



# Pacific herring (*Clupea pallasii*) consumption by marine birds during winter in Prince William Sound, Alaska

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## ABSTRACT

Following the 1989 MV *Exxon Valdez* oil spill (EVOS) and subsequent herring population collapse in Alaska's Prince William Sound (PWS), the Pacific herring (*Clupea pallasii*) fishery was closed. In the 25 yr since EVOS, herring and several herring-dependent marine bird species have failed to reach pre-spill population levels. One hypothesis is that intense predation pressure may be inhibiting herring recovery. To inform herring modeling efforts, this study estimated marine bird consumption of juvenile and adult herring in PWS for 10 winters over an 18-yr period (1989–90 through 2006–2007). Total estimated herring consumption by wintering marine birds averaged  $2409 \pm 950$  t, indicating that avian consumption represents a substantial and inter-annually variable source of herring mortality. Common murre (*Uria aalge*) consumed the greatest portion (16–80%) of herring in all years among marine bird species. Juvenile herring biomass consumed annually by common murre was greater than murre consumption of adult herring biomass. Time lag analyses showed that marine bird consumption of adult herring is negatively correlated with the amount of herring spawn observed in subsequent years, but such effects were not observed more than 2 yr. Our models indicate that during years in which herring recruitment is low or bird populations are particularly large, marine birds can consume up to 10% of the annual adult herring biomass. Our results highlight

the importance of herring to wintering PWS birds. We propose that future management of herring stocks seeks to reduce negative impacts on marine birds that prey on herring.

**Key words:** Alaska, avian predation, bioenergetics, *Clupea pallasii*, common murre, Prince William Sound

## INTRODUCTION

Herring (*Clupea* spp.) are abundant schooling fish that are the target of major commercial fisheries in both the North Pacific Ocean and the North Atlantic Ocean. Herring are also a key forage fish for breeding and wintering seabirds in those same areas (Skov *et al.*, 2000; Suryan *et al.*, 2002; Kuletz, 2005; Overholtz and Link, 2007). Atlantic puffins (*Fratercula arctica*) along the east coast of the Norwegian Sea are estimated to consume more than 160 000 t of age 0+ Atlantic herring (*Clupea harengus*) during the breeding season (Anker-Nilssen and Øyan, 1995). In the Gulf of Maine, seabirds consumed an estimated 9000 t of Atlantic herring in 2002 (Overholtz and Link, 2007). Along the Pacific Coast of Vancouver Island, Common murre (*Uria aalge*) and shearwaters (*Puffinus* spp.) consumed on average 16% of the estimated biomass of age 0- to 2-yr Pacific herring (*Clupea pallasii*; Logerwell and Hargreaves, 1996).

In Alaska's Prince William Sound (PWS), Pacific herring was historically an important fishery with an annual harvest up to 20 000 metric tonnes (t) (Botz *et al.*, 2010). In March 1989 the MV *Exxon Valdez* oil spill (EVOS) occurred in PWS, releasing 42 million litres of crude oil. Subsequent to the spill, the PWS herring population collapsed. While there is still uncertainty as to whether the cause of the collapse was natural variability, disease or the oil spill, the PWS herring population has yet to recover (Hulson *et al.*, 2008; EVOS Trustee Council, 2010). The post-EVOS herring crash in PWS has been implicated in the decline of several marine bird species. Kuletz (2005) concluded that juvenile herring were critical to the Marbled murrelet (*Brachyramphus marmoratus*) and suggested that the population decline in PWS murrelets was linked to the concurrent herring decline.

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Similarly, Irons *et al.* (2000) determined that the effects of EVOS on several marine birds lasted longer than expected, possibly as a result of reduced forage fish abundance. In addition, they found that the most persistent declines were associated with seabirds that overwinter in PWS, whereas birds that migrated south for the winter recovered more quickly.

Although herring is considered more resilient than other marine fish because it matures early in life and is fished with highly selective gear (Hutchings, 2000), herring population declines in general take a decade or longer to recover (Hay *et al.*, 2001). In PWS, a critical bottleneck for herring recruitment is juvenile abundance and the condition of young-of-the-year during late fall and winter (October–March), a period when zero or negative growth rates occur (Foy and Paul, 1999) and mortality rates are highest (Stokesbury *et al.*, 2002). Brown (2003) suggested that abundance of age 1+ juvenile herring should be directly correlated with adult recruitment 2 or 3 yr later unless the local population is under intense predation pressure. Furthermore, she suggested that stable or increasing predator populations in PWS could constrain or further reduce herring recruitment when the juvenile herring population is increasingly composed of smaller and fewer schools over a reduced geographic range.

Herring population recovery and successful management of herring require detailed knowledge of age-specific mortality as well as the factors limiting population growth. In this study a bioenergetics simulation model was used to estimate consumption of Pacific herring by marine birds wintering in PWS. The objectives of this study were: (i) to estimate the biomass of juvenile and adult herring consumed by marine birds during the winter months; and (ii) to compare our consumption estimates with the adult herring biomass available during the same time period. Our results improve the natural mortality estimate for herring stock assessment and can be used by herring fisheries managers to reduce negative impacts to marine birds when establishing future fishing quotas.

## METHODS

### Study area

Prince William Sound is located on the coast of south-central Alaska, primarily between 60° and 61°N. The Sound is separated from the adjacent Gulf of Alaska by large mountainous islands. The coastline is rugged and extensive, with many islands, fjords and bays. Water depths in fjords and bays range from <50 to >400 m; outside of the bays and fjords are many basins and passages of varying depths up to 700 m. Annual

precipitation can be as much as 5.4 m. Sea surface temperatures can be as low as 1°C in late winter, with some inner bays and fjords blocked with ice (Gay and Vaughan, 2001).

### Consumption estimation model

Herring biomass consumption was estimated for 17 marine bird species known and one species suspected (Yellow-billed loon, *Gavia adamsii*) to forage on juvenile and or adult herring during winter (Fig. 1, Table 1). For each winter, a species' herring consumption ( $C$ ) is determined by the equation:

$$C = \sum_{d=1}^{D_s} \sum_{a=1}^{A_s} (S \times E_a) / K_a$$

where  $D$  is the number of days between 15 November and 15 March that a species resides in Prince William Sound,  $S$  is the bird species population size in a given winter,  $A$  is the number of herring age classes consumed (juvenile or adult),  $E_a$  is the daily energy requirement ( $\text{kJ day}^{-1}$ ) of herring of age class  $a$ , and  $K_a$  is the energy content ( $\text{kJ g}^{-1}$ ) of an individual fish of age class  $a$ . Juvenile herring was defined as age 0+ to 2+ and adults as all herring age 3+ and over.

