Predation on Pacific herring (Clupea pallasi) spawn by birds in Prince William Sound, Alaska

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ABSTRACT

We examined bird diets in areas with Pacific herring (Clupea pallasi) spawn at northern Montague Island in Prince William Sound, Alaska. Diets of the five most abundant bird species consisted primarily of herring spawn. Using a bioenergetics model, we estimated that in spring 1994 the five-bird species ate 857.1 metric tons (mt), representing 31% of the estimated spawn deposition. The two most numerous consumers, glaucous-winged gull (Larus glaucescens) and mew gull (Larus canus) consumed 26% and 3%, respectively, of the estimated spawn deposition. Surf scoters (Melanitta perspicillata), surfbirds (Aphriza virgata), and black turnstone (Arenaria melanocephala) together consumed 2% of the spawn deposition. In years with low spawn biomass, such as 1994, the number of herring larvae produced could be significantly affected by normal rates of avian predation. The high consumption by gulls, shorebirds, and surf scoters underscores the importance of herring spawn in the annual cycle of these species and requires further investigation.

Key words: avian predation, bioenergetics, Clupea pallasi, egg loss, glaucous-winged gull, spawn

INTRODUCTION

Pacific herring (Clupea pallasi) spawn in Prince William Sound, 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. The Sound Ecosystem Assessment (SEA) project hypothesized that the recruitment success of herring populations in Prince William Sound is related to predation during early life stages and physical processes that affect overwinter survival within the Sound (Norcross et al., 2001; this volume p. 42). Studies in Washington State, USA, showed that throughout the incubation of herring spawn, egg loss or removal from the original incubation environment can be significant (Palsson, 1984). In Prince William Sound, the percentage of eggs lost during incubation has ranged from 50 to 100% (Biggs-Brown and Baker, 1993; Rooper, 1996).

Herring egg loss is caused by several processes, including predation, physical displacement by wave action, anoxia, and desiccation (Palsson, 1984; Haegle and Schweigert, 1991; Rooper, 1996). Predators of herring spawn include birds, invertebrates, marine mammals, and fishes. In Washington State and British Columbia, epibenthic invertebrates (decapod crustaceans, gastropods, and asteroids) and birds have been identified as the most important egg predators (Munro and Clemens, 1931; Outram, 1958; Palsson, 1984; Haegle and Schweigert, 1991; Rooper, 1996). In those studies, maximum estimates of localized egg losses were 4% to invertebrates (Haegle, 1993b) and 55% to birds (Outram, 1958). Prior to our 1994–95 study, no other studies had investigated predation on herring spawn in Prince William Sound, Alaska. In association with our study, during spring 1995 Rooper (1996) documented herring egg predation at Montague Island in Prince William Sound by two fishes: greenling (Hexagrammidae) and Dolly Varden char (Salvelinus malma). He estimated that greenling consumed 2–9% and Dolly Varden char an insignificant number of herring eggs.

Egg loss has important implications to the management of herring fisheries in Prince William Sound. From 1994 through 1996, commercial herring fishing in Prince William Sound was closed because the adult herring biomass was estimated to be below minimal harvest levels (Sharp et al., 1996). From 1989 to 1997, the Alaska Department of Fish and Game estimated adult herring biomass for the Sound using total spawn biomass estimates, average fish size, sex ratio, and average fecundity. Total spawn biomass was determined from underwater diver transect surveys and adjusted by +10% to correct...
for egg losses occurring before the surveys (Wilcock et al., 1995). Because spawn transect surveys are conducted from 4 to 20 days after the initiation of spawning, we hypothesized that egg loss could be significantly greater than this +10% correction factor. As a result, herring stocks may be considerably underestimated.

Egg loss can be estimated in two ways: (i) by quantifying decreases in egg abundance throughout the incubation period; and (ii) by identifying sources of loss and estimating their magnitude (Haegele and Schweigert, 1991). We used the second approach to estimate herring egg loss to avian populations at Montague Island in Prince William Sound. We carried out a census of populations of the most numerous bird species foraging in spawn areas, measured their diet composition, and used a bioenergetics model to estimate egg consumption by these bird species. Previously, bioenergetics simulation models have been applied to oceanic, coastal and freshwater bird populations to estimate fish consumption (Wiens and Scott, 1975; Furness, 1978; Cairns et al., 1991; Madenjian and Gabrey, 1995; Derby and Lovvorn, 1997; Furness and Tasker, 1997).

