in one of the following categories: swimming below the tideline, 0-3m below the tideline, 0-3m above the tideline, 3-6m above the tideline, 6-10m above the tideline, and >10m above the tideline.

In between scan samples, a foraging bird in the plot was randomly selected and all behavior was recorded for 10 min. or until the bird was lost. We used Psion LZ64 dataloggers and The Observer (ver. 2.0, Noldus Information Technology, Wageningen Netherlands), a behavior recording computer program to record the following information: foraging intensity (intensive, non- intensive, none), activity (foraging, foraging while swimming, swimming, walking, flying, comfort, and rest), and tidal zone location. Other data collected included: species, age, weather, prey identification (if possible), flock size, and foraging habitat (water, exposed intertidal, egg windrow, high tide wrack line, wave wash zone).

Data Analysis

For purposes of this report, 19 April is considered Day 0 (first day of spawn).

We first tested the hypotheses that the distribution of bird species at northern Montague Island is related to the presence of herring spawn using a Wilcoxon paired data test. Based on data collected during the 18.4 km boat surveys during and post spawn, paired data consisted of: proportion of a species or group of species per km of shore surveyed with spawn and, the proportion of total shoreline surveyed where spawn was laid down. The test uses the ranks of the difference between these two variables (proportion of a species - proportion spawned shoreline). Positive values indicate there were more birds in a spawn area than expected; negative values indicate there were fewer birds than expected.

We then calculated an odds ratio:

$(pOb_{spawn}/1-pOb_{spawn}) / (pSur_{spawn}/1-pSur_{spawn})$, where
 pOb_{spawn} = proportion of species observed in spawn; and,
 $pSur_{spawn}$ = proportion of survey in spawn.

We used generalized linear models (glm) to test hypotheses 1,2,3 and 5. Best models for explaining variability in the dependent variable were determined using SuperAnova (Abacus Concepts, Inc., Berkeley, CA) or SAS (SAS Institute, Cary, NC) computer software. A stepwise technique was used to delete and add variables in arriving at a final model. A model was determined to be "best" when it explained the most variability in the dependent variable (as judged by adjusted R^2) with the fewest significant variables. Model assumptions were checked with a visual inspection of residual plots. The natural log transformation of the dependent variable was used when appropriate to improve the fit of the data to the model (i.e. stabilize residual variance). Means presented are least square means as determined by the model. Multiple comparisons are based on Bonferroni/Dunn's Test. For all test results, P -values <0.01 were termed highly significant, <0.05 significant, and 0.05-0.10 marginally significant.

We used the glm to test hypotheses 1 and 2: 1) the distribution, timing, and abundance of black turnstones, surfbirds, mew gulls, and GW gulls is related to the dispersion, timing, and abundance of herring spawn, and; 2) avian consumption of herring spawn is a function of egg density, and diminishes as spawn decreases. Abundance of birds in spawn blocks, the dependent variable, was measured either as birds/m² (for 100x300m transects) or birds/m of shoreline (for aerial and boat surveys). The suite of independent variables analyzed included: ACTIVE SPAWN (all days between first and last day spawn deposition for area; yes, no), SPAWN DAYS (number of days spawn laid; 1-4 days), INCUBATION STAGE (days since first spawn laid; linear and quadratic terms), WAVE EXPOSURE (exposed, semi-protected (for 100x300 transects only), protected), SUBSTRATE (rocky and/or boulder, sand and mud, solid rock with sand in-between, mud on rock outcropping; 100x300m transects only), TIDE HEIGHT, and TIDE DIRECTION (incoming, outgoing). For those aerial and boat blocks with ADF&G spawn biomass transects additional variables included SPAWN WIDTH (defined by perpendicular distance from shoreline), AVERAGE EGG (average egg biomass (1,000's) per sampling station with eggs), and TOTAL EGG (total transect egg (1,000's) biomass). For those survey blocks with more than one ADF&G spawn biomass transect, average spawn width and egg abundance values were used.

We began testing the hypotheses that egg loss resulting from avian predation occurs at higher rates in years when eggs are scarce. At the 10 ADF&G egg loss sites, we related the

density of birds in 100x300m transects to egg loss by LOCATION (+5, 0, -9m from mean low tide) as well as the same suite of independent variables listed above. Using diver-adjusted data provided by ADF&G, a daily egg loss value (ELOSS) was calculated as:

$$\text{ELOSS} = \frac{\text{MAE}_1 - \text{MAE}_2}{D}$$

where, MAE_1 is the mean adjusted estimate for eggs at a sampling station on the first visit, MAE_2 the mean adjusted estimate for the second visit, and D the number of days between the two visits. Two independent variables for each depth (ELOSS1 and ELOSS2) were analyzed in separate models. ELOSS1 is the number of eggs lost per day at that depth between the current visit and the previous visit. ELOSS2 is the number of eggs lost per day at that depth between the current visit and the following visit.

Intensive Behavioral Observations

Because for 1994 we were requested not to collect stomach samples from the major avian species in spawn areas, we used flock scans and focal animal data to test indirectly if herring spawn is a major component in the diet of bird species foraging in herring spawn areas. And, using feeding location as an indication of spawn viability, we used flock scans and focal animal data to also test the hypotheses that viable herring spawn are preferred prey compared to dead and decaying spawn.

Flock scan data was first analyzed using a Kruskal-Wallis non-parametric one-way ANOVA to determine if there was a difference in the mean proportion of a species: a) feeding by location in relation to the tideline; b) feeding by tide; and c) tide direction. We conducted this analysis for GW gull, mew gull, surfbirds, and black turnstones.

We used stepwise glm to relate the proportion of a species feeding or resting/comfort with a suite of environmental variables including: LOCATION (high density eggs, low density eggs, or windrow site), TIDAL ZONE (feeding only), TIDE HEIGHT, LOW MEAN (position relative to low mean tide, for feeding birds only), TIDE, TIDE DIRECTION, interaction of TIDE*TIDE DIRECTION, and HABITAT (water or shore for resting/comfort only). Proportions were weighted by total birds per species for that scan. Only GW gull and mew gull were analyzed with these models. Black turnstones and surfbirds were not analyzed because for the feeding analysis, in >70% of all scans the proportion of birds feeding was 100%, violating assumptions in the model. For resting analysis too few scans of resting were observed for these two species.