For marine bird population estimates ( $S$ ), species estimates and unidentified species group estimates (e.g., 'unidentified gull', 'unidentified loon') were obtained from 10 U.S. Fish and Wildlife Service (USFWS) surveys conducted in March over a period of 18 yr: 1990, 1991, 1993, 1994, 1996, 1998, 2000, 2004, 2005, and 2007 (McKnight *et al.*, 2008; Table 1). All birds were assumed to reside in PWS from 15 November to 15 March ( $n = 120$  days) except Black-legged kittiwake (*Rissa tridactyla*). Our survey data from November 2007 through March 2009 found that Black-legged kittiwake are few or absent from PWS during mid-winter months (mid-December through mid-February), therefore their residency time was adjusted to 60 days.

Diet composition in winter is not readily available for marine birds in Alaska. Therefore, the proportion of herring in the daily diet for the 18 piscivorous species was estimated based on available literature from other regions (Gillespie and Westrheim, 1997) and our own observations made during surveys for marine birds over two winters (M.A. Bishop and K.J. Kuletz, unpubl. data) (Table 1). To account for our uncertainty in these estimates, high variability in parameter estimates were set for the consumption model. Small marine birds such as Red-necked grebe (*Podiceps grisegena*), Horned grebe (*Podiceps auritus*), Mew gull (*Larus canus*), Black-legged kittiwake, Pigeon

**Table 1.** Minimum and maximum population estimates from 10 yr of March marine bird surveys and model input mean values for body mass (kg), proportion of herring in diet, and proportion of herring by age class (adult or juvenile). Unidentified (Unid.) loons, grebes, mergansers, murrets and murrelets are assigned model inputs for the most common species in their respective genera. Population estimates from U.S. Fish and Wildlife Service surveys (McKnight *et al.*, 2008).

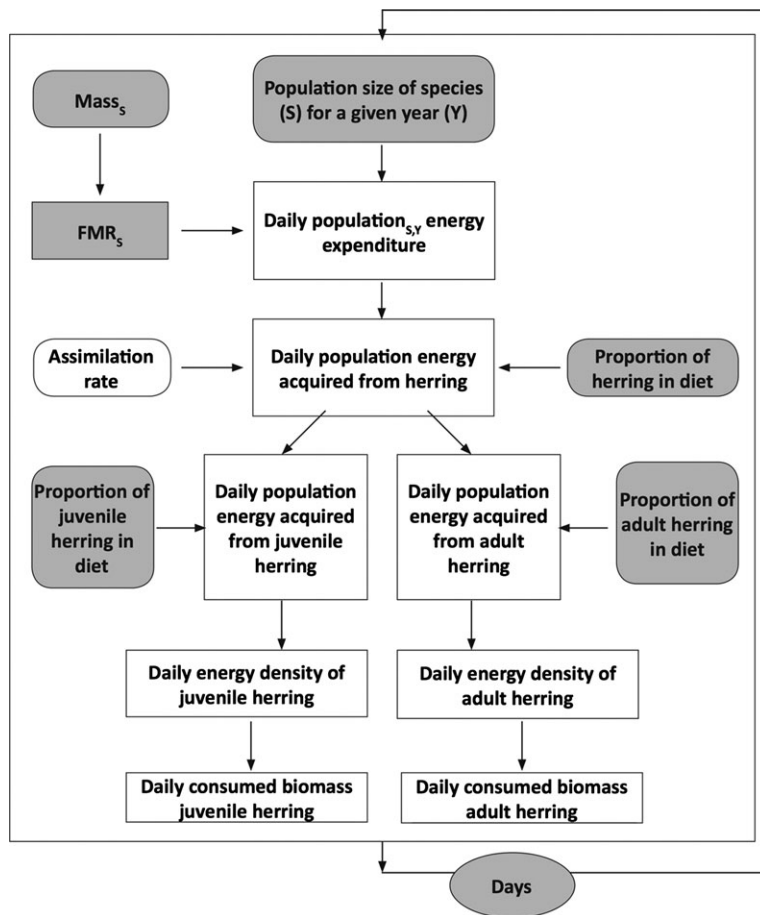
Species	Population range (n = 10)	Body mass (kg) ± SD	Body mass source*	Prop. herring <sup>†</sup>	Prop. adult herring	Prop. juvenile herring
Common loon, <i>Gavia immer</i>	67–2390	4.98 (1.0)	3, 5	0.5	0.7	0.3
Yellow-billed loon, <i>G. adamsii</i>	23–206	4.00 (1.2) <sup>‡</sup>	3	0.5	0.7	0.3
Red-throated loon, <i>G. stellata</i>	0–90	1.52 (0.1)	3	0.5	0.7	0.3
Pacific loon, <i>G. pacifica</i>	0–1437	1.67 (0.1)	3, 11	0.5	0.7	0.3
Unid. loon, <i>Gavia</i> spp.	357–1618	1.67 (0.5)		0.5	0.7	0.3
Red-necked grebe, <i>Podiceps griseogen</i>	572–2571	1.22 (0.2)	3, 13	0.25	0	1.0
Horned grebe, <i>P. auritus</i>	400–3863	0.45 (0.04)	3, 12	0.25	0	1.0
Unid. grebe, <i>Podiceps</i> spp.	135–4209	0.45 (0.04)		0.25	0	1.0
Red-faced cormorant, <i>Phalacrocorax urile</i>	0–458	1.85 (0.1)	2	0.25	0.5	0.5
Double-crested cormorant, <i>P. auritus</i>	124–1041	1.83 (0.1)	6	0.25	0.5	0.5
Pelagic cormorant, <i>P. pelagicus</i>	590–10 958	1.8 (0.5)	3, 7	0.25	0.5	0.5
Unid. cormorant, <i>Phalacrocorax</i> spp.	277–12 431	1.8 (0.5)		0.25	0.5	0.5
Common merganser, <i>Mergus merganser</i>	1171–20 641	1.4 (0.5)	3, 9	0.3	0.1	0.9
Red-breasted merganser, <i>M. serrator</i>	231–7824	0.9 (0.1)	3, 14	0.3	0.1	0.9
Unid. merganser, <i>Mergus</i> spp.	80–6463	0.9 (0.1)		0.3	0.1	0.9
Herring gull, <i>Larus argentatus</i>	60–2031	1.02 (0.1)	4	0.1	0.2	0.8
Glaucous-winged gull, <i>L. glaucescens</i>	8442–42 479	1.33 (0.5)	1	0.2	0.2	0.8
Mew gull, <i>L. canus</i>	1761–29 712	0.45 (0.2)	1	0.1	0	1.0
Black-legged kittiwake, <i>Rissa tridactyla</i>	157–15 903	0.43 (0.1)	3	0.2	0	1.0
Unid. gull <sup>§</sup>	546–18 546	1.33 (0.5)		0.2	0.2	0.8
Unid. gull <sup>§</sup>	546–18 546	0.45 (0.2)		0.1	0	1.0
Unid. gull <sup>§</sup>	546–18 546	0.43 (0.1)		0.2	0	1.0
Common murre, <i>Uria aalge</i>	4863–157 176	0.99 (0.1)	3	0.5	0.5	0.5
Unid. murre, <i>Uria</i> spp.	426–63 528	0.99 (0.1)		0.5	0.5	0.5
Marbled murrelet, <i>Brachyramphus marmoratus</i>	3144–29 193	0.22 (0.04)	3, 8, 10	0.5	0	1.0
Unid. murrelet, <i>Brachyramphus</i> spp.	1309–18 351	0.22 (0.04)		0.5	0	1.0
Pigeon guillemot, <i>Cephus columba</i>	810–2842	0.49 (0.1)	3	0.2	0	1.0