METHODS

We conducted our study at northern Montague Island, in Prince William Sound, Alaska (Fig. 1) from 7 April–15 May 1994 and from 19 April–19 May 1995. Herring spawned at northern Montague Island from 18 to 25 April 1994 along 22.6 km of shoreline and between 27 April–1 May 1995 along 20.2 km of shoreline. Our study area included all shoreline areas with herring spawn. Location of spawn was determined from observations of milt detected during Alaska Department of Fish and Game aerial herring surveys and underwater diver spawn transect surveys (Wilcock et al., 1995).

Bird abundance

Using aerial and nearshore boat surveys, we estimated abundance of the five most numerous birds in spawn areas for spring 1994. These included glaucous-winged gulls (Larus glaucescens), mew gulls (L. canus), surf scoters (Melanitta perspicillata), black turnstones (Arenaria melanocephala), and surfbirds (Aphriza virgata). All surveys were conducted during a 3-h period centred at low tide when maximum spawn was exposed. Aerial surveys (n = 12 surveys) were flown in a Cesna 185 float plane along a path approximately 100–150 m from shore at a survey altitude of 200–250 m and included multiple flight lines where necessary for complete coverage. Nearshore boat surveys (n = 12 surveys) covered 6.4 km of shoreline with spawn between Stockdale Harbor and Montague Point (Fig. 1) and recorded all birds within 120 m of shore plus the shoreline (maximum shoreline width 50 m).

For each species we calculated an average abundance in spawn areas. To estimate gull abundance, we used aerial videography supplemented by aerial observers between Montague Point and Rocky Bay, and nearshore
boat surveys for all other spawn areas. Offshore diving duck abundance was estimated from aerial and boat surveys. Offshore diving ducks were principally surf scoters, but also included white-winged scoters (Melanitta fusca), oldsquaws (Clangula hyemalis), and greater scap (Aythya marila). We extrapolated numbers of glaucous-winged gulls, mew gulls, and surf scoters from flock compositions observed during boat surveys to estimate numbers of individuals for each species in aerial surveys. The two shorebird species, black turnstone and surfbird, are too small and cryptic to be counted from the air. For these two species we determined their numbers from nearshore boat surveys.

Diet

To determine the impact of bird predation on herring eggs, we examined bird diets in spawn areas. We collected surfbirds and black turnstones in 1994 and 1995, and glaucous-winged gulls, mew gulls, and surf scoters in 1995 from foraging flocks in spawn areas. All specimens were weighed, measured, and dissected in the field. We removed contents of the mouth, oesophagus and proventriculus (combined and hereafter referred to as oesophagus), and the gizzard and stored them separately in Gilson’s solution. To determine if birds were selecting for dead or live herring eggs, we estimated percent viable spawn in the oesophagus (excluding the proventriculus) of all birds collected between 4 and 17 May 1995. Clear eggs indicated viability, whereas partially to totally milky-coloured eggs indicated nonviable spawn (Falson, 1984). We used Pearson’s correlation coefficient (r) to evaluate the strength of the relationship between percent viable spawn and date of collection.

In the laboratory, we identified items from stomach samples to the lowest possible taxon. Number, size and weight (wet mass, including shells) for each prey type was recorded. We estimated herring egg numbers by counting and weighing subsamples (one egg, wet mass, \( \bar{x} = 2.29 \times 10^{-3} \) g \( \pm 1.32 \times 10^{-4} \) g (SE); \( n = 45 \)). Identifiable shell fragments (e.g. hinges) could often determine the number of hard-shelled prey items. When no unique shell fragments occurred, we assumed the fragments represented one individual with a length equal to the average length found in stomach contents from this or similar studies (Navarro et al., 1989; P. Martin, unpublished data).

