Abstract.–Egg size has been shown to relate to survival and growth in the early life stages of fish. Combined field and laboratory studies examined variation in the egg size of walleye pollock *Theragra chalcogramma*, a commercially important North Pacific gadoid; and a preliminary assessment of the effect of egg size on larval size was made. Differences in egg size were found over parts of the geographical range, among years, and over the spawning season in Shelikof Strait. Egg size did not appear to correlate with female length, age, or condition. Individual female's egg size decreased significantly over the course of the spawning cycle. Preliminary studies in the laboratory showed that egg size is correlated with larval size and may therefore affect mortality in the early larval stages.

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Variation of Egg Size of Walleye Pollock *Theragra chalcogramma* with a Preliminary Examination of the Effect of Egg Size on Larval Size*

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Variability in egg size may be an important factor in the survival of early life stages of fish. It has been proposed by numerous authors (Blaxter and Hempel 1963, Bagenal 1969, Ware 1975, Hunter 1981, Knutsen and Tilseth 1985) that egg size (dry weight or diameter) influences larval survival through its effects on larval size, growth rates, and activity. Larger eggs provide more energy for growth and development (Hempel and Blaxter 1967, Hempel 1979) and generally produce larger larvae which are able to avoid predators more effectively (Miller et al. 1988), survive longer without feeding (Hunter 1981), search a greater volume of water for prey (Blaxter 1986, Webb and Weihs 1986), and eat prey of a greater variety of sizes (Hunter 1981).

Differences in egg size are thought to reflect adaptations by the spawning stock to varying conditions met by early larvae. Bagenal (1971) proposed that there is a relationship among egg size, time of spawning, and availability of food. Cushing (1967) stated that egg size in Atlantic herring *Clupea harengus harengus* is related to the type of production cycle and its variability.

Hunter (1976) indicated that egg size may be important in studies of starvation and predation as cause of larval fish mortality, because of its effects on time to the onset of irreversible starvation, on feeding success, and on the ability of larvae to avoid predators. Larval size and its relation to egg size has been proposed as a unifying factor integrating the dynamics of larval survival and the mechanisms of recruitment. Miller et al. (1988), in their review of this subject, state that "... even small size differences of larvae at hatching can have significant ecological implications, and that even within a species (e.g., herring), size at hatching might be an adaptive response to local geographic conditions."

Walleye pollock *Theragra chalcogramma* is a semidemersal species ranging from Japan around the North Pacific rim to central California. This species supports important commercial fisheries in the Bering Sea and the Gulf of Alaska. Walleye pollock spawn pelagic eggs which have an incubation time of approximately 15 days in 5°C water. Egg diameters have been reported to range from 1.0 to 1.9 mm (Table 1). Larvae are 3–4 mm standard length (SL) at hatching (Dunn and Matarese 1987). Egg size in walleye pollock varies across its geographic range (Table 1). It also varies within populations (Gorbunova 1954, Yusa 1954, Nishiyama and Haryu 1981, Sakurai 1982), and over the course of the spawning season (Serobaba 1968). The causes and significance of egg size variation in walleye pollock are not well known.

This field and laboratory study assesses sources of variation in walleye pollock egg size and presents results of a preliminary study of the relation-

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Table 1
Geographic variation in walleye pollock egg size.

Location	Average latitude (°N)	Egg size (mm) Mean	Range	Temperature* (°C) (Mean)	Reference
Eastern Pacific					
Puget Sound	47	1.2	1.0–1.3	8.5	This study
Shelikof Strait	57	1.37	1.3–1.4	5.0	This study
Bering Sea	57	1.73	1.3–1.9	3.25	Nishiyama and Haryu 1981
Bering Sea	59	1.57	1.5–1.7	0.95	Serobaba 1968
Bering Sea	59	1.59	1.4–1.8	2.75	Serobaba 1974
Western Pacific					
Japan	38	1.45	1.2–1.7	8.0	Yusa 1954
Peter the Great Bay	43	1.46	1.3–1.7	2.0	Gorbunova 1954
S. Kurile Islands	45	1.53	1.3–1.8	1.43	Gorbunova 1954
N. Kurile Islands	48	1.61	1.4–1.8	1.17	Gorbunova 1954
Sakhalin Island	50	1.58	1.5–1.7	−0.08	Gorbunova 1954
W. Kamchatka	56	1.57	1.3–1.8	1.5	Gorbunova 1954