Focal animal data was analyzed using stepwise glm. First we first tested the hypothesis time spent foraging varied with tidal zone location. Our dependent variable was the proportion the time spent feeding, and the independent variables included: TIDAL ZONE, FORAGE BEHAV (foraging behavior: intensive, non-intensive and no foraging), and the interaction of these two effects. Next we tested the hypothesis that time spent foraging was related to a suite of environmental variables including: LOCATION, TIDE, TIDE DIRECTION, BIRD AGE (2nd year, 3rd year, 4+year, gulls only), FLOCK SIZE, WINDROW FOR (foraging in windrow; yes, no), WRACK FOR (foraging in wrack; yes, no), and WAVE FOR (foraging in wave wash; yes, no), WEATHER, WIND (wind speed), DIRECTION (wind direction), SEA STATE, and TIDE*TIDE DIRECTION.

RESULTS

Distribution and Timing of Herring Spawn

ADF&G aerial spawn surveys located a small amount of herring spawn (<400m) deposited approximately 8km north of Graveyard Point on 18 April. On 19 April, extensive spawn was deposited in the Graveyard Point area, and small amounts at Rocky Bay. Spawning continued from northern Stockdale Harbor to Rocky Bay from 19-25 April (Fig. 1). No spawn occurred south of Stockdale Harbor, (i.e. in Port Chalmers or Gilmor Point areas) nor in Zaikof Bay. Hatching began by 11 May, approximately 22 days after 19 April (Day 0).

Species Composition in Spawn Areas

Boat surveys (n=14) along 18.4 km of northwest Montague Island shoreline between 13 April and 13 May provided the data base for species composition. Two surveys were conducted prespawn (13 and 15 April), and one survey (23 April) was ended early due to weather. Three species of birds accounted for 90% of all observations (n= 204,630 birds) across all surveys: GW gulls (57.3%), mew gulls (13.1%), and surfbirds (19.6%). Sea ducks (primarily scoters and oldsquaws (*Clangula hyemalis*)) accounted for 3.3% of all birds, however, their numbers are underestimated since they often fell outside the 120m boat survey window.

In spawn areas only, these same three species accounted for 90.5% of all observations (GW gulls 57.7%, surfbirds 18.6%, mew gulls 14.2%) (Table 1). We ran a one-way analysis of variance (ANOVA), to determine if gulls were attracted to spawn areas. The response variable was the difference in gull and non-gull densities per block and the independent variable was spawn status (spawn or no spawn). The difference in densities between areas was highly significant ($P<0.01$). In areas with spawn, gull densities were significantly greater

Table 1. Ratios, total numbers and significance of bird species and groups observed on bird surveys in spawn and non-spawn areas. Ratios indicate the relative odds of being observed in a spawn area as opposed to a non-spawn area. Significance levels refer to results from a Wilcoxon test for paired data.

SPECIES	RATIO	TOTAL OBSERVED	P-VALUE
POSITIVE ASSOCIATION			
BONAPARTE'S GULLS	78.7	1,880	P < 0.001
SEA DUCKS	40.0	6,700	P < 0.01
MEW GULLS	29.8	26,211	P < 0.025
DABBLING DUCKS	11.3	187	P < 0.01
GLAUCOUS-WINGED GULLS	14.1	110,736	P < 0.001
HARLEQUIN DUCKS	11.0	4,698	P < 0.001
SURFBIRDS	5.2	40,006	P < 0.001
CALIDRIS SHOREBIRDS	7.1	617	P = 0.025
BLACK TURNSTONES	2.6	3,331	0.05 < P < 0.1
BALD EAGLES	3.6	222	P < 0.025
NEUTRAL			
BLACK OYSTERCATCHERS	1.3	73	P > 0.25
CORVIDS	1.2	401	P > 0.25
CANADA GEESE	1.0	354	P > 0.25
CORMORANTS	0.9	649	P > 0.25
MERGANSERS	0.6	480	0.1 < P < 0.25
MURRELETS	0.4	14	P=0.25
INSHORE DIVING DUCKS	0.4	234	0.1 < P < 0.25
GREBES	0.4	30	0.1 < P < 0.25
NEGATIVE ASSOCIATION			
PIGEON GUILLEMOTS	0.1	15	P < 0.05

than non-gull densities (mean difference = 2.08 birds/m, $P=0.01$). In areas with no spawn, gull and non-gull densities were not significantly different (mean difference = 0.86 birds/m, $P= 0.20$).

Next we tested the hypothesis that a particular species or groups of species (eg. sea ducks) were attracted to spawn using a Wilcoxon paired data test. We found that those species with a positive response to spawn ($n=7$ species, 3 species groups), were generally the most numerous species (Table 1). Black turnstones showed a positive response but were only marginally significant ($0.05 < P < 0.10$). Generally, piscivorous birds showed a neutral (eg cormorants, mergansers, grebes) or negative response (pigeon guillemots) to spawn.

We calculated an odds ratio to indicate the relative odds of a species or group of species, being observed in a spawn area as opposed to a non-spawn area. For example, a ratio of 1 indicates that a species is equally likely to occur in a spawn area as in a non-spawn area. Bonaparte's gull and sea ducks (scoters, oldsquaws), both primarily spring migrants had the highest ratios (78.7 and 40.0 respectively) (Table 1).

Abundance, Timing, and Distribution of Principal Species

Gulls

Aerial surveys ($n=14$) for avian concentrations began at northern Montague Island on 7 April (prespawn) and were completed 15 May, approximately 26 days after the first spawn was laid. Prior to spawn initiation, aerial surveys ($n=3$) recorded gull numbers ranging between 15,600-25,700 (Fig. 2). Some 89-95% of the gulls were concentrated between Stockdale Harbor and Zaikof Bay, where herring schools were located.

Gulls responded immediately to the presence of spawning fish (19-25 April) with >97% of all gulls observed occurring in the 20 km of spawned shoreline. This trend continued throughout the remainder of the study. Gull numbers peaked during active spawn, with >55,000 observed on 24 April flight. From 28 April through 12 May, an average of 29,559 gulls occurred in spawn areas (SE= 2,669; range 20,200-36,800, $n= 7$ flights). By the final flight on 15 May, gull numbers dropped to <8,000 (Fig. 2).

Aerial surveys appear to have underestimated gull numbers for the northwestern shoreline. We compared aerial survey estimates of total gulls for the 18.2 km between Stockdale Harbor and Montague Point with estimates from boat shoreline surveys. On 3 days when both boat and aerial surveys coincided, aerial estimates of total gulls were 23-56% lower than boat estimates (Fig. 3).