For mew gulls, glaucous-winged gulls, and surf scoters, diet analyses did not include gizzard contents due to bias toward refractory components of the diet and differential digestion rates. Gizzard contents of surfbirds and black turnstones were included due to a lack of prey in their oesophagus. For each prey type, we determined percent occurrence and aggregate wet weight including shells (Korschgen, 1980).

For each bird we estimated the proportion of total energy in the forage (kJ) represented by each prey type. Estimated proportions were based on the number, size, estimated dry mass of soft tissue (predigestion), and caloric density (kJ g\(^{-1}\), dry mass) of each prey type, and then averaged for each bird species (Korschgen, 1980).

We estimated herring egg dry mass from samples of 100 herring eggs (\( \bar{x} = 2.72 \times 10^{-1} \) g \( \pm 6.59 \times 10^{-2} \) g, \( n = 11 \)). Dry weights of edible body parts of Mytilus trossulus were estimated using values obtained from a length-weight relationship for Mytilus edulis reported in the literature (Cummins and Wuycheck, 1972) to determine average caloric density (kJ g\(^{-1}\), dry mass) for herring spawn (18.7 kJ g\(^{-1}\), n = 2) and blue mussels (Mytilus trossulus, soft tissue only; 19.9 kJ g\(^{-1}\), n = 4) collected from the study area. We estimated caloric densities for other prey items based on similar species reported in the literature (Cummins and Wuycheck, 1971).

Consumption model

We estimated daily herring spawn consumption for glaucous-winged gulls, mew gulls, surf scoters, surfbirds, and black turnstones. Our bioenergetics model was 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) per individual bird predator: \( C = (FMR/MEC) \times P \times 196 \), where, \( FMR = \) field metabolic rate (kJ day\(^{-1}\)), \( MEC = \) metabolizable energy coefficient of herring spawn, \( P = \) proportion of total energy acquired from herring spawn, as determined from stomach contents of collected birds (aggregate energy), and, \( 196 = \) number of herring eggs needed to produce 1 kJ, as determined from our caloric density and dry weight measurements.

For our model, we assumed MEC of 75% (Castro et al., 1989; Furness and Tasker, 1997). Field metabolic rates for mew gulls and glaucous-winged gulls were calculated from the allometric equation for FMR for all seabirds (Birt-Friesen et al., 1989): \( FMR = 10^{(1.20 \cdot 0.1673 \cdot h_{kgm})} \), where \( M = \) average body mass (kg) based on specimens.
collected at Montague Island. Field metabolic rates for black turnstones and surfbirds were derived from the basal metabolic rate equation for shorebirds (Kersten and Piersma, 1987) and multiplied by 2.5, the standard conversion to FMR for shorebirds (Drent and Piersma, 1990); \( \text{FMR} = 2.5 \times (437M^{0.729}) \); where \( M \) = average body mass (kg) for surfbirds and black turnstones collected on spawn areas during 1994 and 1995. FMR for surf scoters was estimated using Feltham’s (1995) FMR for female common merganser (Mergus merganser; \( \text{FMR} = 1867 \text{kJ day}^{-1} \)), scaled linearly to the mean body mass of surf scoters collected at Montague Island.

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): \( C_n = 0.51M^{0.54} \); where \( C_n \) = daily food consumption (g), and \( M \) = average body mass (kg) per bird species (Nilsson and Nilsson, 1976). For our comparison, we assumed that \( C_n \) represented 100% herring spawn.

Sensitivity analyses
A sensitivity analysis was performed on our herring spawn consumption model using the individual parameter perturbation method (Bartell et al., 1986). Five parameters: body mass, bird abundance between Stockdale Harbor and Montague Point, metabolizable energy coefficient of food, proportion of energy acquired from herring spawn, and field metabolic rate 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. We varied parameters within ranges reported, or within set percentages. We adjusted average body mass and average bird abundance on either side of its nominal value by the percent equivalent of 2 SE. Metabolizable energy coefficient of herring spawn was varied from 65 to 85%. Furness and Tasker (1997) reported that in general MEC for herring spawn was varied from 65 to 85%. Furness and Tasker (1997) reported that in general MEC for herring spawn was varied from 65 to 85%. Furness and Tasker (1997) reported that in general MEC for herring spawn was varied from 65 to 85%. Furness and Tasker (1997) reported that in general MEC for herring spawn was varied from 65 to 85%.

