

Cannibalism on eggs by walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska

Richard D. Brodeur*, Kevin M. Bailey, Suam Kim**

Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, Washington 98115 USA

ABSTRACT: A strong density-dependent relationship has been observed for the walleye pollock *Theragra chalcogramma* population in the Western Gulf of Alaska. It has been suggested that this relationship may be attributed in part to egg cannibalism by the adult spawning stock. This hypothesis was examined by collecting stomach samples of walleye pollock from the main spawning area over 5 yr. Eggs were prevalent in many stomachs, especially in those from the older age classes. The mean number of eggs in the stomachs was not related to the overall amount of food in the stomach but was linearly related to the density of eggs in the water column. Total egg consumption was estimated for 3 years (1986, 1988, and 1989) and was found to be only a small (<1) percentage of the total egg production. Even during a year (1981) of peak adult abundance, the total calculated egg consumption was less than 3 % of the total egg production. A passive filtration model provided estimates similar to those observed in the field. We conclude that egg cannibalism alone would not account for the high egg mortalities observed.

INTRODUCTION

The role of density-dependent versus density-independent processes is of fundamental concern to understanding fish population dynamics. In the case of walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska, a strong negative relationship between the number of new recruits and the spawning stock biomass has been observed (Megrey 1989a, b), suggesting compensation. One mechanism that could lead to such a relationship is cannibalism on young stages (Ricker 1954) and especially on eggs (MacCall 1981). Kim & Gunderson (1989) suggested that cannibalism on eggs by adult pollock, which are concentrated in the area of maximum egg abundance for prolonged periods of time, may be one cause of the substantial (32 to 35 % d⁻¹) early mortality observed in this population.

Walleye pollock form dense spawning aggregations in the deep troughs of Shelikof Strait during late March and early April (Kim 1987, Hinckley et al. 1991). Extensive patches of eggs are produced which occur at high densities (> 50 m⁻³) relative to most other pelagic

spawning teleosts (Kendall et al. 1987). The eggs incubate at depths between 100 and 300 m (Kendall & Kim 1989) for about 2 wk at 5 °C (Haynes & Ignell 1983, Bailey & Stehr 1986). In areas with dense spawning aggregations, pollock egg patches can exhibit mean densities up to 68 times background levels in the strait and persist for the entire incubation time and well into the larval period (Incze et al. 1989).

Although the highly vulnerable egg and early larval stages are susceptible to predation from a diverse array of invertebrate predators, juvenile and adult fishes may often be the source of the greatest predation mortality (Hunter 1984, Bailey & Houde 1989). In this paper, we report on the results of 5 yr of pollock stomach sampling during their peak spawning period in the western Gulf of Alaska. We also report egg predation by other pelagic fishes. Using these data, we estimate the contribution of egg cannibalism to the total egg mortality for the Shelikof Strait population, and the potential role of density-dependent egg mortality in population regulation. A passive filtration model is proposed, and predictions are compared with observed data.

MATERIAL AND METHODS

Data used in this study were gathered aboard the NOAA ship 'Miller Freeman' during surveys of eggs

Present addresses:

- * Pacific Biological Station, Dept of Fisheries and Oceans, Nanaimo, B.C., Canada V9R 5K3
- ** Korean Ocean Research & Development Institute, Polar Research Laboratory, Ansan, PO Box 29, Seoul 425-600, Korea

and spawning adults from 1985 through 1989. An extensive station grid was initially surveyed in order to locate areas of high egg abundance (Incze et al. 1989). Eggs were sampled using 60 cm MARMAP bongo gear equipped with 505 μ m mesh nets, calibrated flow-

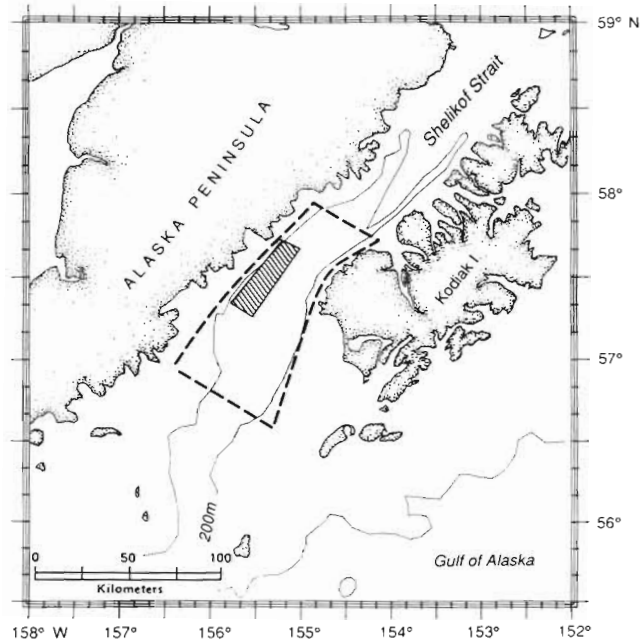


Fig. 1. Location of trawling area (hatched) and area in which adult pollock abundances were estimated (dashed line) from hydroacoustic surveys in Shelikof Strait, Gulf of Alaska

meters and a bathykymograph. Tows were double-oblique from the surface to near bottom. Upon completion of the initial sampling, the areas of highest concentration were resampled for egg abundance.

Potential fish predators were collected using Diamond and Marinovich midwater trawls (1985 to 1988) or pelagic rope trawls (1989). All trawl codends were fitted with fine-mesh (1 cm) liners to capture the full size range of fish predators available. Specific trawl locations (Fig. 1, Table 1) were selected based on the presence of strong acoustic signal readings on a 38 kHz echosounder and chromscope at the depth of high egg abundance. The trawl was lowered to this depth and towed for short periods of time (generally less than half an hour) before retrieval. The depth of the trawl was monitored using a headrope-mounted netsounder. During years when several hauls were made, an attempt was made to space the collections throughout the diel period (Table 1).

