

Consumption of Pacific herring (*Clupea pallasii*) eggs by greenling (Hexagrammidae) in Prince William Sound, Alaska

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Predation is an important process regulating egg survival in marine systems (Bailey and Houde, 1989). Pacific herring (*Clupea pallasii*) spawn demersal adherent eggs on shallow subtidal and intertidal substrates. Consequently, their eggs are available to a variety of predators throughout incubation. Documented predators of herring eggs include birds, invertebrates, marine mammals, and fish (Palsson, 1984). Avian predators were responsible for over 95% of the herring eggs lost in the intertidal zone in Holmes Harbor, Washington, in 1946 (Cleaver and Frannett, 1946), 39% of the intertidal herring eggs lost on the west coast of Vancouver Island from 1947 to 1950 (Outram, 1958), and 70% of the herring eggs lost in Yaquina Bay, Oregon, in 1970 (Steinfeld, 1971). Estimates of egg predation by birds at two sites in British Columbia in 1988 and 1989 were 3.0% and 3.5% of the total eggs deposited by herring (Haegle and Schweigert, 1989; 1991).

Much less is known about the effects of other predators because studies to quantify Pacific herring egg loss from predators other than birds have been rare. In Barkeley Sound, British Columbia, predation by invertebrates accounted for 13.0% of the total herring eggs deposited, whereas gray whales consumed 3.0% of the total eggs deposited (Haegle and Schweigert, 1989). In 1989, herring egg loss due to epibenthic invertebrates was 4.1% of the total eggs spawned in Georgia Strait, Brit-

ish Columbia (Haegle and Schweigert, 1991).

Fish predation on Pacific herring eggs has not been studied in the northeast Pacific, although some studies have been done on the deeper-spawning Atlantic herring (*Clupea harengus*). Historically, abundance of North Sea haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*) with stomachs containing Atlantic herring eggs were used as indicators of the concentrations of herring eggs (Hempel and Hempel, 1971); in years of light spawning, cod and haddock can consume up to 60% of the total eggs deposited.¹ Stomachs of sand eels (*Ammodytes marinus*) have been observed to be full of Atlantic herring eggs (Rankine and Morrison, 1989), and perch (*Perca fluviatilis*) has been found to be the most important consumer of herring eggs in the Archipelago Sea (Rajasilta et al., 1993). For Atlantic herring off the coast of Norway, egg loss due to haddock consumption has been estimated at 4.2% of the total eggs spawned (Toreson, 1991). Total Atlantic herring egg loss due to consumption by winter flounder (*Pseudopleuronectes americanus*) was at least 7% of the total egg abundance at a site in the Northwest Atlantic (Tibbo et al., 1963).

¹ Johannessen, A. 1980. Predation on herring (*Clupea harengus*) eggs and young larvae. International Council for the Exploration of the Sea, Council Meeting/1980, H:33, 12 p.

Lack of knowledge about fish predation on Pacific herring eggs and the importance of herring as a forage fish in the Northeast Pacific Ocean, led us to study predation on herring eggs in Prince William Sound, Alaska. The objective of our study was to estimate total consumption of herring eggs by some fish predators with the Elliot-Persson model (Elliot and Persson, 1978).

Materials and methods

Our study was conducted after herring spawning was completed on northern Montague Island in Prince William Sound, Alaska (Fig. 1), during late April and early May, 1995. Two variable mesh gill nets, 30.5 m long and 2.4 m deep, were used to collect fish near incubating herring eggs in the subtidal and intertidal zones at eight transects. Stretched-mesh sizes ranged from 2.5 to 12.7 cm. Panels of same-size mesh were equal length and depth (6.1 m × 2.4 m), and a total of five panels per net were used. A standardized fishing plan was carried out from one to three transects per day. Two nets were set at the bottom parallel to the shoreline at each transect. Depths fished depended on tide stage; at high tide, depths fished were 0.0 m and -3.0 m, whereas at low tide, depths fished were -1.5 m and -3.0 m in relation to mean low water. Logistical constraints limited fishing to one series of gillnet samples centered around the daylight high tide, and one series of samples centered around the daylight low tide. Each series consisted of three one-hour sets of the two nets, for a total of six gillnet sets over each tide stage, and a total of 96 sets equally spread over the eight transects.