Rate of egg consumption
We estimated the percent of total spawn lost to the five avian predators at northern Montague Island for 1994 by dividing total consumption (TC) by total eggs (TE). Available herring eggs were estimated from underwater diver transects conducted between 28 April–14 May 1994 for all Montague Island spawn areas (J. Wilcock and E. Brown, unpublished data). We calculated TE in billions of eggs as: \( \text{TE} = [N(\bar{y} \times 10^3)] \); where \( N \) = total number of possible transects (e.g. 100 m of shoreline spawn = 316 transects) and \( \bar{y} \) = average estimated total number of eggs (thousands) per transect (Wilcock et al., 1995).

A one-day egg consumption rate was determined at selected spawn transects in north-east Prince William Sound (20 April and 9–10 May 1994) and at northern Montague Island (28 April–8 May 1994). 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 centred 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 two geographical areas within our northern Montague Island study site: 4.3 km of shoreline on the east side of Rocky Bay, and 5.5 km of shoreline at Graveyard Point (Fig. 1). Herring egg biomass for these shorelines had been estimated during diver transect surveys conducted from 28 April–1 May at Rocky Bay (\( \bar{x} = 29 \text{ April}, n = 17 \text{ transects} \)) and 2–6 May at Graveyard Point (\( \bar{x} = 4 \text{ May}, n = 14 \text{ transects} \)). For all consumption estimates, mean values are presented ± SE.

RESULTS

Diet
Stomach analyses showed that herring spawn occurred in 100% of the oesophagi of glaucous-winged gulls (\( n = 13 \)), mew gulls (\( n = 9 \)), and surf scoters (\( n = 8 \)) and accounted for 96–100% of the aggregated wet weights of all ingesta in the foregut (Table 1). Quantity of eggs found in the oesophagus ranged from 0.04 g (16 eggs) in a mew gull to a high of 145.8 g (63 501 eggs) in a glaucous-winged gull to a high of 145.8 g (63 501 eggs) in a glaucous-winged gull.
gull. Compared with gulls and surf scoters, food habits of surfbirds (n = 20) and black turnstones (n = 14) in spawn areas were more varied and included herring spawn, bivalves, gastropods and crustaceans. No herring spawn was found in the guts of five of the surfbirds (25%) and three of the black turnstones (22%).

We found no evidence that avian predators preferred viable to dead and decaying spawn. Percent viable spawn in oesophagi of glaucous-winged gulls ranged from 0 to 50% (x̄ = 18.9%, n = 7), and from 0 to 100% for both mew gulls (x̄ = 66.16%, n = 8) and surf scoters (x̄ = 56.20%, n = 6). No viable spawn was observed in oesophagi of black turnstones (n = 2). We tested a relationship between percent viable spawn in the oesophagus and date of collection. The percentage of viable spawn in the oesophagus was strongly negatively correlated with date of collection for surf scoters (r = -0.73, p = 0.04, n = 6) and glaucous-winged gulls (r = -0.73, p = 0.03, n = 7), but not in mew gulls (r = 0.06, p = 0.45, n = 8).

Consumption model

The estimated proportion of daily energy acquired from herring spawn ranged from 93 to 100% per species. Based on our consumption model, we estimated black turnstones (the smallest predator), and surf scoters had the lowest and highest daily herring spawn consumption rates at 0.16 and 1.07 kg day⁻¹ per individual, respectively (Table 2).

In the sensitivity analyses of our consumption model, a decrease in MEC had the greatest effect on herring spawn consumption estimate per unit of change (Table 3). A 1% decrease in MEC increased consumption by +1.1%. Alternatively, a 1% increase in MEC decreased consumption by only – 0.91%. There was a 1 : 1 direct relationship between percentage change in estimated herring spawn consumption and percent changes in bird abundance, proportion of spawn in the diet, and field metabolic rate. Percentage change in body mass had the least effect on our herring consumption estimate. Depending on the species, a 1% increase in body mass increased herring consumption by 0.67–0.72%. However, of the five input parameter values used in our model, bird abundance contributed the most to prediction errors because of the large variation associated with this parameter. For example, during boat surveys of Stockdale Harbor to Montague Point the variation in bird abundance ranged from a low of 38% of the average number of glaucous-winged gulls to a high of 93% of the average number of black turnstones (Table 4).