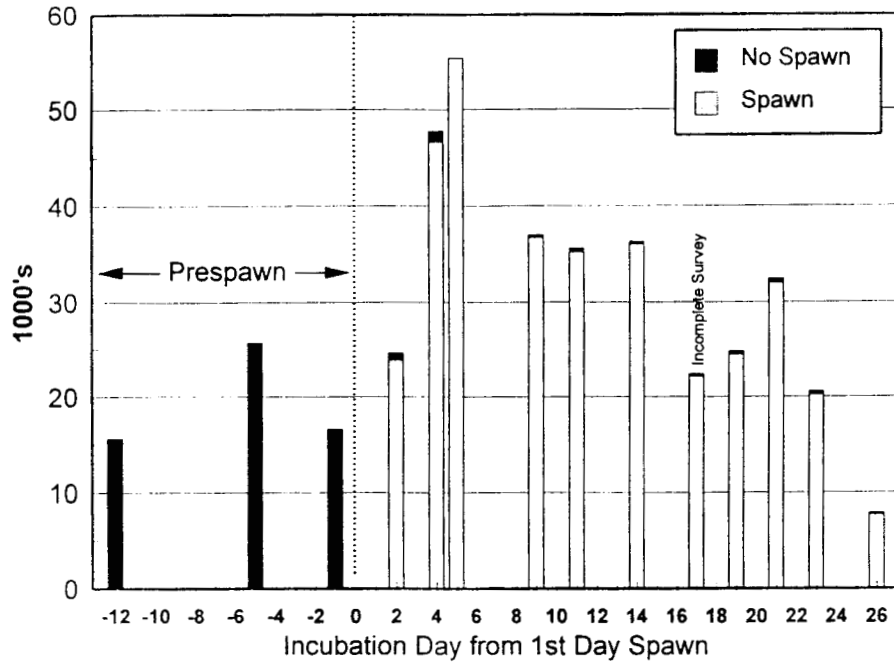


Figure 2. Gull estimates from 96 km aerial shoreline surveys (n = 14) including spawn areas (20 km). Northern Montague Island, spring 1994.

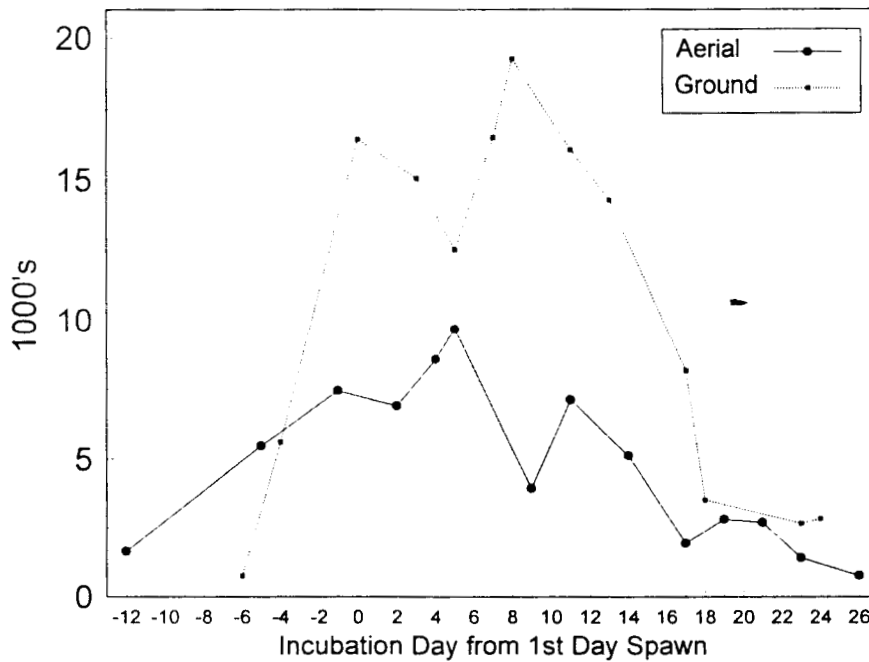


Figure 3. Comparison between aerial (n = 14) and boat shoreline surveys (n = 13) for gulls. Graveyard Point and Stockdale Harbor areas, Northern Montague Island, spring 1994.

Boat surveys along northwestern Montague indicated differences in the timing of gull species on spawn areas. GW gulls, both a winter resident and spring migrant, peaked on the first day of spawn deposition, 19 April, and stayed at high levels until 6 May (Fig. 4). Most mew gulls winter south of PWS, migrating to and through PWS from mid-March through May. In 1994 at Montague Island, mew gulls first appeared in significant numbers (>1,000 per survey) on 22 April, peaked 27 April, and steadily declined in numbers (Fig. 4). Bonaparte's gull (*Larus philadelphia*) a common spring migrant and locally common breeder, occurred in negligible numbers (<20 birds) prior to 22 April, peaked on 27 April (n=486), and thereafter declined rapidly with <10 birds recorded on the final 13 May survey.

We combined aerial transects and examined gull densities by three broad geographic areas with spawn: Graveyard Point (5.6km, from northern Stockdale Harbor to Montague Point), Montague Point (5.4km including the spits on north shore of Rocky Bay), and Rocky Bay (8.8 km spawn). Between 23 April-12 May, highest densities of gulls were recorded in the Montague Point area on all but one flight (range 2,270-5,610 gull/km) (Fig. 5).

We ran a glm on gull densities (dependent variable, ln transformed) observed on aerial surveys. Two analyses were performed. First only areas where spawn was laid down were included. The independent variables included WAVE EXPOSURE, LOCATION (grouped blocks of Rocky Bay, Montague Point, Graveyard Point), INCUBATION STAGE (linear and quadratic), and ACTIVE SPAWN (yes, no). This analysis covered 8 aerial surveys from 21 April-15 May 1994. A stepwise procedure of adding and deleting variables was used to arrive at a model. The final model ($P<0.01$), included LOCATION and INCUBATION² as significant variables and explained 34.4% of the variation in gull densities. The quadratic term indicates that gull densities increased up to a point and then decreased as the incubation of herring roe progressed. The mean densities between the three locations were significantly different, with Montague Point (2,356 birds/km) > Rocky Bay (988 birds/km) > Graveyard Point (366 birds/km). This model explains 60.5% of the variation in gull densities.

When we ran the glm again using smaller aerial blocks as the LOCATION independent variable. The final model ($P<0.01$), once again included LOCATION and INCUBATION² as significant variables. This model explains 60.5% of the variation in gull densities. Mean densities by location ranged from 89.2 birds/km at the north end of Stockdale Harbor to 2,927.6 birds/km by Montague Point. Comparison of the two models suggests that variation in gull densities is better explained by examination at the finer spatial scale (eg. at the block level rather than grouped blocks).