Fish captured were identified by species and measured for fork length. Time of catch, net soak time, and tide stage were also recorded for each fish. Fish stomachs were removed and preserved in 10% buffered formalin. Stomach contents were categorized by type of prey (herring eggs, vegetation, crustaceans, etc.) and weighed to the nearest 0.01 g. Wet weights of each group of stomach contents were recorded, and herring eggs were subsampled to determine the

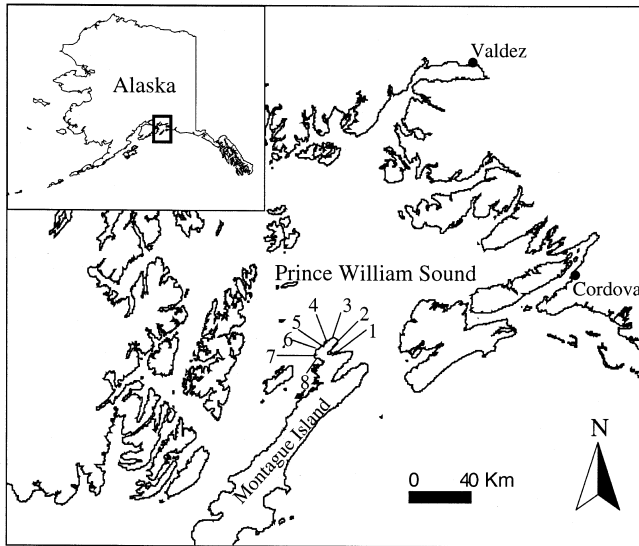


Figure 1

Study transects on Montague Island in Prince William Sound, Alaska, where gill nets were used to collect fish predators of herring spawn in 1995.

number of eggs per g. By multiplying the wet weight of herring eggs contained in each stomach by the number of eggs per g, the total number of herring eggs in each stomach was estimated.

Based on stomach-content analysis, estimates of daily ration were calculated only for greenling species. Because of the small number of each greenling species caught, these species were combined to estimate herring egg consumption. Estimates of daily ration were calculated by using the Elliot and Persson (1978) model,

$$C_t = \frac{(S_t - S_0 e^{-Rt}) \times Rt}{1 - e^{-Rt}}, \quad (1)$$

where C_t = food consumption during daylight hours;
 R = the calculated gut clearance rate;
 t = the number of daylight hours; and
 S_0 and S_t = average stomach contents at time 0 and time t , respectively.

Estimates of stomach contents were obtained by examining fish caught during gillnet sampling and were assumed to be constant over daylight hours. The gut clearance rate (R) was calculated from a relationship of species evacuation rate versus temperature for marine and freshwater fish:

$$R = 0.0175T - 0.0442 \quad (\text{Worobec, 1984}). \quad (2)$$

The average temperature (T) over the incubation period at a Montague Island transect was used in Equation 2. We had to extrapolate the equation in Worobec (1984) because their temperature range was warmer than ours. Initial consump-

tion of food at the onset of daylight was calculated according to the Elliot-Persson model by using the equation

$$C_{\text{initial}} = S_{\text{average}} - S_0 e^{-Rt}, \quad (3)$$

where S_{average} = the average eggs per stomach from gill-net samples; and
 t = the nighttime hours.

Adding C_{initial} and C_t gives an estimate of the daily consumption (C_d) of herring eggs over 24 h. Total consumption over the incubation period was then calculated by

$$C_{\text{total}} = C_d \times D \times I, \quad (4)$$

where C_d = the calculated daily consumption in numbers of eggs;
 D = predator density; and
 I = length of the incubation period in d.

Two previous studies estimated nearshore fish abundance on Montague Island. The first study estimated greenling density by using SCUBA surveys (Jewett et al.²) and the second study estimated nearshore fish biomass (Rosenthal³). We used both these estimates in separate calculations of Equation 4 to derive consumption estimates for greenling.