\*Data sources for mass: <sup>1</sup>Bishop and Green (2001); <sup>2</sup>Causey (2002); <sup>3</sup>Dunning (2007); <sup>4</sup>Evans *et al.* (1995); <sup>5</sup>Evers *et al.*, 2010); <sup>6</sup>Hatch and Weseloh (1999); <sup>7</sup>Hobson (1997); <sup>8</sup>Kuletz (2005); <sup>9</sup>Mallory and Metz (1999); <sup>10</sup>Nelson (1997); <sup>11</sup>Russell (2002); <sup>12</sup>Stedman (2000); <sup>13</sup>Stout and Nuechterlein (1999); <sup>14</sup>Titman (1999).

<sup>†</sup>Proportion estimate based on Gillespie and Westrheim (1997) and PWS survey observations (M.A. Bishop and K.J. Kuletz, unpubl. data).

<sup>‡</sup>Standard deviation was calculated using an available sample size of four individuals.

<sup>§</sup>For each survey year, unidentified gull population estimates were divided by three, with each population estimate assigned body mass and diet inputs corresponding to Glaucous-winged gull (one-third of all unidentified gulls), or Mew gull (one-third) or Black-legged kittiwake (one-third).



**Figure 1.** Model schematic for winter Pacific herring consumption by 18 marine bird species in Prince William Sound. Round-cornered rectangles indicate inputs sampled from a distribution. Shaded boxes indicate species-specific model inputs. All values within the box were iterated for each day.

guillemot (*Cepphus columba*) and Marbled murrelet cannot consume adult herring, so the mean proportion of adult herring consumed was assumed to be 0. Large marine birds such as loons can target larger (>200 mm) adult herring (Vermeer and Ydenberg, 1989), so we estimated a higher proportion of adult herring than juvenile herring in their diet. For Common murre and other medium-sized birds such as cormorants, we estimated equal proportions of adult and juvenile herring (Table 1). Common murre consume a wide range of herring sizes (75–276 mm total length (TL); Ouwehand *et al.*, 2004), but prefer herring with body depths <40 mm (Swennen and Duiven, 1977). PWS herring ranging from age 0+ to 9+ fall within this TL size range (Alaska Department Fish and Game, unpubl. data), and body depths <40 mm have been recorded during winter months in PWS adult herring as large as 236 mm TL (~ age 5+; this study). Estimated proportions reflect the amounts of  $\text{kJ day}^{-1}$  acquired from juvenile and/or adult herring.

To calculate  $E_a$ , the daily energy requirement ( $\text{kJ day}^{-1}$ ) from herring age class  $a$ , the total daily energetic expenditure (field metabolic rate),  $F$

( $\text{kJ day}^{-1}$ ), for an individual bird was determined using allometric equations formulated by Birt-Friesen *et al.* (1989). For gulls and kittiwakes, the equation for seabirds using flapping flight in cold waters was applied:  $\log F = 3.24 + (0.727 \times \log x)$ , where  $x$  is body mass (kg). For the remaining species the equation  $\log F = 3.13 + (0.646 \times \log x)$  was used for seabirds in cold waters. Body mass data was obtained for each species (Table 1) from records within Alaska and PWS when available. Otherwise, body mass data were obtained from Dunning (2007) and the respective *Birds of North America* species account. The  $E_a$ , daily energy requirement ( $\text{kJ day}^{-1}$ ) for herring of age class  $a$  was calculated as:

$$E_a = (F/0.75) \times (H \times P_a)$$

where  $F$  is the total daily energy requirement, 0.75 is the assumed assimilation rate (Furness and Tasker, 1997),  $H$  is the proportion of herring in the diet, and  $P_a$  is the proportion of each age class of herring.

Herring energy density ( $K$ ) declines over winter (Foy and Paul, 1999) but varies with age. The following linear equations were used to calculate the energy

density ( $\text{kJ g}^{-1}$ ) of an adult herring ( $K_a$ ) (R. Heintz, Auke Bay Laboratories, NOAA, U.S.A., pers. comm.) and a juvenile herring ( $K_j$ ) (T. Kline, Prince William Sound Science Center, U.S.A., pers. comm.) on a given day:

$$K_a = (9.64 - 0.0199 \times d)$$

$$K_j = (5.67 - 0.0108 \times d)$$

Where  $d$  = days since 15 September (for adult herring) and  $d$  = days since 15 November (for juvenile herring). Differences in start date for juvenile and adult herring are based on the timing during which adult and juvenile herring were captured and analyzed in their respective bioenergetics studies.