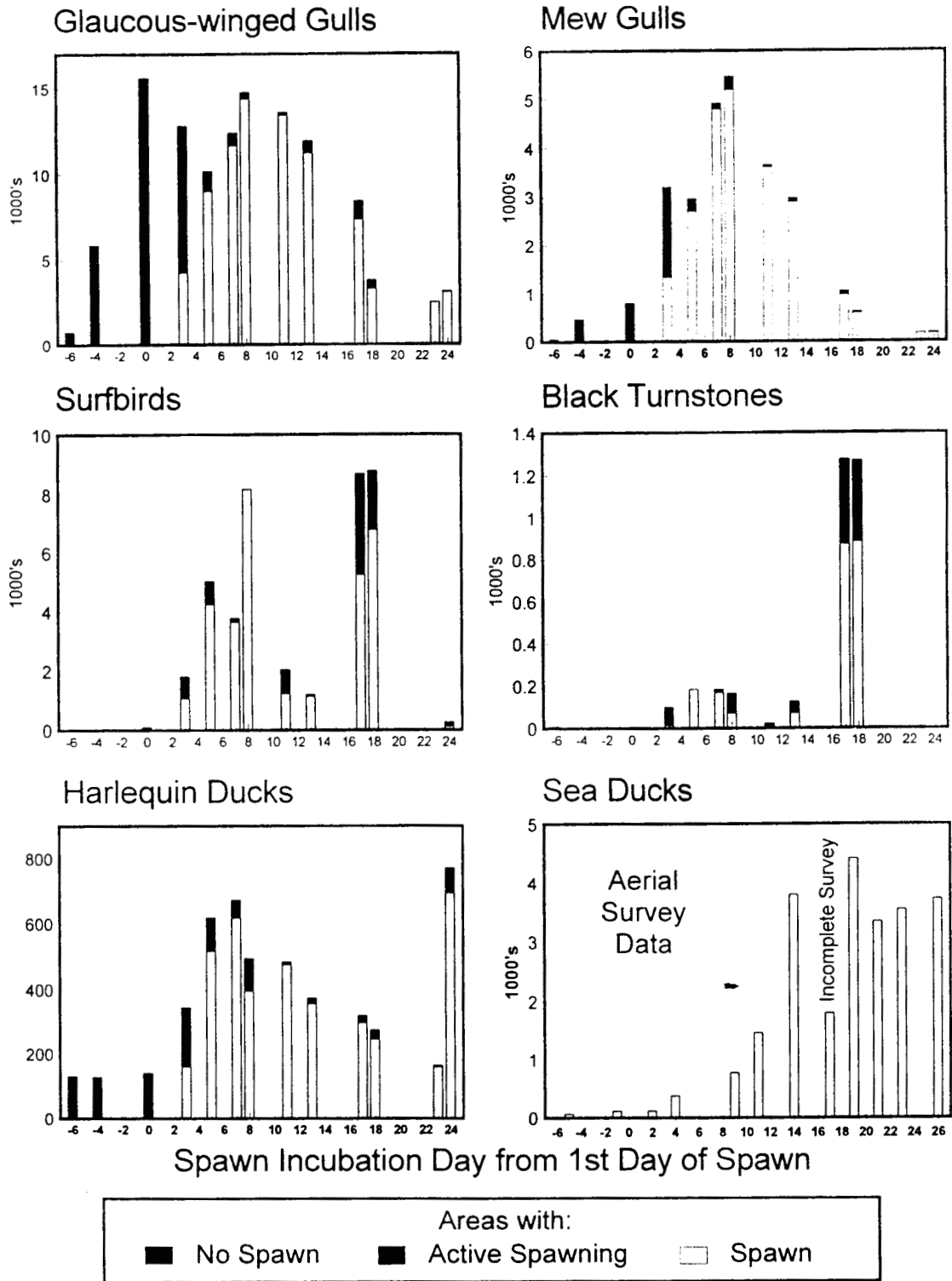


Figure 4. Bird abundance by days since spawn initiation for most common species based on 18.4 km boat surveys (n=13). Sea duck abundance based on 96 km aerial shoreline surveys. Spawn incubation day 0 = 19 April. Northern Montague Island, spring 1994.

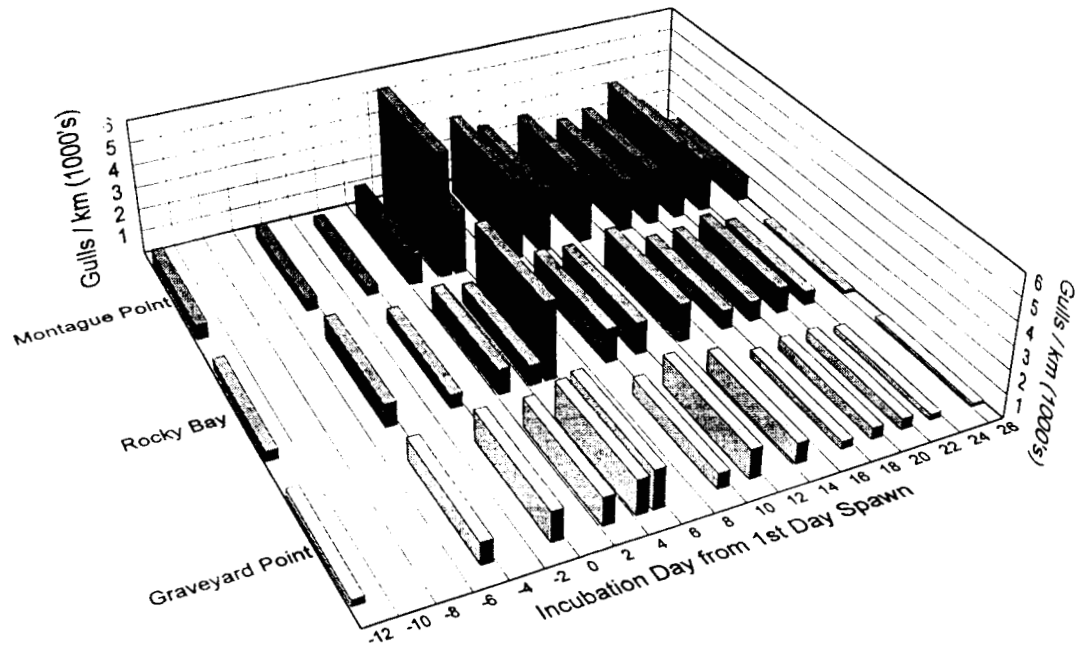


Figure 5. Gull densities in spawn areas by incubation days from the initiation of spawn. Northern Montague Island, spring 1994.