In the first calculation we used greenling density estimates in the subtidal zone from Jewett et al. (1995); total consumption per m² was compared directly with the average number of eggs per m² estimated in 1995. To use the biomass estimates from Rosenthal (1980), we changed the daily ration in egg numbers to a daily ration in egg biomass. Assuming isometric growth for greenling and using the end points of greenling length and weight ranges reported in Rosenthal (1980), we calculated the weight of each greenling caught during gillnet sampling. Using these two calculations for each fish sampled, we then estimated the daily ration as a percentage of body weight. Then, incorporating biomass estimates for greenling in Prince William Sound from Rosenthal (1980) and the number of incubation days for herring eggs in 1995, we calculated the total weight of eggs consumed per km² by converting Equation 4 to

$$C_t = B_g \times C_w \times I, \quad (5)$$

² Jewett, S. C., T. A. Dean, R. O. Smith, M. Stekoll, L. J. Halderson, D. R. Laur and L. McDonald. 1995. The effects of the *Exxon Valdez* oil spill on shallow subtidal communities in Prince William Sound, Alaska 1989–93. *Exxon Valdez Oil Spill Restoration Project Final Report* (Restoration Project 93047; subtidal study number 2A), Alaska Dept. of Fish and Game, Habitat and Restoration Division, Anchorage, Alaska, 178 p.

³ Rosenthal, R. J. 1980. Shallow water fish assemblages in the northeastern Gulf of Alaska: habitat evaluation, species composition, abundance, spatial distribution and trophic interaction. In *Environmental assessment of the Alaskan continental shelf*, p. 451–540. Final reports of principal investigators, 17: biological studies, NOAA/NOS, Office of Oceanography & Marine Services.

Table 1

Total gillnet hours fished and mean catch per hour for each fish species captured at Montague Island, Alaska, in 1995. Numbers in parentheses indicate total number of fish captured during sampling.

Transect	Hours fished	Catch (no. of fish) per hour				
		Greenling (two species)	Dolly Varden	Starry flounder	Red Irish lord	Great sculpin
1	13:48	(0)	0.435 (6)	0.072 (1)	(0)	(0)
2	14:26	(0)	0.069 (1)	(0)	(0)	(0)
3	13:28	0.446 (0)	(0)	(0)	(0)	(0)
4	13:52	0.072 (1)	(0)	(0)	(0)	0.072 (0)
5	13:32	0.296 (4)	(0)	(0)	0.074 (1)	0.074 (1)
6	12:15	0.082 (1)	(0)	(0)	(0)	(0)
7	14:34	0.069 (1)	0.069 (1)	(0)	(0)	(0)
8	14:39	(0)	(0)	(0)	(0)	0.068 (1)
Average CPUE		0.120 (13)	0.072 (8)	0.009 (1)	0.009 (1)	0.027 (1)

where C_t = the total biomass of eggs consumed per km²;

B_g = the biomass of greenling;

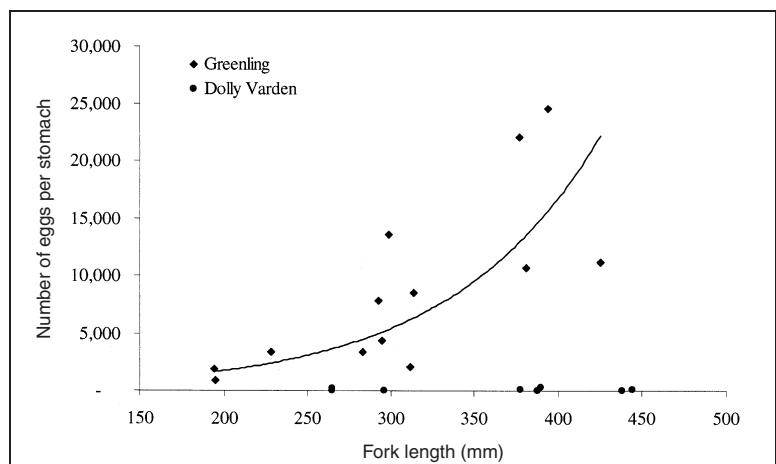
C_w = the daily ration as a percentage of fish weight; and

I = the length of the incubation period in d.