To account for uncertainty in our parameter estimates, a Monte Carlo simulation approach was used. For each species and for each survey year, 1000 model simulations were run (Fig. 1). All analyses were performed using R (version 2.12.2; R Development Core Team, 2011). Input parameters for marine bird body mass and species population in PWS were assigned lognormal distributions. To accommodate the high uncertainty about the actual amounts of herring in winter diets, the distributions of: (i) proportion of herring and (ii) proportion of adult herring in the diet, were assigned uniform distributions with maxima and minima at their nominal value (Table 1)  $\pm 0.25$  and bounded between 0 and 1. However, if the proportion of adult herring was assigned a value of 0 (Table 1; e.g., Black-legged kittiwake), the parameter value was fixed at 0 and not sampled from a distribution. For all species, proportion of juvenile herring was then calculated as the remainder of herring in the diet. Assimilation efficiency was assigned a beta distribution whose shape parameters were based on a mean of 0.75 and a standard deviation of 0.025 (Roby *et al.*, 2003).

For unidentified loons, grebes, mergansers, murres and murrelets, model inputs were used for the most common species in that group. For example, Thick-billed murre (*Uria lomvia*) and Kittlitz's murrelet (*Brachyramphus brevirostris*) are rare in PWS during winter, therefore unidentified murres and murrelets were assigned the parameter inputs of common murre and marbled murrelet, respectively. For input distributions of gulls, one-third of unidentified 'gulls' from each survey were assigned to each of the three species: Glaucous-winged gull (*L. glaucescens*), Mew gull, and Black-legged kittiwake. The unknown gulls that were designated as Black-legged kittiwake were assigned a residency time of 60 days, consistent with that of identified Black-legged kittiwakes.

### Sensitivity analysis

Sensitivity of herring consumption model parameters were measured using a Monte Carlo error analysis method (Bartell *et al.*, 1986; Hunsicker and Essington, 2008). The consumption model was run 10 000 times and a parameter's influence on the model uncertainty was assessed using relative partial sums of squares (RPSS). In this method, consumption of juvenile and adult herring were each regressed against all model parameters (the full model) and the contribution of each model parameter on the total sum of squares was then determined by comparing the full model with a model that omits one parameter at a time. The difference in the total sum of squares between the full model and the model missing one parameter enables us to partition the total sum of squares among each model parameter. Thus the RPSS scores for all parameters sum to the total sum of squares, or  $r^2$ , for the full model (Rose *et al.*, 1991). Each parameter was assigned a nominal value equal to the mean of that parameter across all species and drawn randomly from the statistical distribution previously described for each parameter.

Model sensitivity was examined for coefficients of variation (CV) of 0.02, 0.10 and 0.20 for adult and juvenile herring consumption individually. Nominal parameter values ( $\mu$ ) were: population ( $\mu = 6\ 039$ ), bird mass ( $\mu = 1.185\ \text{g}$ ), proportion of herring in diet ( $\mu = 0.32$ ), proportion of adult herring in diet ( $\mu = 0.26$ ), daily energy requirement for seabirds in cold waters [ $\log \mu = 3.13 + (0.646 \times \log(\text{mass}))$ ], assimilation rate ( $\mu = 0.75$ ), juvenile herring energy content [ $5.67 - 0.0108 \times (\text{number of days since November 15})$ ] and adult herring energy content [ $8.4261 - 0.0199 \times (\text{number of days since September 15})$ ].

### Lag analysis

The potential impact of marine bird consumption in 1 yr on herring populations 1–5 yr later was investigated using linear regression models. Due to the relatively low number of data points in this analysis, correlations were expected to be highly subject to extreme values. During the 1992–93 winter, high numbers of Common murre were present, resulting in much higher consumption in that year. Thus the lag analysis was also performed while excluding 1992–93.

In the lag models, three metrics for herring abundance were used (Table 2). Miles of spawn and mile days of spawn were based on Alaska Department of Fish and Game (ADFG) aerial surveys (Botz *et al.*, 2010; S. Moffitt, ADFG, U.S.A., pers. comm.) and are indicative of spawning biomass. Estimates of adult

**Table 2.** Metrics used for lag analysis to indicate spawning biomass of adult herring.

Year	Miles of spawn (aerial survey) <sup>1</sup>	Mile days of spawn (aerial survey) <sup>*,†</sup>	Adult herring (tonnes) (acoustic estimate) <sup>‡,§</sup>
1990	94.1	164.4	NA
1991	58.0	71.5	NA
1992	74.7	119.8	NA
1993	20.4	50.3	18 812
1994	14.6	23.1	12 555
1995	20.4	28.2	12 070
1996	27.2	37.3	23 203
1997	42.7	64.3	37 400
1998	38.7	62.0	17 655
1999	25.4	40.7	17 301
2000	19.5	31.7	7280
2001	16.0	14.8	6330
2002	21.5	23.6	10 700
2003	25.2	26.1	23 200
2004	29.7	30.4	12 700
2005	29.9	31.7	20 100
2006	19.9	21.7	13 000
2007	NA	18.3	20 400
2008	NA	45.4	17 900
2009	NA	29.8	20 400
2010	NA	30.8	17 500

NA = Data not available.

<sup>\*</sup>1990–2009 data from Botz *et al.* (2010).

<sup>†</sup>2010 data from S. Moffitt (Alaska Department Fish Game, U.S.A., pers. comm.).

<sup>‡</sup>1993–2009 data from Thorne and Thomas (2008, 2011).

<sup>§</sup>2010 data from R. Thorne (Prince William Sound Science Center, U.S.A., pers. comm.).

herring biomass are taken from acoustic surveys in fall (1992 and 1993) or spring (1995–2010) (Thorne and Thomas, 2008, 2011; R. Thorne, PWS Science Center, U.S.A., pers. comm.) and represent a direct measure of spawning biomass. No reliable direct estimates of juvenile biomass exist for PWS herring so it was not possible to perform a lag analysis using juvenile biomass estimates. Miles of spawn or mile days of spawn are the closest potential indices of juvenile biomass in a given year but mortality in year 0 is likely too high (*cf.* Stokesbury *et al.*, 2002) for such comparison to be made.