Once the trawl was aboard, a representative subsample of the length distribution of each potential predator was set aside for stomach sampling. Regurgitation effects were minimized by rejecting fish with flaccid stomachs or with food in the oral cavity. From 1985 to 1987, pollock stomachs were examined at sea under a dissecting microscope and eggs were removed and stored in 10 % formalin for later identification and staging. Stomachs of both walleye pollock and eulachon *Thaleichthys pacificus*, the only other abun-

Table 1. Station and tow data for egg predation sampling by year. All times and locations listed are for the start of the tow

Year	Haul	Date	Time (local) (h)	Lat. (N)	Long. (W)	Gear depth (m)	Bottom depth (m)
1985	1	8 Apr	11:49	57° 44'	155° 00'	237	257
1986	1	5 Apr	12:39	57° 17'	155° 34'	265	274
	2	5 Apr	17:52	57° 15'	155° 31'	183	276
	3	9 Apr	00:28	57° 36'	155° 18'	197	298
	4	9 Apr	01:44	57° 35'	155° 17'	205	301
	5	9 Apr	13:32	57° 34'	155° 22'	152	323
	6	9 Apr	17:20	57° 35'	155° 19'	228	311
1987	1	3 Apr	18:00	56° 27'	156° 11'	225	274
	2	3 Apr	04:11	57° 37'	155° 18'	230	284
1988	1	4 Apr	14:01	57° 41'	155° 09'	222	302
	2	4 Apr	15:24	57° 40'	155° 12'	210	298
	3	4 Apr	22:13	57° 40'	155° 09'	247	292
	4	5 Apr	04:43	57° 41'	155° 10'	263	302
	5	12 Apr	01:26	57° 38'	155° 18'	227	336
	6	12 Apr	02:31	57° 39'	155° 17'	197	323
	7	12 Apr	12:33	57° 38'	155° 17'	243	320
	8	12 Apr	13:56	57° 39'	155° 17'	274	325
1989	1	7 Apr	09:03	57° 34'	155° 18'	230	320
	2	7 Apr	12:38	57° 38'	155° 14'	243	295
	3	7 Apr	15:43	57° 38'	155° 16'	238	306
	4	7 Apr	19:38	57° 38'	155° 13'	241	292
	5	10 Apr	02:17	57° 38'	155° 16'	225	309
	6	10 Apr	04:35	57° 38'	155° 16'	184	328
	7	15 Apr	00:43	57° 39'	155° 18'	215	340

dant pelagic predator, were preserved whole at sea and analyzed in the laboratory during the last 2 years of sampling. The entire contents of these stomachs were removed and the relative fullness of each stomach was visually assessed and assigned a rank from 0 (empty) to 5 (fully distended). The contents were identified to major taxonomic categories and weighed to the nearest 0.001 g only for the years 1988 and 1989.

A daily ration (D) for walleye pollock was estimated for each year i (1986, 1988 and 1989 only) using the following model:

$$D_i = F \times R \times 24 \quad (1)$$

which requires an estimate of gastric evacuation rate (R) and the mean weight or number of prey over a 24 h period (F) (Eggers 1977). Boisclair & Leggett (1988) found this method yielded similar daily ration estimates to those of the more statistically rigorous Elliott & Persson (1978) model.

Estimates of R are usually determined in the laboratory. We used estimates of juvenile walleye pollock evacuation rates given by Smith et al. (1989) appropriate to the temperatures and meal sizes for our study. We have assumed that the evacuation rate for eggs is about the same as for other food types. Since evacuation rates are known to be dependent on body size, we scaled the rates for juveniles to the mean predator size in each year according to the relationship given in Smith et al. (1989).

As a check on the suitability of these evacuation rates, we attempted some preliminary experiments at sea using adult walleye pollock (39 to 53 cm) collected in brief midwater trawls. These fish were maintained in a large covered deck tank supplied with filtered seawater at around 5 °C for 24 h prior to use in the experiments. The pollock were each then force-fed a gelatin capsule containing 50 fertilized eggs and allowed to digest these for set periods of time. Previous experiments had shown that it takes 1 to 2 h to break down the gelatin capsules in pollock stomachs. Three fish were then sacrificed at 4, 8, 12, 16 and 24 h after feeding and the eggs remaining in the stomach were recovered.

The number of eggs consumed during each year i (C_i) was estimated by the following:

$$C_i = D_i \times N_i \times I \quad (2)$$

where N_i = abundance of consumers; I = incubation time in days (= 14). This assumes that all the spawning takes place simultaneously and that all predators are in the area of maximum spawning throughout this 2 wk period. Neither of these assumptions is entirely valid. However, data for 1981 indicate that the 14 d around the peak spawning time encompasses around 90 to 95 % of the annual egg production (Kim & Gunderson

1989). Although some adults may move out of the main spawning area before all the eggs have hatched, this fraction is generally very small. Hence, our estimates may be considered the maximum possible consumption by the predators.

The abundance of potential predators in the area of maximum egg density was determined from hydroacoustic and trawl surveys conducted on the 'Miller Freeman' 1 to 2 wk before the egg survey. Predator abundances were estimated based on hydroacoustic transect densities averaged for the 50 m directly above bottom within a standardized area of ca 8500 km² (Fig. 1) during the 3 years (1986, 1988, and 1989) for which a sufficient number of stomachs were examined. These abundances represent 76.9, 77.4, and 74.2 %, respectively, of the total Shelikof Strait hydroacoustic abundance estimates from the 3 years. Each transect density was weighted by the number of observations made along that transect. The total abundance was apportioned to the various year classes based on age frequency distributions available from trawl catches in the area of maximum egg density (E. Nunnalee & N. Williamson, NMFS, Seattle, unpubl.).