### Table 1. Frequency of occurrence (%) and aggregate percent weight of foods in gut contents of five avian species. Birds collected from herring spawn areas on northern Montague Island, April–May 1994, 1995

<table>
<thead>
<tr>
<th>Species</th>
<th>Glaucous-winged gull (n = 13)</th>
<th>Mew gull (n = 9)</th>
<th>Surf scoter (n = 8)</th>
<th>Surfbird (n = 20)</th>
<th>Black turnstone (n = 14)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Clupea pallasi eggs</td>
<td>100 100 100 96 100 100 75 70.5 69 74</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bivalves</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mytilus trossulus</td>
<td>- - - - - - 80 27.7 19 1.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crustaceans</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Balanus sp.</td>
<td>- - - - - - 5 0.2 19 23.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unidentified amphipod</td>
<td>- - - - - - 5 &lt; 0.1 - -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amphithoe sp.</td>
<td>- - - - - - 5 &lt; 0.1 - -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unidentified pagonus</td>
<td>- - - - - - 10 0.3 - -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gastropods</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alia sp.</td>
<td>- - - - - - 10 0.7 - -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Littorina secans</td>
<td>- - - - - - 10 0.1 - -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Margarites sp.</td>
<td>- - - - - - 10 0.4 - -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unidentified gastropod</td>
<td>- - - - - - 5 &lt; 0.1 - -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insects</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diptera larvae</td>
<td>- - - 11 4.2 - - - - - -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nematodes</td>
<td>8 &lt; 0.1 - - - - - - - - - -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unidentified organic material</td>
<td>8 &lt; 0.1 - - - - - - - - - -</td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

% occ., percent occurrence: number of individuals with prey item/total number of individuals. % wt., aggregate weight: total weight of prey item for all individuals/total weight of all prey items for all individuals.

Table 2. Bioenergetics model input parameters and daily herring spawn consumption by avian species. Daily consumption compared with Nilsson and Nilsson (1976) daily food consumption model.

<table>
<thead>
<tr>
<th>Species</th>
<th>Body mass (g) ± SE (n)</th>
<th>Field metabolic rate (kJ day⁻¹)</th>
<th>Energy % eggs (n)</th>
<th>Eggs ingested (day⁻¹)</th>
<th>Eggs ingested [kg (wet) day⁻¹]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glaucous-winged gull</td>
<td>1326 ± 54 (9)</td>
<td>1451</td>
<td>100 (12)</td>
<td>380 052</td>
<td>0.87</td>
</tr>
<tr>
<td>Mew gull</td>
<td>453 ± 18 (5)</td>
<td>709</td>
<td>95 (8)</td>
<td>185 662</td>
<td>0.43</td>
</tr>
<tr>
<td>Surf scoter</td>
<td>1160 ± 52 (6)</td>
<td>1783</td>
<td>100 (7)</td>
<td>466 934</td>
<td>1.07</td>
</tr>
<tr>
<td>Surfbird</td>
<td>206 ± 7 (15)</td>
<td>345</td>
<td>93 (20)</td>
<td>84 161</td>
<td>0.19</td>
</tr>
<tr>
<td>Black turnstone</td>
<td>151 ± 2 (16)</td>
<td>275</td>
<td>99 (14)</td>
<td>71 375</td>
<td>0.16</td>
</tr>
</tbody>
</table>

$^a$Based on $C = 0.51M^{0.85}$, where $C =$ daily food consumption (kg) and $M =$ average body mass (kg) per bird species.