## RESULTS

Total herring consumption by marine birds averaged  $2409 \pm 950$  t per year for the 10 winters (1989–90 through 2006–07). Consumption varied inter-annually with a maximum of  $4998 \pm 2140$  t during the 1992–93 winter and a minimum of  $865 \pm 228$  t in 1989–90,

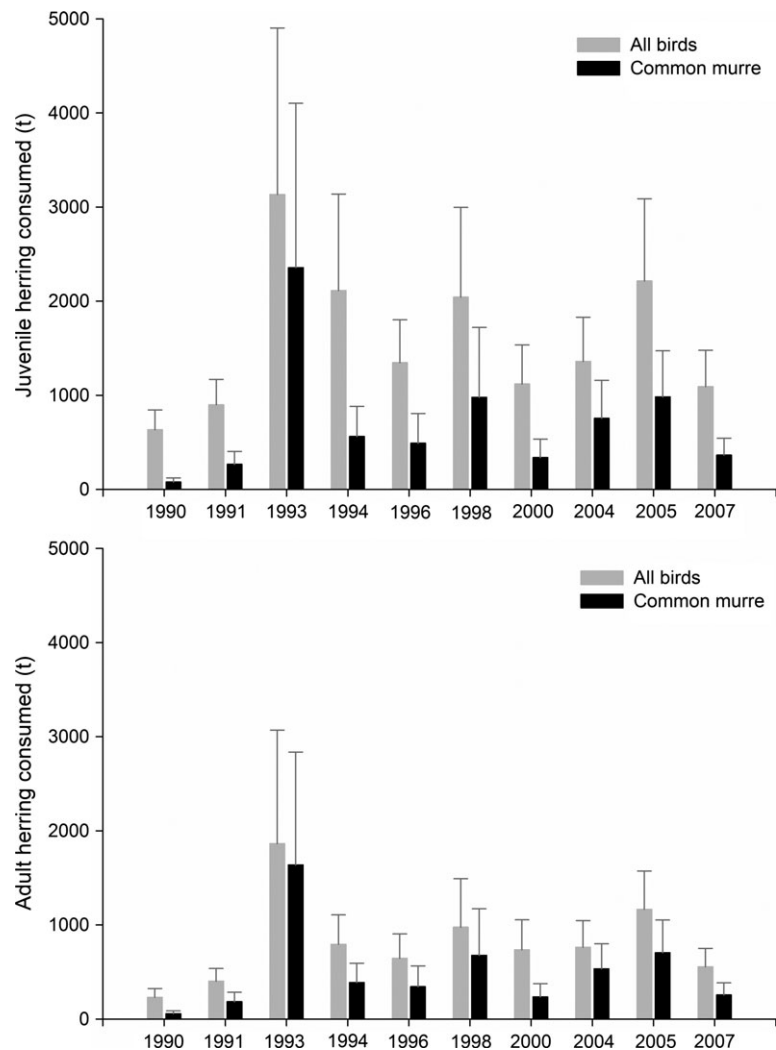
the first winter following EVOS. Marine birds consumed more juvenile ( $\bar{x} = 1596 \pm 820$  t) than adult ( $\bar{x} = 812 \pm 479$  t) herring in all winters (paired *t*-test,  $P < 0.001$ ; Fig. 2). The greatest difference (1319 t) between juvenile and adult herring consumption occurred during the 1992–93 winter, when Common murre made up the greatest proportion (72%) of the population.

Marine bird consumption was an important source of adult herring mortality. On average, 6.1% of the available adult herring biomass was consumed each winter. This estimate is exclusive of consumption during the winters 1990–91 and 1991–92, for which biomass estimates are unavailable. Our model showed that in winters with relatively low adult herring biomass, such as 1999–2000, or winters with relatively high numbers of marine birds, such as 1992–93, as much as 10% (1864 t) of the adult biomass can be removed by avian predators (Fig. 3). We were unable to estimate the proportion of juvenile herring removed as there was no data for total available juvenile herring.

Common murre (including unidentified murre) was the most abundant marine bird in PWS and the largest herring consumer. Murres constituted 10.7% ( $7439 \pm 2904$ ) to 72.3% ( $220\,704 \pm 160\,543$ ) of the winter marine bird population ( $\bar{x} = 36.8 \pm 17.2\%$ ,  $n = 10$ ). Murre consumption represented 15.7–79.9% ( $\bar{x} = 43.9 \pm 18.1\%$ ,  $n = 10$ ) of total herring biomass consumed by marine birds. In eight of the 10 winters, murres consumed the most adult herring ( $\bar{x} = 501 \pm 449$  t). Common murre was also the largest consumer of juvenile herring ( $\bar{x} = 718 \pm 656$  t) (Fig. 2). Among the other marine bird species, Glaucous-winged gull was the second largest consumer of juvenile herring during all winters ( $\bar{x} = 324 \pm 490$  t). Pelagic cormorant (*Phalacrocorax auritus*) and common loon (*Gavia immer*) were the largest consumers of adult herring during 1989–90 and 1999–2000 winters, respectively (Fig. 4).

### Sensitivity analysis

The full models for juvenile and adult herring consumption revealed decreasing  $r^2$  values as the CVs were increased from 0.02 ( $r^2 = 0.998$  for both juvenile and adult herring) to 0.20 ( $r^2 = 0.639$  for adults and  $r^2 = 0.648$  for juveniles), indicating an increasing degree of non-linearity with increasing CV. For both juvenile and adult herring consumption, the RPSS score for each model parameter decreased as the CV was increased (Fig. 5) with the exception of assimilation efficiency, which increased for both juvenile and adult herring consumption.



**Figure 2.** Winter consumption of juvenile herring (above) and adult herring (below) by all marine birds compared with Common murre (including unidentified murre) as estimated from Monte Carlo simulations. Winter = 15 November through 15 March; bars = mean herring consumption; error bars =  $\pm 1$  SD. Year on the x-axis corresponds to the previous–present year's winter (e.g., 1994 refers to winter 1993–94). No bird population estimates were available for 1992, 1995, 1997, 1999, 2001–2003 or 2006.