In order to measure filtration rates of adult pollock, fish were collected in midwater hauls and individually placed in 300 l polyethylene enclosures filled with filtered seawater and containing a known concentration (1 per liter) of buoyant eggs. These enclosures were then suspended in the deck tank aboard the research vessel and covered with dark plastic. The fish were then removed at predetermined time intervals (<1 h) and their stomachs excised and examined for eggs.

RESULTS

Occurrence of eggs in stomachs

Eggs were found in at least some pollock stomachs collected from each of the 24 hauls made (Table 2). With the exception of most of the collections made during 1989, pollock eggs were found in at least half the stomachs containing food in each haul. Egg numbers varied greatly among hauls but generally showed a decrease in maximum and mean eggs consumed in the last 2 years (Table 2).

Only 1 of the 69 eulachon (length range 102 to 240 mm) examined from 7 hauls in 1988 and none of the 65 eulachon examined from 6 hauls made during 1989 (97 to 229 mm) contained eggs. Since eulachon were in spawning condition when collected and their stomachs contained only trace amounts of food, we will assume that any egg consumption by eulachon at this time of year was insignificant and restrict all further data analyses to pollock.

Table 2. *Theragra chalcogramma*. Stomachs examined and incidence of cannibalism upon eggs by walleye pollock by year. (nc: data not collected)

Year	Haul	No. of stomachs	Length range (cm)	No. with food	No. with eggs	Mean no. eggs	Max. no. eggs
1985	1	46	41–53	44	44	46.71	242
1986	1	103	22–57	nc	46	1.33	22
	2	103	11–55	nc	71	4.71	27
	3	97	19–52	nc	63	2.94	41
	4	98	33–59	nc	95	26.96	249
	5	70	21–58	nc	47	5.03	31
1987	6	99	34–56	nc	95	24.12	248
	1	99	19–64	53	31	0.71	10
1988	2	96	29–63	74	60	2.89	22
	1	29	27–53	24	16	4.41	31
1989	2	25	21–53	18	9	0.96	9
	3	30	20–49	17	14	1.50	7
	4	17	32–62	11	11	2.06	15
	5	20	21–50	16	14	4.20	20
	6	7	11–36	5	5	3.14	11
	7	22	12–44	17	13	5.09	24
	8	20	11–60	15	9	3.75	31
	1	35	10–50	34	11	2.06	31
	2	35	10–52	32	14	1.23	8
	3	35	21–56	31	10	0.77	5
	4	27	11–51	25	5	0.22	2
	5	34	11–61	24	10	4.06	91
	6	45	11–68	36	11	1.07	10
	7	25	35–60	21	21	13.52	64

Eggs from 21 walleye pollock stomachs collected during 1985 were assigned to early (1 to 5 d old), middle (6 to 7 d old) and late (8 to 14 d old) stages of development. In the sample of 981 eggs, 85.5, 3.2, and 7.5 % were determined to be early, middle, and late stages, respectively. Of the remaining eggs, 1.4 % were unfertilized and 2.3 % were too digested to be reliably staged.

Proportion of diet consisting of eggs

Walleye pollock consumed a variety of foods during the 2 years in which detailed stomach analysis was done. Pollock eggs were the dominant food by number

during 1988, comprising almost two-thirds (64.3 %) of the total number of prey items consumed (Fig. 2). By weight, however, eggs were the fourth most important prey comprising about 5 % of the total food weight. The percentage of eggs in the total food consumed ranged from 57 to 78 % and 1 to 16 % by number and weight, respectively, in the individual hauls. The most important prey overall by weight were decapods, resulting mainly from the occurrence of several large pandalid shrimp (*Pandalus* spp.) in the stomachs from one station. Euphausiids (mostly *Thysanoessa* spp.) were the second most important food by both weight and number during 1988 (Fig. 2).

Small prey dominated the diet numerically during 1989, with copepods, pollock eggs, and larvaceans

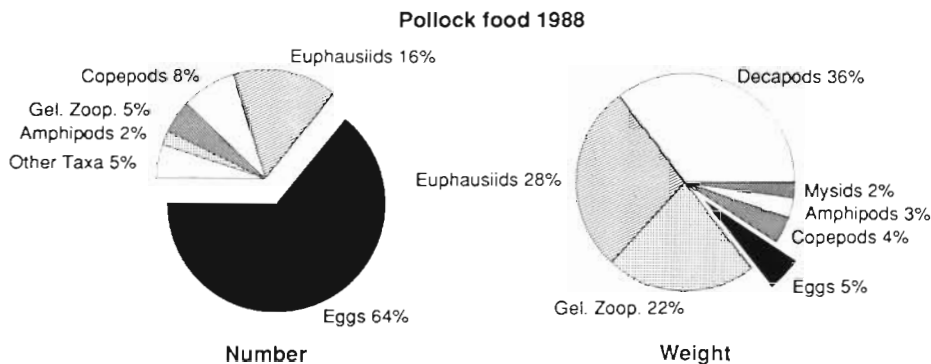
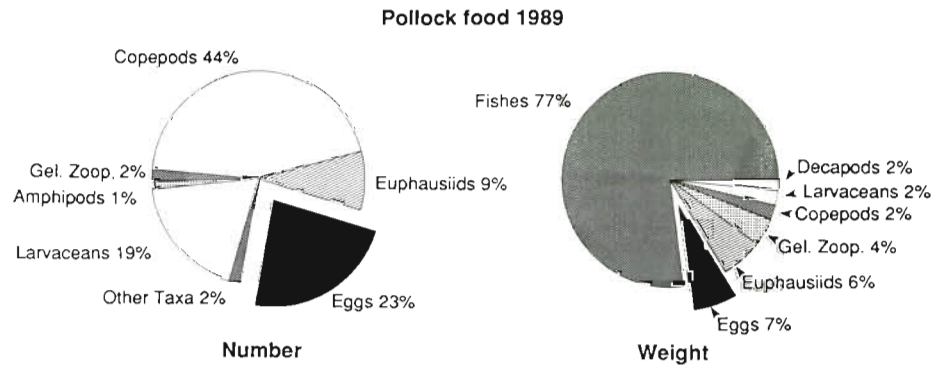