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Slope (10⁻³)</th>
<th>Body mass</th>
<th>Number of birds</th>
<th>Field metabolic rate</th>
<th>Proportion herring spawn</th>
<th>Metabolizable energy coefficient of food</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glaucous-winged gull</td>
<td>0.08</td>
<td>63.77</td>
<td>63.77</td>
<td>63.77</td>
<td>−64.19</td>
<td></td>
</tr>
<tr>
<td>Mew gull</td>
<td>5.5</td>
<td>8.25</td>
<td>8.25</td>
<td>8.25</td>
<td>−8.30</td>
<td></td>
</tr>
<tr>
<td>Surf scoter</td>
<td>−4.98</td>
<td>4.98</td>
<td>4.98</td>
<td>4.98</td>
<td>−5.02</td>
<td></td>
</tr>
<tr>
<td>Surfbird</td>
<td>4.31</td>
<td>5.91</td>
<td>5.91</td>
<td>5.91</td>
<td>−5.95</td>
<td></td>
</tr>
<tr>
<td>Black turnstone</td>
<td>0.30</td>
<td>0.42</td>
<td>0.42</td>
<td>0.42</td>
<td>−0.42</td>
<td></td>
</tr>
</tbody>
</table>

Table 4. Avian abundance in spawn areas and estimated spawn consumption for the five most numerous bird species at northern Montague Island, 19 April–15 May 1994. Avian abundance and spawn days (number of days birds occur in spawn areas) determined from aerial videography, aerial surveys, and boat surveys.

<table>
<thead>
<tr>
<th>Species/survey area</th>
<th>Number of birds ± SE (n)</th>
<th>Spawn days</th>
<th>Eggs (10⁶)</th>
<th>Metric tons</th>
<th>Percentage of spawn consumed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glaucous-winged gull</td>
<td>26 000 ± 3563 (12)</td>
<td>24</td>
<td>237.1</td>
<td>544.8</td>
<td>82.2</td>
</tr>
<tr>
<td>Rocky Bay – Montague Point</td>
<td>7 326 ± 1401 (12)</td>
<td>25</td>
<td>69.6</td>
<td>159.9</td>
<td>11.0</td>
</tr>
<tr>
<td>Stockdale – Montague Point</td>
<td>6 384 ± 1184 (12)</td>
<td>26</td>
<td>30.8</td>
<td>70.7</td>
<td>5.0</td>
</tr>
<tr>
<td>Mew gull</td>
<td>2 042 ± 503 (12)</td>
<td>27</td>
<td>10.2</td>
<td>23.5</td>
<td>1.7</td>
</tr>
<tr>
<td>Surf scoter</td>
<td>1 045 ± 272 (12)</td>
<td>26</td>
<td>12.7</td>
<td>29.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Rocky Bay – Montague Point</td>
<td>466 ± 103 (17)</td>
<td>27</td>
<td>5.9</td>
<td>13.5</td>
<td>1.0</td>
</tr>
<tr>
<td>Stockdale – Montague Point</td>
<td>3 070 ± 930 (10)</td>
<td>25</td>
<td>6.5</td>
<td>14.8</td>
<td>0.1</td>
</tr>
</tbody>
</table>
| Surf scoter               | 254 ± 118 (9)            | 19         | 0.3        | 0.8         | 2001 Blackwell Science Ltd., Fish Oceanogr., 10 (Suppl. 1), 149–158.
Egg losses to avian predators

Based on aerial and nearshore boat surveys, we estimated 857.1 mt of herring were consumed by the five major avian predators over 27 days (Table 4). Over 66% of egg consumption occurred before 4 May, day 16 of incubation and the average date for underwater diver estimates of herring biomass. Using average fecundity and average body mass of spawning females to determine eggs per female (21 881 eggs/female; Wilcock et al., 1995), estimated bird consumption represents spawn from 4885 mt of adult herring. Glaucous-winged gulls were the most numerous spawn consumers, with an estimated 8.1 × 10^5 bird days between 20 April and 15 May. These gulls were also the largest consumers, accounting for 82% of estimated eggs removed by the five species.