This estimate of egg biomass consumed was applied to the biomass estimates of eggs spawned on Montague Island to obtain a percentage of the total herring eggs consumed by greenling.

Results

Six fish species were caught during gillnet sampling: rock greenling (*Hexagrammos lagocephalus*), kelp greenling (*Hexagrammos decagrammus*), Dolly Varden char (*Salvelinus malma*), starry flounder (*Platichthys stellatus*), red Irish lord (*Hemilepidotus hemilepidotus*) and great sculpin (*Myoxocephalus polyacanthocephalus*). The most common fish caught were the two greenling species, followed by Dolly Varden and great sculpin; only one red Irish lord and one starry flounder were caught. Average catch for all species was relatively low, ranging from 0.009 fish per h (SE=0.008) for starry flounder and red Irish lord to 0.120 fish per h (SE=0.052) for the greenling species combined (Table 1). Only greenling and Dolly Varden consumed herring eggs; all 13 greenling stomachs contained eggs, whereas just 4 of 8 Dolly Varden stomachs contained eggs. Stomachs of other fish species contained a combination of unidentifiable fish and invertebrates. The average number of eggs per stomach was 87 (SE=40.4) for Dolly Varden, and 8785 (SE=2107.6) for greenling. The number of herring eggs

**Figure 2**

Number of eggs per stomach for combined greenling species ($n=13$) and Dolly Varden char ($n=8$) captured by gillnetting at herring spawning bed transects in 1995. The line represents the predicted exponential increase in eggs per stomach with increasing fork length; r^2 for the predicted versus the observed relationship was 0.55.

per greenling stomach increased exponentially with length (Fig. 2).

A pattern in greenling and Dolly Varden catch distributions was apparent; Dolly Varden were caught exclusively in embayments, whereas all greenling, except one, were caught on the outer coast of Montague Island. The average temperature during incubation at -1.5 m depth was 5.8°C at transect 4, resulting in an estimated instantaneous evacuation rate of 0.057 per h. The daily ration calculated with that evacuation rate was 11,984 eggs per d (Table 2).

Subtidal surveys of fish abundance in Prince William Sound found an average of 0.0889 greenling per m² on

Table 2

Calculations for estimating daily consumption of herring eggs by greenling with the Elliot-Persson model.

Elliot-Persson model for estimating daily consumption (Eq. 1)	
1 Consumption during daylight hours (assuming constant stomach fullness), C	
t = average daylight hours from 29 April to 20 May 1995	16.67
Instantaneous evacuation rate (R)	0.057
S_0	9264
S_t	9264
C_t	8816
2 Initial consumption at onset of feeding, $C_{initial}$	
Decrease in stomach contents during night, $S_t = S_0 e^{-Rt}$	
S_0	9264
t = average nighttime hours from 20 April to 20 May 1995	7.33
Instantaneous evacuation rate (R)	0.057
S_t	6096
$C_{initial} = S_0 - S_t$	3168
3 Total consumption over 24 hours = $C_{initial} + C_t$	11,984

island points in shallow waters from 2 to 20 m deep on Montague Island (Jewett et al., 1995). According to the daily ration calculated above, daily consumption of herring eggs by greenling would be 1065 eggs per m^2 . In 1995, the incubation period for herring eggs was 21 d in Prince William Sound; therefore total removal during incubation would have been 22,373 eggs per m^2 . In 1995, the average number of eggs per m^2 was 606,831, on Montague Island.⁴ Therefore, using the daily consumption above, we estimated that 3.7% of the eggs deposited were consumed by greenling over the course of incubation.