Model uncertainty for consumption of juvenile herring was most sensitive to changes in the proportion of herring in the diet and the assimilation rate, followed by the population size of a given bird species, the percent of the diet that was adult herring, and the daily energy requirement of a given bird species. Model uncertainty was negligibly sensitive to changes in bird mass and the daily herring energy content. Consumption of adult herring varied in the order of the first three parameters – percent of adult herring in the diet was followed by percent of total herring in the diet and then by assimilation efficiency. The remaining parameters followed a similar trend to that for juvenile herring consumption.

#### Lag analysis

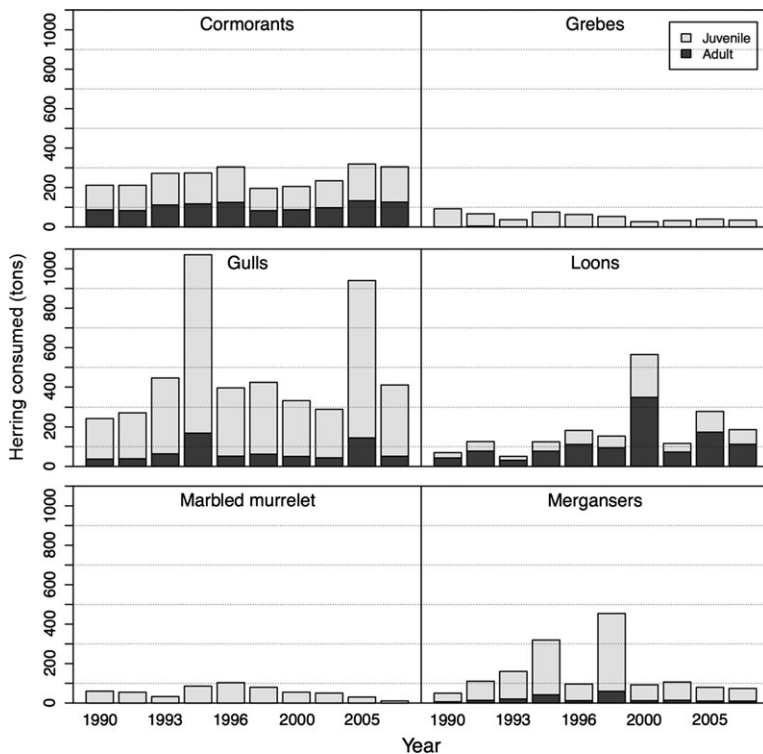
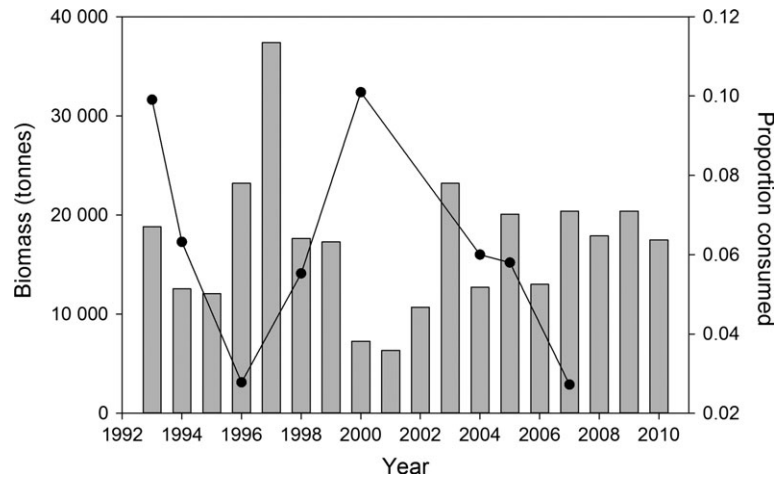
Lag analyses revealed significant negative correlations of 1–4 yr between marine bird herring consumption and subsequent spawning biomass. However, when the

1992–93 winter was excluded from these analyses, most results were not significant ( $P > 0.1$ ). However, several significant correlations did still exist. Consumption of adult herring was negatively correlated with miles of spawn ( $P = 0.015$ ,  $r^2 = -0.593$ ) and mile days of spawn ( $P = 0.05$ ,  $r^2 = -0.41$ ) 1 yr later (i.e., more consumption this year means less spawn next year). Two years after marine birds consumed adult herring, a negative correlation was also observed with mile days of spawn ( $P = 0.015$ ,  $r^2 = -0.54$ ). Marine bird consumption of juvenile herring showed a negative impact on miles of spawn ( $P = 0.049$ ,  $r^2 = -0.418$ ) 1 yr after juvenile herring were consumed.

#### DISCUSSION

This study demonstrates the importance of marine bird consumption as a source of herring mortality. The model showed that in winters with relatively low adult

**Figure 3.** Estimated proportion of adult herring biomass consumed by marine birds (dots) for eight survey years compared to available adult herring biomass (bars). Adult biomass estimates for 1993–2009 taken from Thorne and Thomas (2008, 2011); biomass estimate for 2010 from R. Thorne (Prince William Sound Science Center, U.S.A., pers. comm.).



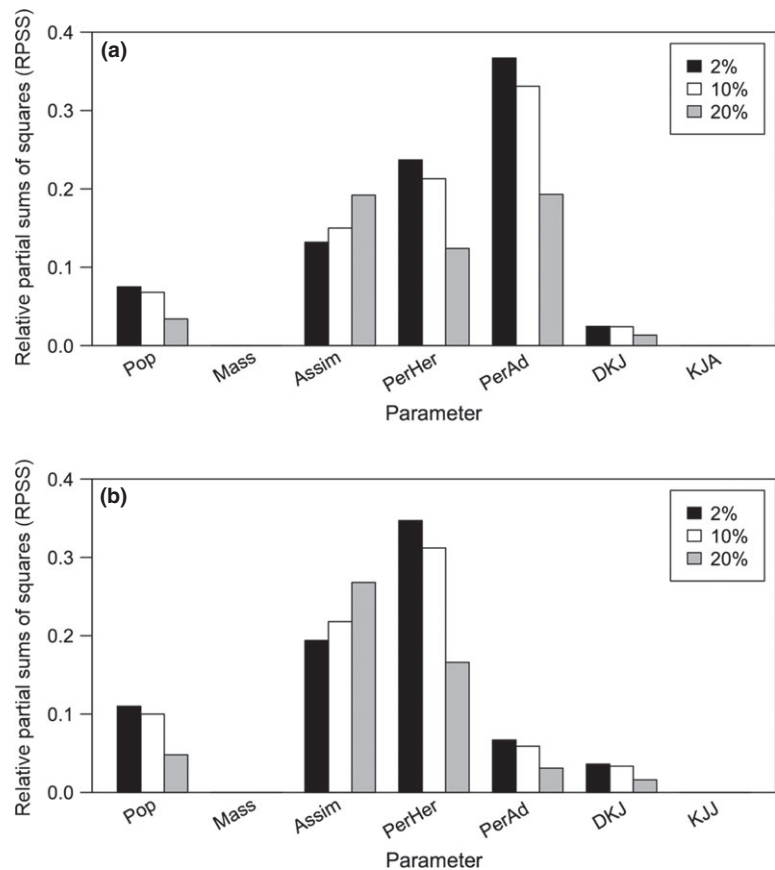
**Figure 4.** Pacific herring consumption (t) by major marine bird species or species groups in Prince William Sound during winter (15 November through 15 March). Consumption estimates are for 10 winters for juvenile (light grey) and adult (black) herring. Year on the x-axis corresponds to the previous–present year’s winter (e.g., 1994 refers to winter 1993–94). No bird population estimates were available for 1992, 1995, 1997, 1999, 2001–2003 or 2006.