Sea and Harlequin Ducks

Few sea ducks were recorded during aerial surveys prior to and during active spawn. Beginning 28 April, rafts of 450 and 325 ducks were observed at Graveyard Point and Rocky Bay, respectively, and by 30 April a third raft of 400 sea ducks was noted at Montague Point area. Total numbers across all spawn areas ranged from 3350-4400 ducks between 3 May and the final 15 May flight (Fig. 3). Most sea duck rafts were composed of mixed species, and included primarily surf scoters, oldsquaws, with lesser numbers of greater scaup (*Aythya marila*).

Harlequin ducks (*Histrionicus histrionicus*) were the fourth most numerous species recorded on boat surveys. This nearshore diving duck is a winter resident in PWS, and the Port Chalmers-Graveyard Point area is a historic wintering area (US Fish Wildlife Service, unpubl. data). Harlequins showed a bimodal peak, the first 7 days after spawn deposition, and a second peak on the last boat survey (13 May) as spawn was hatching (Fig. 4).

Surfbirds and Black Turnstones

These two shorebird species were among the most numerous species recorded on boat surveys (Table 1). Both are transient spring migrants through PWS. Surfbirds were not recorded in large numbers until post spawn deposition, and did not peak until 6-7 May. Only small flocks of black turnstones were recorded in spawn areas, with a pronounced peak recorded on 6-7 May, the same time as surfbirds (Fig. 4).

Relationships between Bird Numbers and Spawn Abundance

We tested the hypotheses that avian consumption of herring spawn (as indicated by bird numbers) is a function of egg density and diminishes as spawn decreases. We tested this hypotheses from bird data collected at three spatial scales: 100x300m transects at ADF&G spawn deposition transects, data from boat shoreline spawn blocks along northwestern Montague, and aerial survey data for all spawn areas.

Spawn Deposition Transects

We first analyzed data from the 100x300 spawn deposition transects (hereafter referred to as spawn deposition transects). These transects (n=17) were conducted immediately before ADF&G divers estimated egg numbers. Using a regression analysis, only the data sets for GW gulls, total gulls, and total birds could be analyzed with a normal error term because the other birds/species groups did not occur frequently enough on the transects.

A simple regression to investigate the relationship between total GW gull numbers and the concurrent egg estimate indicated that all three biomass variables (SPAWN WIDTH,

AVERAGE EGGS, and TOTAL EGGS) were highly significant in explaining the variation in GW gulls numbers. Adjusted R^2 s for these three models ranged from 49% (SPAWN WIDTH) to 81% (TOTAL EGGS). In a multiple regression model with all three independent variables entered into the model, only TOTAL EGGS was significant ($P < 0.01$). This indicates that while all three variables explain the same variation in GW gull numbers, TOTAL EGGS explains an additional amount that the other two do not.

We ran a stepwise glm models to determine the relationship between total birds and total GW gulls and biomass variables and included an additional suite of independent variables (Table 2). For both models, the same two variables were significant: TOTAL EGGS ($P < 0.001$) and SPAWN DAYS ($P < 0.02$ for GW gulls, and $P < 0.01$ for all birds). The similar results are due to the dominance of GW gulls in the all birds data set. The models were both significant with adjusted $R^2 = 84.7\%$ for GW gulls, and adjusted $R^2 = 82.7\%$ for all birds.

We tested the hypothesis that a threshold level of spawn was determining GW gull densities. The dependent variable, TOTAL EGGS, had two levels: $< 2,000$ eggs ($n = 12$ transects) and $> 2,000$ eggs ($n = 5$ transects). The variable was significant with the average number of GW gulls on spawn transects with $> 2,000$ eggs at 370 gulls compared to 63 gulls at transects with $< 2,000$ eggs. The adjusted R^2 for the model was 21.4%.

Boat Shoreline Surveys

Using results of eight boat surveys after final spawn (25 April) was laid, we ran simple regressions on total birds and total GW gulls in spawn blocks with ADF&G biomass estimates ($n = 14/38$ spawn blocks). As in the spawn deposition transects, we found a similar relationship between spawn biomass and total birds and total GW gulls. All three variables (SPAWN WIDTH, AVERAGE EGGS, and TOTAL EGGS) were highly significant in explaining the variation in bird numbers for both regressions.

We ran stepwise glms to determine the relationships between total GW gulls and totals of all other birds in spawn blocks with ADF&G biomass estimates and other independent variables. For GW gulls, two biomass variables, TOTAL EGGS and SPAWN WIDTH, as well as SPAWN DAYS, INCUBATION STAGE², and WAVE EXPOSURE were highly significant (adjusted $R^2 = 52.7\%$, Table 2). For all other birds (including mew gulls), the biomass variable SPAWN WIDTH, along with SPAWN DAY and INCUBATION STAGE² were highly significant (adjusted $R^2 = 47.8\%$).

We examined the relationship between GW gulls densities and TOTAL EGGS using two

Table 2. Results from generalized linear models on abundance of glaucous-winged gulls in spawn areas. Table entries indicate significance of variables: ** P-values < 0.01; * P-values < 0.05; -- not significant; NA not significant.

Variables	Spawn Deposition Transects	Boat Surveys	Aerial Surveys ^a	Egg Loss Transects
SPAWN DAYS	*	**	NA	**
INCUBATION STAGE	--	--	*	--
INCUBATION STAGE ²	--	**	**	**
WAVE EXPOSURE	--	**	--	**
SUBSTRATE	--	NA	NA	**
TIDAL HEIGHT	--	--	NA	--
LOCATION	NA	NA	**	--
EGG LOSS 1	NA	NA	NA	*
SPAWN WIDTH	--	**	--	NA
AVERAGE EGGS	--	--	--	NA
TOTAL EGGS	**	**	--	NA
SPAWN LEVEL (<>10,000 eggs)	NA	NA	**	NA
Adjusted R²	84.7	52.7	52.9	38.4
n	17	116	76	43
Visits	1	8	7	3-6

^a for all gulls

spawn levels: <2,000 eggs and >2,000 eggs. The variable was highly significant although the relationship was not as strong as seen on the spawn deposition transects (adjusted $R^2=11.5\%$ versus 21.4% on spawn deposition transects). The average density of GW gulls in blocks with >2,000 eggs at 0.45/m shoreline ($n=78$ blocks) compared to 0.09/m shoreline ($n=38$ blocks) in blocks with <2,000 eggs.