The weight of the estimated daily ration (11,984 eggs) for greenling was 38.3 g, or weight of the eggs in a greenling stomach multiplied by 1.29. From this conversion factor, daily ration as a percentage of greenling body weight was estimated as 6% per d. Results from dive surveys from Rosenthal (1980) have shown a greenling biomass at Zaikoff Point on Montague Island of approximately 35,000 kg/ km^2 . Multiplying this biomass estimate by the daily ration as a percentage of body weight and by the number of incubation days in 1995, yields an egg consumption estimate of 44,100 kg/ km^2 . In 1995, an estimated 5,922,673 kg of eggs were deposited over a 3.05- km^2 area on Montague Island.² If one assumes that all greenling move into subtidal and intertidal areas to feed on eggs deposited there, then greenling would have consumed 2.3% of the total eggs deposited.

Discussion

Calculation of daily ration by the Elliot-Persson method presented here assumes that greenling maintain a full stomach throughout the entire daylight period. The exponential increase in eggs per stomach with greenling length suggests that our assumption that greenling maintain a constant state of gut fullness is correct because greenling stomach volume should increase exponentially with body length. Our method for estimating total consumption of herring eggs by greenling also assumes that there is no numerical response to availability of eggs. If greenling move from deeper water to the band of herring eggs, the estimate of consumption may be higher. Migration of greenling to the spawning beds from areas where no spawn was deposited would also have increased the consumption estimate.

By sampling during slack tide periods, total consumption of eggs may have been underestimated. If greenling were actively feeding during the time when they encountered gill nets, their stomach contents may not have been representative of the entire daylight period. Greenling stomach contents may have been less during times of active feeding than during the rest of the day. Gill nets are also known to be both size selective and species selective (Hay et al., 1986; Methven and Schneider, 1998). Selectivity, therefore, probably influenced our results both on account of the nets selecting for a small range of greenling sizes and selecting only species that exhibited behaviors that made them susceptible to capture. If the average length of greenling captured during sampling was larger than the average length of greenling in the total population, we may have overestimated the total consumption of eggs. However, the estimate of total consumption of herring eggs is likely to have been underestimated for Prince William Sound, because the estimate is only for two species of fish. Because greenling make up only 56% by number and 59% by biomass of the fish species at Montague Island (Rosenthal, 1980), many other species inhabiting the zone covered by herring eggs would have access to the rich food source the eggs provide. Our results are similar to other studies in the Atlantic where predation on herring eggs by fish has typically been estimated at less than 10% of the total herring eggs (Tibbo et al., 1963; Toreson, 1991).

A concurrent study of egg loss in Prince William Sound has shown that herring egg loss from spawning beds increases at shallower depths (Rooper et al., 1999). Consumption of eggs by bird species indicate avian predators may be responsible for removals of large numbers of eggs (27%),⁵ most of which are lost in the intertidal zone. The different levels of predation in the intertidal and subtidal zones by birds and fish may be the underlying cause of the higher egg loss rates observed at shallower depths. If predation is an important factor regulating survival of eggs to time of hatching, then herring behavior may lend itself to compensatory mortality. Concentration of herring

⁴ Wilcock, J., and K. Hyer. 1998. Personal commun. Alaska Department of Fish and Game, P.O. Box 669, Cordova, AK 99754.

⁵ Bishop, M. A., and P. Green. 1998. Unpubl. data. USFS-CRDI, PO Box 1460, Cordova AK 99574.

stocks into a relatively small area during spawning and the resulting spatial concentration of eggs in the spawning beds could lead to high egg losses owing to predation even in years of low herring biomass. This in turn could drive the abundance of herring eggs even lower, as predators continued to concentrate on an ever-dwindling resource.

In summary, our study estimated that two greenling species consumed between 2.3% and 3.7% of the total herring eggs deposited on Montague Island in Prince William Sound in 1995. Greenling represent only a portion of the fish species in Prince William Sound; therefore predation by other fish species would probably increase the consumption estimates. Although consumption of herring spawn by fish species has not been extensively studied in the Pacific, the results of our study indicate the importance of predation by fish species on the mortality of herring eggs in spawning beds.

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