Fig. 2. *Theragra chalcogramma*. Percent by number and weight of the major food categories found in the stomachs of walleye pollock in Shelikof Strait in 1988. The portion of the diet made up of pollock eggs is isolated for emphasis. (Gel. Zoop. = gelatinous zooplankton)

Fig. 3. *Theragra chalcogramma*. Percent by number and weight of the major food categories found in the stomachs of walleye pollock in Shelikof Strait in 1989. The portion of the diet made up of pollock eggs is isolated for emphasis. (Gel. Zoop. = gelatinous zooplankton)



accounting for 86.3 % of the total food consumed (Fig. 3). Because of the preponderance of copepods in some stomachs, eggs were relatively less important numerically but were actually of greater importance in terms of biomass compared with the 1988 results. Fish were the dominant prey by weight during 1989 and consisted almost entirely (> 99 %) of age-1 juvenile pollock (length range 9 to 12 cm) found in adult pollock collected in hauls 4 and 6.

Diel consumption of food

Collections were grouped into 4 h time intervals in order to examine diel trends in feeding. Mean stomach fullness, as expressed by both percent body weight and fullness code, exhibited significant diel variations (Kruskal-Wallis Test, $p < 0.001$) peaking during the early morning (06:00 to 10:00 h) and declining throughout the remainder of the day (Fig. 4). Both the mean number of eggs per stomach and the percentage of stomachs containing eggs were similar for most time periods (Fig. 4) but showed a substantial increase during the night (22:00 to 02:00 h). These increases are attributed mainly to the large numbers of fresh eggs in pollock stomachs collected during 1989 in haul 7 (Table 2).

Dietary variations by age and maturity

The size distribution of fish analyzed during 1988 and 1989 shows several distinct modes corresponding to the different pollock age groups present in the strait (Fig. 5). The first 2 modes, centered around 120 and 220 mm, represented 1 and 2 year-olds; these immature fish were examined separately from the age-3+ pollock in spawning condition. Although stomach fullness, expressed by both percent body weight and fullness code, was much higher in the age-1 fish than in either of the other groups, these fish consumed a similar mean number of eggs as the age-2 fish, and significantly

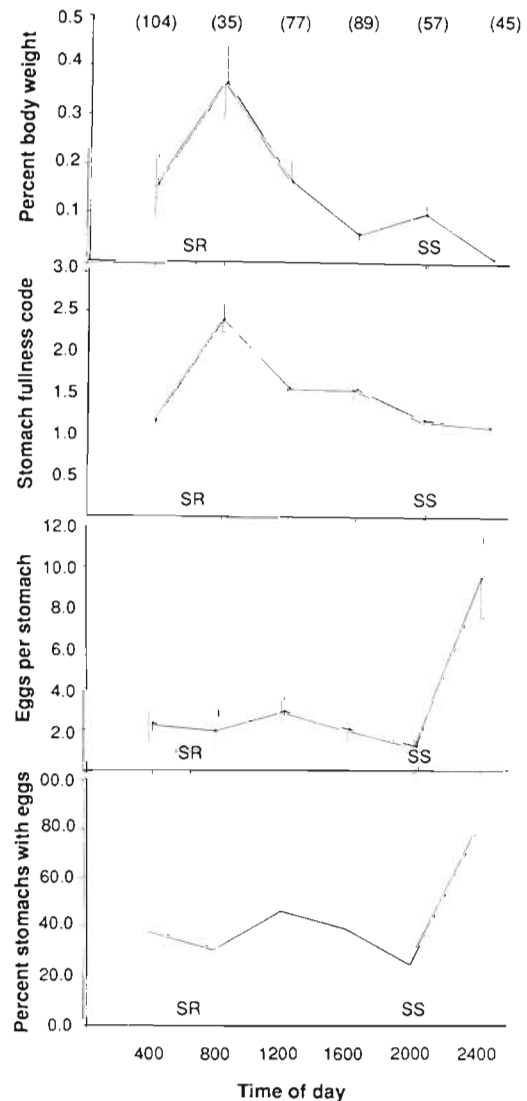


Fig. 4. *Theragra chalcogramma*. Percent of total body weight made up by stomach contents, stomach fullness code, mean number of eggs per stomach and percentage of stomachs containing eggs by 4 h time periods for 1988 and 1989. The number of stomachs examined during each period is shown in parentheses in the upper figure. Data are means ± 1 SE. Approximate times of sunrise (SR) and sunset (SS) are indicated

(Mann-Whitney Test, $p < 0.001$) fewer mean eggs than the age-3+ fish (Table 3). Walleye pollock eggs were found in only 5 of the 62 (8.1 %) age-1 fish and 3 of 22 (13.6 %) age-2 fish examined compared with 165 of 323 (51.1 %) of the age-3+ fish. Since the majority of the stomachs we examined from both years were age-3 and older, the proportions of walleye pollock eggs by both weight and number within this group increased only slightly (< 1 % in all cases) from those shown in Figs. 2 & 3.