herring biomass, or winters with relatively high numbers of marine birds, such as 1992–93, as much as 10% of the adult biomass and >3100 t of juvenile herring can be removed by avian predators. This is especially important because PWS herring populations have remained low since 1993 (Thorne and Thomas, 2011). While other Pacific herring populations along the west coast of the United States and Canada have

occasionally yielded large recruitment events from low levels of spawning biomass, PWS herring populations have historically not exhibited such patterns (Funk, 2007). This underscores the potentially large effect that predation could have on a population with poor recruitment (Bakun, 2006).

Pacific herring are the most abundant forage fish in PWS during winter (Stokesbury *et al.*, 2000). Juvenile





**Figure 5.** Relative partial sums of squares for model parameters of the herring consumption model. (a) Adult herring; (b) juvenile herring. Three coefficients of variation (CV) were used to test the sensitivity of average model parameter values: black, CV = 0.02; white, CV = 0.10; grey, CV = 0.20. *Pop*, bird population; *Mass*, bird mass; *Assim*, assimilation efficiency; *PerHer*, percent of herring in the diet; *PerAd*, percent of the herring diet that are adult herring; *DKJ*, daily energy budget for a species; *KJJ*, juvenile herring condition index; *KJA*, adult herring condition index.

herring overwinter at depths <30 m in bays and inlets (Stokesbury *et al.*, 2000), whereas adults tend to aggregate in deeper waters of more protected areas that are often close to major spring spawning locations (Thomas and Thorne, 2003). Common murre, the most abundant marine bird during winter in PWS, is capable of diving to depths of 180 m or more (Piatt and Nettleship, 1985). This diving ability allows murres to pursue and consume both juvenile herring and the typically deeper adult herring. Although the age composition of herring consumed by murres in PWS has not been verified, surveys conducted in PWS in two winters (November, January and March) recorded the highest densities of Common murre in and around historic spring spawning locations, indicative of adult herring overwintering areas (M.A. Bishop and K.J. Kuletz, unpubl. data). In addition, Thomas and Thorne (2003) regularly used flocks of Common murre as indicators of adult herring when selecting areas for adult herring hydroacoustic surveys.

With a diet composition estimated at 50% herring and populations that were often one to two orders of magnitude greater than other marine birds in PWS, Common murre consumed far more herring

than any other marine bird species in PWS in eight of the 10 winters. Furthermore, Common murre populations were highly stochastic, with a 10-yr average CV of 0.47, far greater than the CVs that were testable for other model parameters in our sensitivity analyses. This means that the high consumption of herring by murres is also unpredictable, or at least highly variable. For example, high overall herring consumption from all species during the 1992–93 winter was largely due to elevated numbers (~221 000) of Common and unidentified murre in PWS. That same winter, large flocks of murre numbering from the 100s to the 1000s, as well as a die-off of several thousand murre were observed in inshore waters throughout the northern Gulf of Alaska. Piatt and Van Pelt (1997) concluded that these murres likely originated from the Gulf of Alaska and moved inshore over the winter in response to reduced food availability in the Gulf associated with an El Niño Southern Oscillation event.

Years with high marine bird populations can reduce PWS herring populations. Alternatively, years with low herring biomass could result in the reduced

occurrence of herring schools as well as the density of schools and thereby reduce predator–prey encounter rates. In the Bering Sea, Benoit-Bird *et al.* (2011) found that for the closely related Thick-billed murre, murre patch selection was influenced by density of prey (krill) within a patch and its vertical accessibility (depth) rather than krill abundance within a patch or to the size of the patch. Prey depth, even for fish, was the main determinant of Thick-billed murre foraging behaviour (Benoit-Bird *et al.*, 2011). In PWS, Ainley *et al.* (2003) detected no relationship during the breeding season between densities of Black-legged kittiwake and forage fish schools visible at the surface (primarily herring and sand lance, *Ammodytes hexapterus*); however, they did find that the presence–absence of foraging kittiwakes was related to where forage fish schools were likely to occur. Because of the tendency for juvenile herring to concentrate in more shallow waters and for adult herring to concentrate in predictable areas near spawning areas (Stokesbury *et al.*, 2000; Thomas and Thorne, 2003), during winters with low herring availability in PWS marine birds may be able to consume herring in greater numbers than might have been expected on the basis of total biomass. Predator effects could be even more intensified for herring populations susceptible to disease outbreaks or other major perturbations, including oil spills.

Marine birds consumed more biomass of juvenile herring than adult herring; however, the percentage of juvenile herring consumed relative to the total biomass available can not be determined without estimates of total juvenile biomass in PWS. Avian predation on juvenile herring may exacerbate low juvenile survival, but the impact of avian consumption of juveniles on future herring recruitment is difficult to quantify. Nonetheless, our results suggest that predation by marine birds may have an important top-down effect on herring populations up to 2 yr after the consumption of adult herring. This result is consistent with the expected impact of removing individuals from a spawning population, as indicated by the reduced miles of spawn. The significant negative correlation between consumption of juvenile herring by marine birds and miles of spawn (an index of adult abundance) 1 yr later is likely due to a high degree of correlation between annual consumption of adult and juvenile herring by marine birds. However, 3–5 yr later, we would expect many extrinsic factors to have acted upon herring populations, and would not be likely to find linear relationships between herring consumption by birds and herring biomass (or spawn) at such time scales.