Daily percent loss to birds of the total eggs spawned ranged from 0.2 to 21.3% at Montague Island (\(\bar{x} = 3.4 \pm 1.8\%\), \(n = 9\)), and 0–17.8% at north-east Prince William Sound (\(\bar{x} = 2.7 \pm 2.0\%\), \(n = 7\)) at 100 × 300 m transects conducted in conjunction with underwater diver spawn surveys. All five predators except surf scoters were observed on these transects. Daily consumption rates for eastern Rocky Bay and Graveyard Point were much lower. On the east side of Rocky Bay, based on underwater diver transect survey results, we estimated 429.0 mt of available spawn on 29 April 1994. From 30 April through 15 May (approximate spawn hatch), estimated daily percent loss to gulls and surf scoters combined ranged from 0.2 to 1.6% (\(\bar{x} = 0.8 \pm 0.2\%\), \(n = 5\)), with an estimated 13.6% of available eggs removed over the 16-day period. At Graveyard Point from 5 to 15 May 1994, the estimated daily percent egg consumption rate for all five predator species ranged from 0.4 to 2.8% (\(\bar{x} = 1.3 \pm 0.4\%\), \(n = 5\)) with 14.5% (42.3 mt) of an estimated 292.2 mt removed over the 11-day period.

DISCUSSION

At Montague Island in Prince William Sound, herring spawn is an abundant but ephemeral resource lasting for approximately 25–30 days each spring. We documented herring spawn consumption by the five most numerous avian species: glaucous-winged gulls, mew gulls, surf scoters, surfbirds, and black turnstones. All five of these species are more likely to occur in spawn areas than non-spawn areas (M. Bishop and S. Green, unpublished data). Diet analyses show that when in spawn areas, glaucous-winged gulls, mew gulls, surf scoters, surfbirds, and black turnstones 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 tidal height, where −1.2 m = Mean Low Low Water; J. Wilcock, personal communication). Surf scoters can access herring spawn regardless of tidal 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 five species ranged from four to five 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 four species of avian piscivores (Nilsson and Nilsson, 1976). This equation underestimates daily consumption because it does not take into account (i) differences in the relative field metabolic rates between species groups (for example shorebirds and seabirds); and (ii) different caloric values and digestibility of prey items. Because this equation was developed for a food source with relatively high energy density (6.2 kJ g\(^{-1}\)) it may not be suitable for use with herring eggs.

There are possible sources of error in our bioenergetics model. To date, field metabolic rate has not been directly measured for any Larus gull. We used an allometric equation for ‘all seabirds’ derived from double-labelled water studies of 16 free-living seabird species (Birt-Friesen et al., 1989). The ‘all seabirds’ equation provides a conservative estimate of field metabolic rate, thus generating a conservative estimate of daily consumption (0.87 kg day\(^{-1}\) for glaucous-winged gulls) when compared with estimates derived from allometric equations for cold water seabirds and for cold water, flapping flight seabirds (0.97 kg day\(^{-1}\) and 1.3 kg day\(^{-2}\) for glaucous-winged gulls, respectively).

Estimates of bird abundance exhibited the largest variation of all model parameters. Variation in bird abundance is due to spring migratory movements as well as shifts in resident bird distribution in response to herring spawn availability. Glaucous-winged gulls and mew gulls are relatively abundant throughout the winter in Prince William Sound (Lance et al., 1999). Gull numbers increase in the Sound by several thousand between mid-April and mid-May as local breeders return from southern wintering areas and transient migrants stop en route to their more westerly breeding grounds. In nearby colonies,
egg-laying usually begins the second week of May (Isleib and Kessel, 1973). Black turnstones and surfbirds are transient migrants through Prince William Sound, stopping in large flocks primarily between 23 April and 10 May (M. Bishop and S. Green, unpublished data). While surf scoters do not breed in Prince William Sound, they occur in abundant numbers throughout the year. Large migrant flocks stop over from late April through May en route to their interior breeding areas (Isleib and Kessel, 1973). Weather plays an important role in the timing of migration for all of these species, with large numbers of birds often arriving and departing in front of low-pressure systems.