Overall food consumption and number of eggs per stomach were analyzed by stage of maturity for the walleye pollock stomachs collected during 1989, the only year for which maturity data were available (Table 4). There were significant differences in the mean stomach fullness, expressed as a percent of total body weight, and the number of eggs per stomach (Kruskal-Wallis Test, $p < 0.001$ for both) among the 4 maturity groups. The highest egg consumption and lowest stomach fullness were found for the actively spawning individuals, whereas the lowest egg consumption and highest stomach fullness were found for immature and developing fish (Table 4).

Relation to abundance in the plankton

The mean number of eggs found in the stomachs for each haul was positively related to egg density throughout the water column determined from plankton collections at the nearest grid station. The relation between these 2 variables was best described by a log-log function (Fig. 6). The 95 % confidence interval of the regression coefficient was 0.308 to 1.986. This range included a slope of 1.0 and therefore suggests that these eggs were consumed in proportion to their abundance in the plankton.

Egg evacuation experiments

Although there was some variation among individual fish, the number of eggs left in the stomach remained

high for the 8 h immediately after feeding but then declined rapidly after that time (Fig. 7). After 24 h, there were few eggs left in the stomachs and 1 of the 3 stomachs contained no eggs at all.

Egg consumption estimates

Using yearly mean abundance of eggs found in the stomachs and size-adjusted evacuation rates, we estimated the number of eggs consumed per day for age classes combined and for fish ages 3 and older (Table 5). These estimates show a substantially higher consumption for 1986 than for either 1988 or 1989. The estimate of total egg consumption by the entire population, as estimated from hydroacoustic surveys in 1986, was only about twice that of 1988, the next highest year (Table 5).

Given the uncertainties in the estimates we used for evacuation rates and adult population abundances, we calculated egg consumption rates using alternative values for these 2 parameters to estimate maximum potential consumption. We first assumed that the evacuation rates could be twice those used in Table 5. We also used the total spawning biomass in the western Gulf of Alaska determined from cohort analysis (Hollowed & Megrey in press) as well as the more localized abundance determined by hydroacoustic estimates. Although most of the walleye pollock in the western Gulf of Alaska spawn in Shelikof Strait, the cohort analysis may include a small percentage of pollock which spawn elsewhere; therefore, these abundances are probably overestimates and were used to reflect the maximum possible predator abundance. Egg consumption estimates based on combinations of these 2 digestion rates and adult abundances were compared with annual estimates of egg production (Hollowed & Megrey 1990) based on age-specific maturity rates, fecundity, and abundance estimates for the 3 years. Using the most liberal estimates for both the evacuation rates and adult walleye pollock population estimates, pollock consumption ranged from 0.10 to 0.22 % of the total egg production for the 3 years (Table 6).

Table 3. *Theragra chalcogramma*. Trends in food and egg consumption with increasing size of walleye pollock collected in Shelikof Strait during 1988 and 1989. Numbers in parentheses: standard errors of the mean

Age group	Length range (mm)	No. of fish sampled	Mean percent body wt	Mean fullness code	Mean no. eggs stomach ⁻¹	Percent occurrence of eggs
1	100–140	62	0.40 (0.07)	2.14 (0.18)	0.226 (0.127)	8.1
2	183–250	22	0.08 (0.04)	1.45 (0.31)	0.227 (0.146)	13.6
3+	267–679	323	0.08 (0.02)	1.28 (0.06)	3.650 (0.491)	51.1

Fig. 5. *Theragra chalcogramma*. Length distributions of pollock examined from 1988 and 1989 stomach sampling

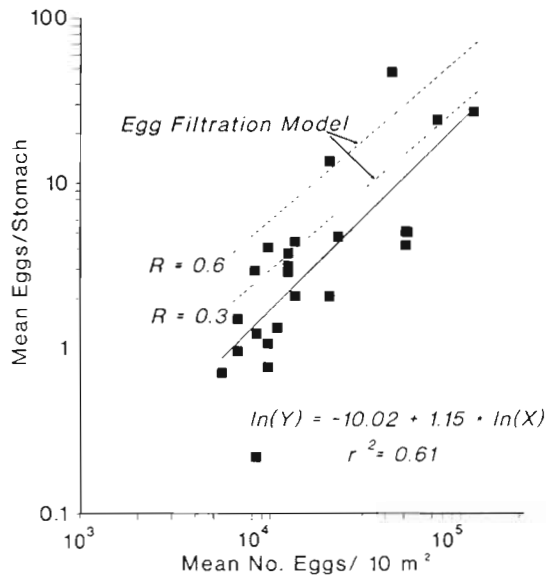
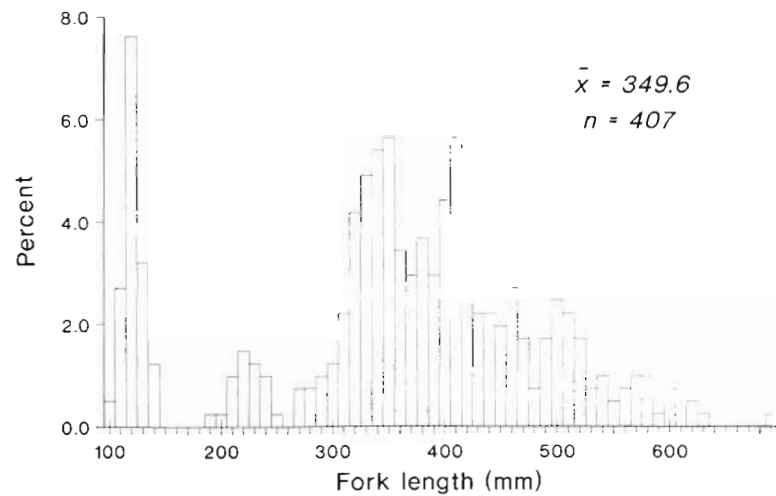