Aerial Surveys

At the broadest spatial scale, we analyzed the relationship between gull densities on aerial surveys and spawn biomass across all spawn areas (20km). This analyses covered surveys starting on 28 April 1994. Biomass variables included two SPAWN LEVEL (<10,000 total eggs, >10,000 total eggs). The final model ($P<0.01$) included INCUBATION STAGE (linear and quadratic), SPAWN LEVEL and LOCATION (grouped blocks) (Table 2). The adjusted R^2 for the model was 52.9%. Mean densities were significantly different between LOCATIONS, with Montague Point (2,266 birds/km) > Rocky Bay (806 birds/km) > Graveyard Point (246 birds/km). Transects with spawn level >10,000 eggs had a significantly higher mean density (1,592 birds/km) than transects with <10,000 total eggs (332 birds/km).

Substituting individual blocks instead for grouped blocks as the LOCATION variable in the model, results in a model with only INDIVIDUAL BLOCKS and INCUBATION STAGE as significant. This model explains 75.3% of the variation in gull densities. Mean densities for transects ranged from 55 birds/km at northern Stockdale Harbor to 3,533 birds/km around Montague Point.

Relationships between Bird Numbers and Egg Losses

We conducted a total of 43, 100x300m transects for bird species and abundance at the ten ADF&G egg loss sampling sites. Number of visits per site ranged from 3-6 with an average of 4.3 visits per site ($SE=0.37$). We ran stepwise glms to determine if there was a relationship between numbers of GW gulls and mew gulls and egg loss (estimated by ADF&G diver samples). In addition to egg loss, we included an additional suite of environmental variables (Table 2).

For GW gulls, ELOSS1 (daily egg losses since the previous visit) was significant when included in the model (Table 2), but ELOSS2 (daily egg loss between the current visit and the following visit) was not significant when included. For mew gulls, substrate was highly significant and spawn days significant in explaining the variation in total mew gulls at the current visit, however neither egg loss variable was significant in either model (adjusted $R^2=31\%$ and $R^2=21\%$ respectively).

Foraging Behavior

Two-way anovas were run on GW gulls, mew gulls, and surfbird densities in boat survey blocks containing spawn to determine spatial and temporal changes in foraging behavior. In all models, INCUBATION (i.e. date) and LOCATION (i.e. blocks) were the two factors. Surveys from 22 April to 13 May 1994 (n=10 surveys) were considered. Only those blocks where the species of interest was observed were included in the analysis.

With the difference in densities of foraging and nonforaging GW gulls in spawn areas as the dependent variable, only INCUBATION was significant ($P < 0.02$). Foraging and nonforaging densities were not significantly different on eight of the ten surveys. Nonforaging densities were greater on the other two dates (22 April and 6 May) (Fig. 6). For mew gulls, both INCUBATION and LOCATION were highly significant. For all surveys, there were significantly more mew gulls feeding than not feeding (Fig. 6).

When the difference in GW gull and mew gull densities foraging on water and foraging on shore were the response variables, both INCUBATION and LOCATION were significant. On four surveys for GW gulls, and on six surveys for mew gulls, densities foraging on shore were significantly greater than those foraging on the water, with no differences on other surveys. Densities did vary by location by both species, although with 38 blocks no pattern was apparent.

For surfbirds, neither INCUBATION nor LOCATION was significantly related to foraging and non-foraging densities ($P > 0.1$ for both). However, in examining the means table for date, it appears that more foraging occurred on 24 April and 7 May, than the other dates, on which the two behaviors did not differ (Fig. 6).

Flock Scans

We examined in more detail foraging behavior by species through flock scans and focal animal sampling. At three locations we recorded 81 flock scans on 10 days between 28 April and 11 May. For both black turnstones and surfbirds, a significantly higher proportion fed 0-3m above the tideline than other zones (Table 3) and fed at low and mid tides than at high tide (Fig. 7). For both species there was no difference in mean proportion by tide direction ($P = 0.26$ turnstones; $P = 0.29$ surfbirds).

Both GW gulls and mew gulls fed by standing in all intertidal zones and swimming below the tideline. For both species there was a highly significant difference in the proportion of gulls feeding by tidal zone (Table 3), but no significant difference in the mean proportion