Metabolizable energy coefficient had the greatest effect on estimated herring spawn consumption per unit of change. Metabolizable energy was estimated at 75% in our model. Foods with higher lipid contents have higher MECs (Brekke and Gabrielson, 1994). However, lipid content of herring spawn (Clupea spp.) is low, ranging from 2.0 to 3.5% of wet mass (Kaitaranta et al., 1979; Kaitaranta and Ackman, 1981) and 11.9–14.6% of dry mass (Sidwell, 1981; Tocher and Sargent, 1984); and spawn maturation causes no significant reduction in lipid content (Kaitaranta and Ackman, 1981). Given the low lipid content, we believe that the MEC estimate of 75% is conservative (i.e., high).

Although body mass had the smallest effect on predicted 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 five species showed high body fat/lean dry mass; M. Bishop and S. Green, unpublished data). Endogenous reserves are needed for both migration and breeding. This is particularly true for the two migrant shorebird species. As long distance migrants, surfbirds and black turnstones theoretically arrive at Montague Island near the end of April with their nutrient stores depleted. Not only do they have to replenish their reserves to continue migration but also once they reach the breeding ground they may need to draw on those reserves for clutch formation and territory defence.

Egg consumption
Total eggs available at Montague Island in 1994 were initially estimated at 2716 mt (1.183 x 10^9 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 4733 mt (2.061 x 10^9 eggs, Willette et al., 1998) using a formula that modelled 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 five bird species removed 857.1 mt of herring spawn, representing 31% of the initial estimate of spawn biomass at Montague Island or 18% 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) modelled egg loss in Prince William Sound for four seasons (1990–91, 1994–95). He found that 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 (1996) calculated an egg loss rate for each depth based on air exposure. He estimated a daily egg loss rate at 6.7% and average percent egg loss throughout 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 days in British Columbia, only an estimated 3–18% of total spawn was consumed, including only 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 enclosure experiments conducted in the Pacific North-west. Estimated losses to avian predators using enclosures ranged from 34 to 97% (Cleaver and Franett, 1946; Outram, 1958; Steinfeld, 1971). However, methodology is often a problem: at least two studies have reported higher losses inside enclosures, resulting from invertebrate predators (Palsson, 1984) or intra- and intervariability in diver counts (Rooper, 1996). At the same time, enclosure studies have primarily measured losses in the intertidal zone, whereas our estimate is for both inter- and subtidal areas.

A more accurate way to adjust total spawn biomass estimates 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. Second, conduct underwater diver spawn deposition surveys in a geographically sequential order whereby all surveys for an area are completed during a short time period. Third, calculate losses to gulls by area using our bioenergetics model.

One factor influencing the estimated high proportion of spawn removed in 1994 was the low spawn biomass

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relative to other years. Based on herring spawn indices between 1974 and 1994 in Prince William Sound, the lowest values for kilometres of shoreline with spawn and for estimated spawn biomass both occurred in 1994. In contrast, peak spawn deposition biomass for this 20-year period was seven times the 1994 estimate (Sharp et al., 1996). Whilst we were not able to address interannual variation in bird numbers in this study, we do not believe that bird numbers would vary proportionally to the amount of spawn available. The glaucous-winged gull, the greatest avian predator on spawn, is both an abundant year-round resident and migrant breeder in the Sound (Isleib and Kessel, 1973). Because migration and early nesting coincide both spatially and temporally with herring spawn deposition and incubation, the overall abundance of glaucous-winged gulls throughout spawn areas is probably similar among years.

CONCLUSIONS
While the rates of herring spawn consumption for the five avian predators are approximations, our model suggests that these predators are a significant component in the loss of herring spawn. Currently, the estimated biomass of herring spawn is used to assess herring stocks for commercial fisheries in Prince William Sound and other Pacific Coast areas. Methods to estimate herring spawn loss for stock assessment vary across areas, and often change. Nevertheless, our bioenergetics model provides management an improved method to estimate herring egg losses to birds in order to correct spawn biomass estimates from diver surveys.

Glaucous-winged gulls are the dominant consumer of herring spawn at northern Montague Island in Prince William Sound. In years with low spawn deposition, the number of herring larvae produced could be significantly affected by normal rates of avian predation. 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 meeting energy requirements for both breeding and migration. Future investigations into the ecological significance of herring spawn in the life history of these avian species are warranted.

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