Fig. 6. *Theragra chalcogramma*. Relationship between mean number of eggs in the stomachs and egg density in the plankton at the nearest tow location for all years. Solid line and the equation is the regression line fit to the data. Dashed lines delimit the range of eggs per stomach predicted by the egg filtration model between fast and slow gastric evacuation rates

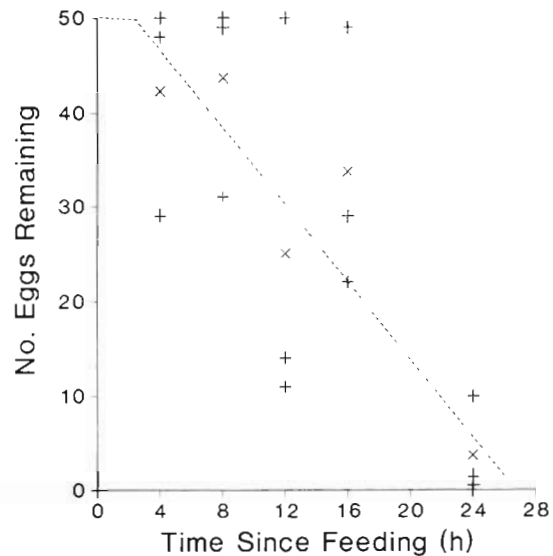


Fig. 7. *Theragra chalcogramma*. Egg numbers remaining in the stomachs at the time intervals shown from shipboard experiments conducted at 5 °C. (+) Actual number of eggs recovered at each time interval; (x) mean of the 3 observations. Dashed line was fit to the mean values and includes a lag period of 2 h to account for digestion of the gelatin capsules (see text)

Table 4. *Theragra chalcogramma*. Trends in overall food consumption and egg consumption with maturity stage of walleye pollock collected in Shelikof Strait during 1989. Numbers in parentheses: standard errors of the mean

Maturity stage	No. of fish sampled	Mean percent body wt	Mean no. eggs stomach ⁻¹	Percent occurrence of eggs
Immature and developing	99	0.37 (0.07)	0.360 (0.011)	14.0
Mature	20	0.06 (0.05)	1.600 (0.907)	35.0
Spawning	65	0.02 (0.01)	6.062 (1.733)	58.5
Spent	52	0.10 (0.04)	4.038 (1.527)	42.3

Table 5. *Theragra chalcogramma*. Mean egg abundances, daily egg consumption per fish, and total annual consumption for all pollock and age-3 and older pollock in the main spawning area in Shelikof Strait

Year	Mean no. eggs stomach ⁻¹	Mean fish weight (g)	Evac. rate h ⁻¹	Eggs consumed d ⁻¹	Adult abundance	Total egg consumption
All ages						
1986	15.53	477.7	0.0316	11.78	3.04×10^8	5.01×10^{10}
1988	3.11	246.5	0.0431	3.22	4.58×10^8	2.06×10^{10}
1989	2.85	382.8	0.0356	2.44	1.55×10^8	5.27×10^9
Age 3+						
1986	19.48	770.9	0.0203	9.49	1.63×10^8	2.16×10^{10}
1988	3.42	283.2	0.0375	3.08	3.83×10^8	1.65×10^{10}
1989	3.87	523.9	0.0284	2.64	1.10×10^8	4.07×10^9

Egg filtering model

Because pollock are not actively feeding during the spawning season and not likely to see eggs at depths of 200 to 300 m, it seems plausible that eggs are passively ingested by retention on the gill rakers during ventilation. A simple passive filtration model was constructed to compare predictions of egg consumption against field data. The model used is as follows:

$$E = V \times R \times B \times D \quad (3)$$

where E = egg consumption (number consumed d⁻¹); V = ventilation volume (l d⁻¹ kg⁻¹) which is a function of O₂ consumption rate and O₂ utilization; R = retention efficiency, here assumed to be 100 %; B = fish biomass (kg); and D = egg density (no. l⁻¹). B and D are data inputs, and V was approximated (lacking data on walleye pollock) from the relationship between respiration rate and ventilation volume of trout with 10 % oxygen utilization at 5 °C (from Shelton 1970). The respiration rate of walleye pollock at 5.5 °C is from Smith et al. (1988):

$$Y = 1.55X + 19.84 \quad (4)$$

where Y = oxygen consumption (μl g⁻¹ h⁻¹); and X = temperature (5.5 °C). The ventilation volume thus calculated was 0.864 m³ d⁻¹ kg⁻¹.

The number of eggs filtered per hour in the lab experiments was highly variable (range 2 to 88) averaging 17.3 eggs h⁻¹. Using our model, we predict that our experimental fish at an average weight of 0.65 kg would filter around 23 l h⁻¹ and, at a density of 1 egg l⁻¹ used in the experiments, consume 23 eggs h⁻¹.

Daily egg consumption was calculated from the filtration model for the range of egg densities observed (assuming eggs are all in the bottom 100 m). The mean number of eggs per stomach was calculated from Eq. (1) by solving for F with R at 0.03 and 0.06, which represented slow and fast evacuation rates, respectively. The mean fish size used was 0.5 kg (from Table 5). Predicted numbers of eggs per stomach fit observed data fairly well, especially at high egg abundances (Fig. 6). The model tended to overestimate eggs per stomach at low egg densities.