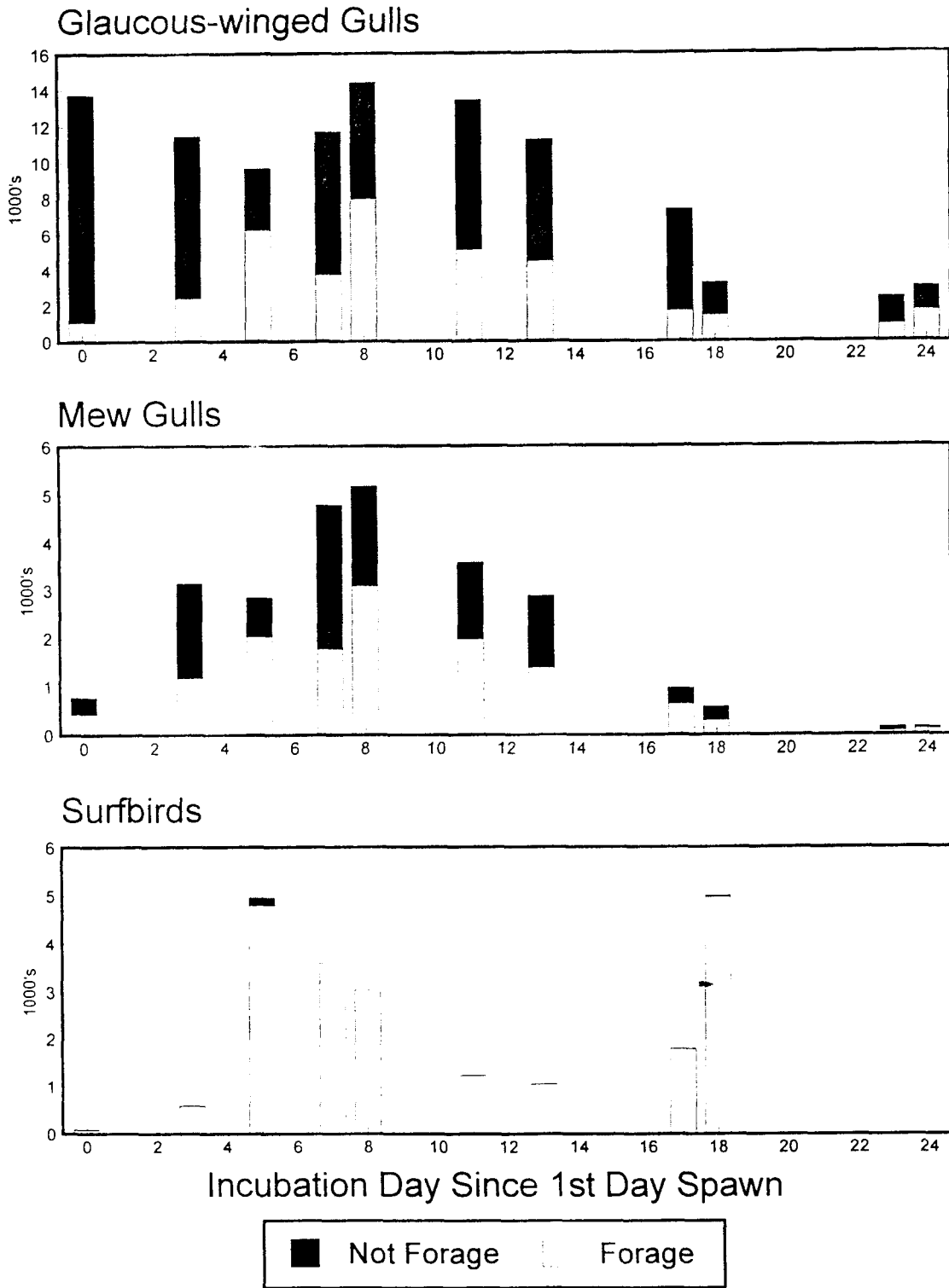


Figure 6. Total number of birds foraging and not foraging in spawn areas for the three most common species. Based on boat surveys of 7.6 km of shoreline with spawn (n = 13), Northern Montague Island, spring 1994.

Table 3. Total scans with foraging birds by tidal zone with herring spawn. Northern Montague Island, spring 1994.

Species	Total Scans	Tidal Zone Location					
		Below		Above			
		Swim	0-3m	0-3m	3-6m	6-10m	>10m
Black Turnstones	55	0	0	51	8	0	0
Surfbirds	39	0	1	35	5	0	0
GW Gulls	40	29	7	20	5	4	1
Mew Gulls	39	39	7	31	2	1	1

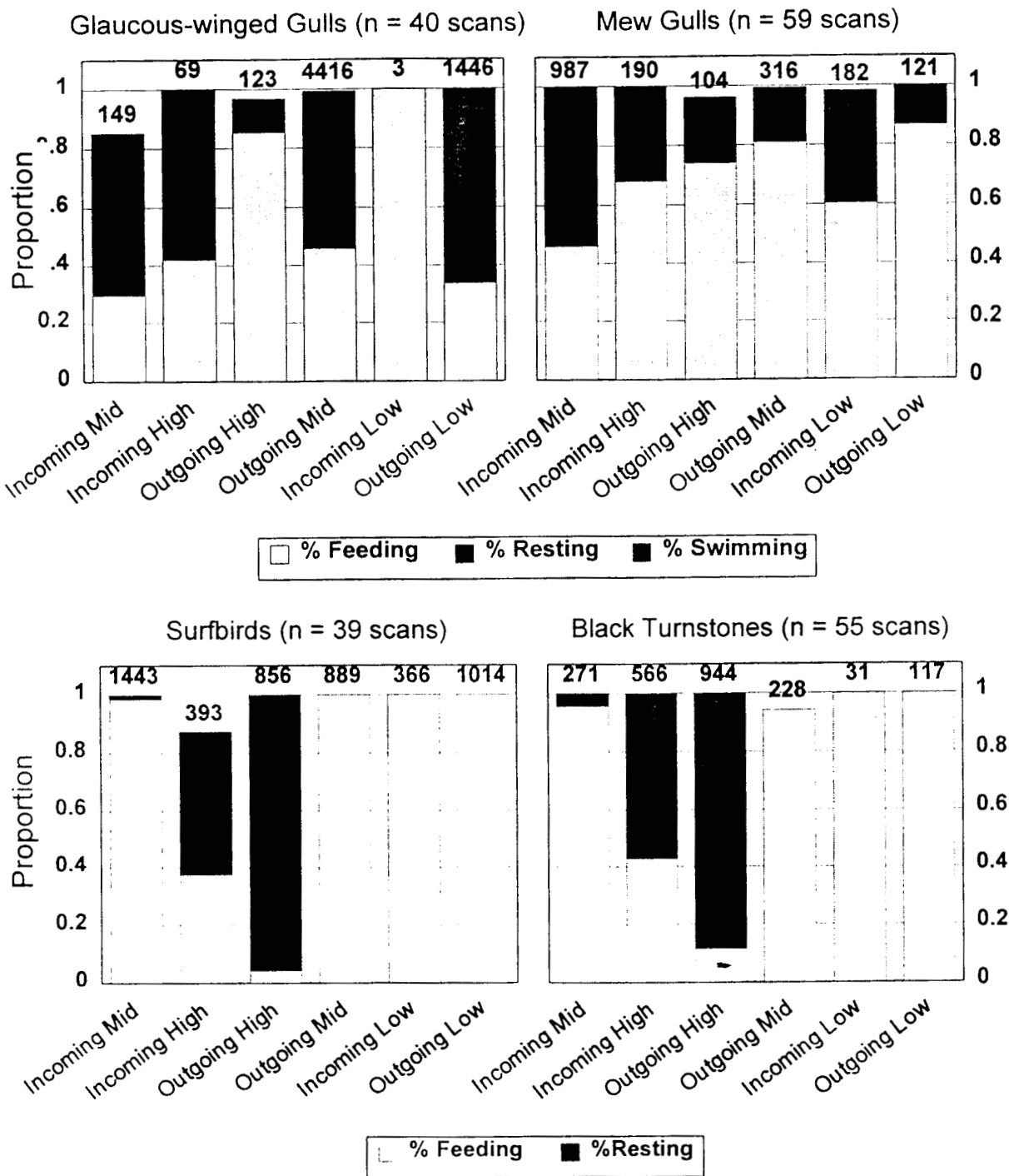


Figure 7. Relative proportion of Glaucous-winged Gulls, Mew Gulls, Surfbirds and Black Turnstones engaged in feeding, resting, or swimming by tide height and flow. Based on flock scans in spawn areas. Numbers above columns = total number of birds across all scans. Northern Montague Island, spring 1994.

feeding by tide or tide direction for either species (GW gull tide $P=0.27$, tide direction $P=0.68$; mew gull tide $P=0.60$, tide direction $P=0.46$) (Fig. 7).