#### *Model uncertainty and future directions*

The present model is based on three key assumptions. First, it assigns all juvenile herring (age 0+ to 2+) an energetic equation associated with age 0+ herring, an age of reduced energetic condition but the only age for which a reliable energetic index for juveniles is currently available. Age 0+ herring provide lower energy content to marine birds and thus the assumption that all juveniles consumed were age 0+ biases the metabolic requirement towards higher avian consumption rates for juvenile herring.

In addition, the present model assumes that all individual birds have equal access to herring and that prey consumption is not density-dependent. Herring concentrate in localized regions within PWS and schools vary in density both seasonally and spatially. Because of the localized nature of herring schools, only a portion of the marine bird population is able to feed on herring at any given time. An individual's ability to feed on herring is limited by its ability to locate herring densities adequate for efficient food-finding and capture, its foraging ability, and the intra- and inter-specific competition. The decision to target a particular prey species and success in acquiring prey is at least partially a function of prey (Axelson *et al.*, 2001; Enstipp *et al.*, 2007) and predator densities. The extent to which marine birds and their co-predators in PWS switch target species when alternative prey are more available is not well documented, but these relationships would undoubtedly affect the biomass of herring consumed. In the Bering Sea in summer, Thick-billed murre abundance at a 'regional' scale was correlated with total prey abundance and vertical accessibility, but not with any single prey species (Benoit-Bird *et al.*, 2011). Similarly, Common murre in PWS may be drawn to regions within PWS because of overall prey diversity and availability, but could then target an energy-dense prey such as herring.

Our sensitivity analyses showed that model uncertainty was most sensitive to changes in the amounts of herring (and adult herring) in bird diets, the assimilation efficiency, the population size, and the daily energy requirement for a given species but was least sensitive to changes in the mass of the bird and the energy content of the herring themselves. Taking into consideration the role of input distributions on model sensitivity, our results underscore the importance of improving estimates for the proportions of adult and juvenile herring in seabird diets. Both herring diet parameters are at present incorporated with uniform distributions, which provide little statistical basis for choosing a particular parameter estimate. Because most marine birds swallow their prey while under

water, the majority of diet information on marine birds is from the summer months, when birds are more easily observed feeding their young at the colony.

Currently there is a dearth of information on seabird diets during the winter. Diet composition in winter has not been studied for marine birds in PWS and little is known about winter diets of marine birds in other parts of the Gulf of Alaska. Roughly 300 km west of PWS at Kachemak Bay, diets of Common murre and Marbled murrelet during the 1977–78 winter were dominated by mysids and capelin (*Mallotus villosus*), respectively, herring being recorded in the diet of Common murre but not Marbled murrelet (Sanger, 1987). In PWS, Marbled murrelet diets in summer were documented over several decades. Murrelet diets changed from being dominated by Pacific sand lance in the 1970s to being dominated by Pacific sand lance and walleye pollock (*Gadus chalcogrammus*) in the late 1980s (Kuletz *et al.*, 1997) and in the 1990s by sand lance and Pacific herring (Suryan *et al.*, 2002; Kuletz, 2005). Our Monte Carlo and sensitivity analyses determined as much as 20% variability in the diet proportions, but zooplankton or other prey dynamics could potentially result in even higher degrees of variability in the case of environmental anomalies, inter-decadal climate oscillations, or catastrophic events such as an oil spill. Further empirical data on seabird diets will improve our estimates of composition variability and the probabilistic assumptions employed regarding such parameters.

With the exception of Black-legged kittiwake, the bird population estimates in our model do not reflect within-season variability; all population data came from March surveys. In some instances, however, higher numbers of birds (e.g., the Marbled murrelet) occur early in winter and decline by March, whereas the opposite trend of higher numbers in March than November have been observed for Common murre. For Glaucous-winged gull, March populations have varied dramatically, with lower numbers associated with birds departing PWS for the Copper River Delta to forage on spring-spawning Pacific eulachon (*Thaleichthys pacificus*; M.A. Bishop and K.J. Kuletz, unpubl. data).

#### Management implications

We examined 18 marine bird species that occur in PWS in winter and that forage on herring. The predominant avian predator on herring in PWS in winter is the Common murre, and this species exhibits dramatic inter-annual variation in abundance which affects its impact on the herring population. Species such as the Marbled murrelet are currently at low levels relative to historic population sizes (Kuletz *et al.*,

2011). In the case of murrelets, an increase in population size to historic levels would undoubtedly increase consumption of juvenile herring, which appears to be a preferred prey of murrelets.

Although marine birds may consume a proportion of the herring population, they represent only one group of predators in PWS. Predatory fish such as the abundant Pacific cod (*Gadus macrocephalus*) forage on herring of a range of sizes (M.A. Bishop and S.P. Powers, unpubl. data). Steller sea lions (*Eumetopias jubatus*) and humpback whales (*Megaptera novaeangliae*) feed extensively on Pacific herring (Thomas and Thorne, 2001, 2003; Rice *et al.*, 2010). In addition to consuming large quantities of Pacific herring, humpback whales and other marine mammals can facilitate forage flocks and marine bird foraging efficiency (Obst and Hunt, 1990; Thomas and Thorne, 2001). A better understanding of levels of predation by these multiple predator groups, and their potentially synergistic effects on herring mortality, will help to refine mortality estimates within herring population models used in fishery management.

The consumption model used showed that during some winters, marine birds consume up to 10% of the annual adult herring biomass. This suggests that marine birds are important top-down inhibitors of herring recovery. Nevertheless, when establishing future herring fishing quotas or managing herring stocks, consumption by marine birds should be taken into account in order to ensure sufficient herring prey for birds. Based on a series of studies that included the northern Gulf of Alaska, Cury *et al.* (2011) recommended at least one-third of forage fish stocks be set aside as a minimum fish biomass to sustain long-term seabird productivity. As marine bird consumption estimates from our model do not exceed the recommended minimum biomass, we agree that fish managers should reserve one-third of forage fish biomass for marine birds.

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