DISCUSSION

There are several sources of bias associated with our egg consumption calculations which may impact our results. As in any study that utilizes trawl-caught fishes, a potential for feeding in nets during capture exists in our study. Eggs consumed in the codend could

Table 6. *Theragra chalcogramma*. Estimated yearly egg consumption rates for adult pollock (age 3+) from Shelikof Strait calculated using combinations of 2 different evacuation rates and abundances levels for the 3 years. See text for derivation of the different models. Percent consumed is given in parentheses below each value

Year	Total egg production	Total egg consumption			
		Low abundance Slow evacuation	Low abundance Fast evacuation	High abundance Slow evacuation	High abundance Fast evacuation
1986	2.113×10^{14}	2.163×10^{10} (0.010)	4.326×10^{10} (0.020)	2.345×10^{11} (0.111)	4.690×10^{11} (0.222)
1988	1.074×10^{14}	1.650×10^{10} (0.015)	3.301×10^{10} (0.031)	9.041×10^{10} (0.084)	1.808×10^{11} (0.168)
1989	1.010×10^{14}	4.074×10^9 (0.004)	8.149×10^9 (0.008)	5.085×10^{10} (0.050)	1.017×10^{11} (0.101)

originate from either previously spawned eggs floating in the plankton or from eggs extruded from ripe females as they are compressed in the net. We believe that the first method of post-capture ingestion is unlikely since the codend mesh size was large enough (1 cm) to allow particles much larger than pollock eggs to pass through. Although some contamination from the second situation is possible, most of the eggs found in the stomachs were fertilized and many were at advanced stages of development (as exemplified by the 1985 eggs we staged) and well digested.

Another source of error may be the assumption that evacuation rates for eggs ingested in the field are similar to those found by Smith et al. (1989) for juvenile pollock feeding on shrimp in the laboratory at similar temperatures. Although we were not able to find any studies which compared the evacuation rates of fish eggs to those of other prey under the same conditions, the few laboratory and field studies available on egg clearance times suggest that these are relatively short, generally less than 24 h (Hunter & Kimbrell 1980, Daan et al. 1985). To account for potential error in evacuation rates, we used a range of values (ca 17 to 34 h) in our calculations which bracketed 24 h. Our preliminary field experiments using adult pollock force-fed gelatin capsules containing a known number of eggs showed almost complete evacuation in about 24 h at 5 °C. This time to complete evacuation of eggs may be high because of the use of the capsules and the potential stress to the fish caused by force-feeding. Thus the field experiments demonstrated that the range of evacuation rates we used was probably realistic. Based on our field data, walleye pollock show a distinct diel periodicity in feeding such that stomach fullness is at a maximum during the early morning and then declines at a rate sufficient to empty the stomach by the next feeding cycle.

The lower cannibalism rates in the younger age groups (ages 1 and 2) may be related to their vertical distribution in the water column. Pollock in Shelikof Strait show vertical stratification by age groups with a substantial increase in mean age with depth (Muigwa 1989, E. Nunnallee, NMFS, Seattle, unpubl.); the majority of the adult spawners are found in the deepest layers. The younger age classes were relatively rare in our predator haul collections, and we suspect that they were captured mainly at shallower depths during the descent and ascent phases of the hauls. Kendall & Kim (1989) found the highest egg densities in the lowest layers during the 1985 spawning season with over 70 % of the eggs found at depths > 218 m and only 2.5 % of the total egg abundance found at depths shallower than 157 m. These authors also found a good correlation between the density of eggs in depth-stratified plankton tows and the number of eggs in pollock

stomachs sampled from trawl hauls in the same layers. Significantly higher egg abundances were found in stomachs collected from the deeper layers. Thus we feel that our abundance estimates calculated from only the lower layer spawning concentrations (47.3 % of the entire water column abundance in 1988) better approximate the actual population consuming pollock eggs than those calculated from all layers.

Eggs preyed upon by adults were primarily those in the early stages of development. This corresponds to the known vertical distribution of eggs, with the younger stages located deeper, overlapping the habitat of mature adults (Kendall & Kim 1989). Following hatching, the larvae rise in the water column and are generally distributed in the upper 60 m of the water column (Kendall et al. 1987). Residence at this depth during the vulnerable yolk-sac or early larval period may provide larvae with a refuge from fish predators residing at greater depths below the thermocline. Based on hydroacoustic and survey data, abundances of fishes in the surface layers during the late spring months are generally low in Shelikof Strait. Examination of a limited number ($n = 29$) of juvenile and adult pollock stomachs collected from 3 hauls taken in the upper 100 m during the late larval period (24 May to 1 June 1988) revealed no evidence of cannibalism on pollock larvae (Brodeur unpubl.). Eulachon, the only other abundant pelagic fish found in Shelikof Strait, also reside near the bottom in spring (Williamson in press).

We believe that the cannibalism we observed on eggs is not the result of active selection of eggs over other potential prey, but rather a passive ingestion during normal gill ventilation. Several lines of evidence support this conclusion. Pollock eggs are generally smaller than most of the normal prey items of adult pollock such as adult copepods, euphausiids, and fishes (Dwyer et al. 1987), and the overall biomass of these evasive prey may be several orders of magnitude greater than that of pollock eggs. Pollock eggs were often the only items found in the stomachs in actively spawning individuals during the spawning season, at a time when feeding motivation appears to be at its lowest level during the year (Dwyer et al. 1987). We found that actively spawning fish had little food in their stomachs overall compared with non-spawning fish yet they consumed a substantial number of eggs. Also, light levels at the depths where most of the cannibalism occurs are probably insufficient for pollock to visually cue on eggs. Finally, predicted results from a passive filtration model fit observed data surprisingly well, considering the crude approximations of adult behavior, physiology, and vertical distributions used in the model. An explanation for the filtration model tending to overestimate egg consumption at low egg densities might be

that the eggs are older and more vertically dispersed at low densities (Kim 1987).