When we modeled the proportion of mew gulls and GW gulls feeding at any time two independent variables were significant: LOCATION (i.e. high egg density, low egg density, and wind-row blinds) and TIDAL ZONE. For mew gulls this model explained 48.3% of the variation and for GW gulls 66.4%. The comparisons of mean proportions feeding by LOCATION and TIDAL ZONES were:

GW gulls	low egg density > high egg density > wind row
mew gulls	low egg density = windrow > high egg density;
GW gulls	0-3m above > swimming = 0-3m below > 3-10m above tideline;
mew gulls	0-3m above = swimming; 0-3m above > 0-3m below > 3-10m; swimming = 0-3m below; swimming > 3-10m above.

When we modeled the proportion of mew gulls resting or in comfort activities at any time, LOCATION ($P<0.01$, high egg density > low egg density blind = windrow blind), HABITAT ($P<0.01$, shore > water) and LOW MEAN (position relative to low mean tide) ($P<0.01$, slope = -0.002) were significant in explaining the variability (adjusted $R^2=48.6\%$). For GW gulls, LOCATION ($P<0.01$, high egg density site = windrow site > low density site) and HABITAT ($P<0.01$, shore > water), were significant in explaining the variability in resting and comfort behavior (adjusted $R^2=81.1\%$).

Focal Animals

When we modeled the proportion the time spent feeding for black turnstones, TIDAL ZONE (0-3m above > 3-6m above > 0-3m below), and FORAGE BEHAV (intensive > non-intensive = no foraging) were highly significant (adjusted $R^2=57.8\%$). For surfbirds only TIDAL ZONE was highly significant (0-3m above > 0-3m below; adjusted $R^2=30.3\%$) in explaining the variability in time spent feeding.

For mew gulls, the interaction of TIDAL ZONE*FORAGE BEHAV was significant ($P<0.02$) in explaining the variability of proportion of time spent feeding (adjusted $R^2=31.6\%$). For GW gulls, only FORAGE BEHAV (intensive = non intensive > no forage) was significant ($P<0.02$) in explaining the variability of proportion of time spent feeding (adjusted $R^2=86.0\%$). For all 4 species, we found no significant effects when we modeled the proportion of time feeding with a suite of environmental variables (LOCATION, TIDE, TIDE DIRECTION, BIRD AGE, FLOCK SIZE, WINDROW FOR, WRACK FOR, WAVE FOR, WEATHER, WIND, DIRECTION, SEA STATE, and TIDE*TIDE DIRECTION).

DISCUSSION

During 1994 in PWS, herring eggs were available to avian predators for approximately 30 days. An estimated 19t of herring spawned, with 99% of it over a 20km area at northern Montague Island. We found that three species accounted for >90% of the birds in spawn areas: GW gulls (57.7%), mew gulls (14.2%), and surfbirds (18.6%). Sea ducks (scoters, oldsquaws, greater scaup) were the fourth most numerous birds. GW gulls, mew gulls, and sea ducks have been documented to consume herring eggs during previous studies conducted primarily on British Columbia and Washington spawning grounds (see Haegele 1993a for review). Small numbers of surfbirds and black turnstones collected at Montague Island in 1989 confirmed their consumption of herring eggs (Martin 1993).

Our results suggest that rate loss due to predation is not constant due to both timing and patchiness of spawn deposition. GW gulls, the most numerous predator, peaked immediately after spawn deposition. Mew gulls, surfbirds, and sea ducks, however, are spring migrants and did not appear in substantial numbers until 8 days after initial spawn deposition. In years when herring spawn is deposited early or late (e.g. before 10 April, after 9 May), avian predation on spawn could be much lower because of spring migrants either not having arrived or already departed. Predation rates could be greater for years when herring spawn is deposited at the end of April and early May because of high gulls numbers with initial spawn deposition, along with the peak arrivals of sea duck, mew gull, and shorebird migrants. And, predation rates could be higher during years with reduced herring spawn, such as 1994. This is because predator populations are potentially remaining the same, despite reduced amounts of herring.

Birds appear to be responding to egg abundances with the attractiveness of a foraging area depending on some threshold egg density. Biomass variables (spawn width, total eggs, spawn levels < > 10,000 eggs) as well as the number of days spawn was laid were all significant in explaining the variation in birds densities, when examined at three spatial scales (Table 2). In the case of the spawn deposition transects when bird densities were recorded immediately prior to when ADF&G egg estimates were made, spawn days and total eggs were the only significant variables, among a suite of other environmental variables tested.

Most spawn is deposited in the area from the intertidal zone to -30ft (-9.9m) with the largest portion of eggs deposited in the lower intertidal and subtidal zones (Biggs et

al in press). Herring eggs in the intertidal zone are exposed at various tidal stages and available to walking birds, whereas subtidal attached and unattached herring eggs are available across all tidal cycles to avian predators that swim and/or dive (i.e., gulls, ducks, piscivorous birds).

Survival of eggs (i.e. viability) in the intertidal zone appears to be highly related to air exposure (Roper et al. 1995). Haegele (1993a) reported that gulls fed on spawn when it was exposed in the intertidal zone and in windrow. For both mew and GW gulls, however, we documented a high proportion feeding while swimming and while standing below the tideline (0-3m), with no difference in feeding by tide. Surfbirds and black turnstones fed at or near the tideline, and tended to feed more on the low and mid tides. Thus, while these four species do feed on exposed spawn which has less likelihood of survival (Roper et al 1995), all four species are also feeding on substantial amounts of viable spawn because of their preference to feed at or below the tideline.

In 1994 we were unable to estimate spawn losses to avian predators. Haegele (1993a) estimated egg losses per bird based on body weight (Nilsson and Nilsson 1976) This method, however, does not take into account different foraging strategies, the percent spawn in each species' diet, caloric content of herring spawn nor its assimilation efficiency (cf. Castro and Myers 1993). At the same time, some of the avian predators could be hyperphagic this time of year in preparation for breeding. Or, in the case of surfbirds and black turnstones, migration costs may require higher amounts of spawn to be ingested.

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