Although the egg production estimates are also subject to some sampling error, they are of the same order of magnitude as independent estimates based on field data (5.0×10^{14} for 1986; Bates 1990). Both estimates of egg abundance indicate that the number of eggs produced is several orders of magnitude above the estimated number consumed. Despite the low consumption rates we found during the later years of our study, the high numbers of eggs found in the stomachs during some years could have affected recruitment dynamics during years of peak walleye pollock abundance. The empirical relationship between egg density in the plankton and consumption by pollock was linear, suggesting a density-independent functional response. This is in contrast to the situation suggested for filter-feeding anchovy off California and South Africa where egg consumption rates increased at higher egg densities (Hunter & Kimbrell 1980, Valdés et al. 1987). The few data points we have at the higher egg densities, however, lie along or above the predicted regression equation (Fig. 6), suggesting that this relationship could be nonlinear at high densities. Therefore, the annual losses due to cannibalism could have been significant during the early 1980s when walleye pollock population sizes and egg densities were extremely high relative to the years we examined.

Although stomach content data is not available from this period, we attempted to examine the magnitude of predation at these high stock levels based on the data on hand. If we extrapolate our egg density to eggs per stomach relationship [$\ln(\text{eggs per stomach}) = -10.02 \times 1.15 \ln(\text{egg density})$] beyond our existing data up to the mean egg density found in the egg patch during 1981 (221 571 eggs 10 m^{-2} ; Incze et al. 1989) and use evacuation rates adjusted for the estimated mean weight (516.9 g) of age-3 and older fish from the hydroacoustic cruises that year (Kim & Gunderson 1989), we arrive at a mean of 60.1 eggs per stomach and a daily consumption of from 41.5 to 83.1 eggs per fish (Table 7). These

estimates are higher than the mean estimates for the years for which we do have data, but these mean numbers of eggs per stomach are substantially less than the highest number of eggs per stomach recorded in our analysis (Table 2); hence, we feel that it is not an unrealistic number. Adult abundances (for fish age 3 and older) and egg production estimates were calculated as before from cohort analysis (Hollowed & Megrey in press) and from the 1981 hydroacoustic surveys (Kim & Gunderson 1989). Our estimates of the egg consumption by walleye pollock during 1981 lie between 0.6 and 2.1 % of the total egg production (Table 7).

This estimate is supported by applying the filtration model to the 1981 egg abundance data. In 1981, the average number of eggs per m^3 was 223; therefore, the average fish would be expected to passively filter 112.4 eggs d^{-1} , assuming a retention efficiency factor of 1.0. An adult fish biomass of $3.8 \times 10^9 \text{ kg}$ in 1981 would filter $3.29 \times 10^9 \text{ m}^3 \text{ d}^{-1}$. Estimating that eggs inhabit a volume of $11.4 \times 10^{11} \text{ m}^3$, adults would filter 0.29 % of available water per day. Therefore egg loss would be 4 % over the 14 d incubation period. This value lies above our field estimates at slow and fast evacuation rates (Table 7), but the assumption of 100 % retention efficiency of eggs by adult pollock may not be realistic.

In summary, we conclude that cannibalism is unlikely to be a major source of the high egg mortality seen in 1981; the remaining losses must be attributable either to transport out of the sampling area or to consumption by invertebrate predators or smaller pelagic fishes (e.g. Pacific sand lance *Ammodytes hexapterus*) unavailable to our trawls. As a consequence of relatively low egg mortality due to cannibalism even in a high adult stock biomass year, we further conclude that pollock egg cannibalism is unlikely to be a major factor in density-dependent stock recruit relationships in this population.

Extensive predation by adult pollock on juveniles has previously been documented for the Bering Sea walleye pollock population (Dwyer et al. 1987, Bailey 1989,

Table 7. *Theragra chalcogramma*. Estimated egg consumption and production for 1981 based on slow and fast evacuation rates and abundance and egg production rates from cohort analysis (Megrey unpubl.) and hydroacoustic estimates (Kim & Gunderson 1989)

Evac.	Mean eggs stomach ⁻¹	Mean fish weight (g)	Evacuation rate h ⁻¹	Eggs consumed d ⁻¹	Adult abundance	Total egg consumption	Total egg production	Percent consumed
Cohort analysis								
Slow	60.10	516.9	0.0288	41.54	7.38×10^9	4.29×10^{12}	4.02×10^{14}	1.066
Fast	60.10	516.9	0.0576	83.08	7.38×10^9	8.58×10^{12}	4.02×10^{14}	2.133
Hydroacoustic surveys								
Slow	60.10	516.9	0.0288	41.54	7.88×10^9	4.58×10^{12}	7.17×10^{14}	0.639
Fast	60.10	516.9	0.0576	83.08	7.88×10^9	9.17×10^{12}	7.17×10^{14}	1.279

Livingston 1989), but the relationship between the magnitude of cannibalism and subsequent recruitment of the year class is unclear (Francis & Bailey 1983, Bailey et al. 1986). Cannibalism on juveniles has not been documented in the limited feeding studies conducted to date on the pollock population of the Western Gulf of Alaska (Megrey 1989a). However, the high consumption of 1-yr-old pollock by the older age groups we observed during 1989 merits further study as a possible density dependent mechanism operating in this population.

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