*Temperature at bottom or depth of highest egg abundance (averaged using minimum and maximum of reported range).

ship between egg size and larval size. Size variation in walleye pollock eggs due to annual, seasonal, and geographical factors was examined from eggs caught in ichthyoplankton surveys in the Gulf of Alaska from 1981 to 1986. Variation due to female age, length, and condition was studied using eggs taken from spawning females caught at sea and from females held in the laboratory. Effects of egg size on larval size at hatching and at yolksac absorption were investigated in rearing experiments, using eggs from captive females and eggs taken in ichthyoplankton surveys.

Methods

Field studies

Walleye pollock eggs were collected in the Gulf of Alaska between 1981 and 1986 with 60-cm bongo nets (0.505-mm mesh), deployed with standard MARMAP procedures (Posgay and Marak 1980).

Eggs selected for measurement were chosen from archived samples (Table 2) taken in different years (1981–86), months (March–May), and areas (Shelikof Strait, the Semidi Islands to the Shumagin Islands, and west of the Shumagin Islands; Fig. 1). Variation in mean egg size among individual sampling stations was examined by measuring 25–50 eggs from up to 10 stations per year/month/area combination. Eggs at similar stages of development (early blastula to early germ ring) were measured with an ocular micrometer on a dissecting microscope at 40× magnification. All eggs were preserved in 3–5% buffered formalin.

Because mean egg sizes were significantly different ($F = 4.75$, $p < 0.0005$) among sampling stations, nested analysis of variance models with unequal cell sizes were used to test year, month, and area effects, with stations as the nested factor. Variation in egg size among years (within area and month), among months (within year and area), and among areas (holding year and month constant) had to be tested separately, due to the incompleteness of the available dataset, including missing months and areas in some years (Table 2).

The General Linear Models procedure of SAS-PC (SAS Inst. 1985) was used in this analysis. The F-statistic was derived using the Satterthwaite approximation (Gaylor and Hopper 1969 as cited in Sokal and Rohlf 1981), except in one case where the criteria for using this test were not satisfied; in this case a simple approximation test (Sokal and Rohlf 1981) was used.

Effects of maternal age, size, and condition on egg diameter and dry weight were examined using eggs from females caught by midwater trawl in Shelikof Strait in late March, 1986 (Table 2). Hydrated (fully ripe) eggs were collected from spawning females, and preserved in 5% buffered formalin. For each female, fork length (FL), gonad- and liver-free body weight, and liver weight were determined and otoliths removed for ageing. Body weight and liver weight were used as indices of condition.

Sixty eggs per female were measured. Because hydrated eggs taken from the ovary are sometimes slightly nonspherical, egg diameters were measured on the axis that fell along the transect to make sure measurements were random. Five to ten eggs per fish were subsampled for dry weight; eggs were measured,

Table 2

Stratification of walleye pollock egg samples measured for differences in egg size by year, area, and month, and to examine the effect of female size, age, and condition on egg size. Samples were collected on ichthyoplankton cruises in the western Gulf of Alaska.

	Shelikof Strait			Semidi Is. to Shumagin Is.	West of Shumagin Is.
Year	March	April	May	April	April
1981	M	Y,M	M		
1982	M	Y,A,M	M	A	A
1984	M	Y,M	M		
1985		Y			
1986	F	Y			

Samples used to study the effect of year (Y), area (A), month (M), and female (F) age, size, and condition.

washed with distilled water, placed individually in preweighed aluminum boats, dried for 24 hours at 60°C, and weighed on a Cahn 29 electrobalance to the nearest 0.001 mg.

An analysis of variance procedure was used to examine egg size within and among fish. A multiple regression model was used to examine the effect of female length, age, and condition on egg diameter and egg weight. The factors in the regression were fork length, age, body weight (minus ovary weight and liver weight), and liver weight. The model used was

$$Y = B_0 + B_1X_1 + B_2X_2 + B_3X_3 + B_4X_4$$

where Y = egg diameter (mm) or egg dry weight (mg),
X_1 = fork length (cm),
X_2 = age (yr),
X_3 = body weight (minus ovary and liver weight, g),
X_4 = liver weight (g).

Interaction terms were not included in the model until after a test of the overall significance.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

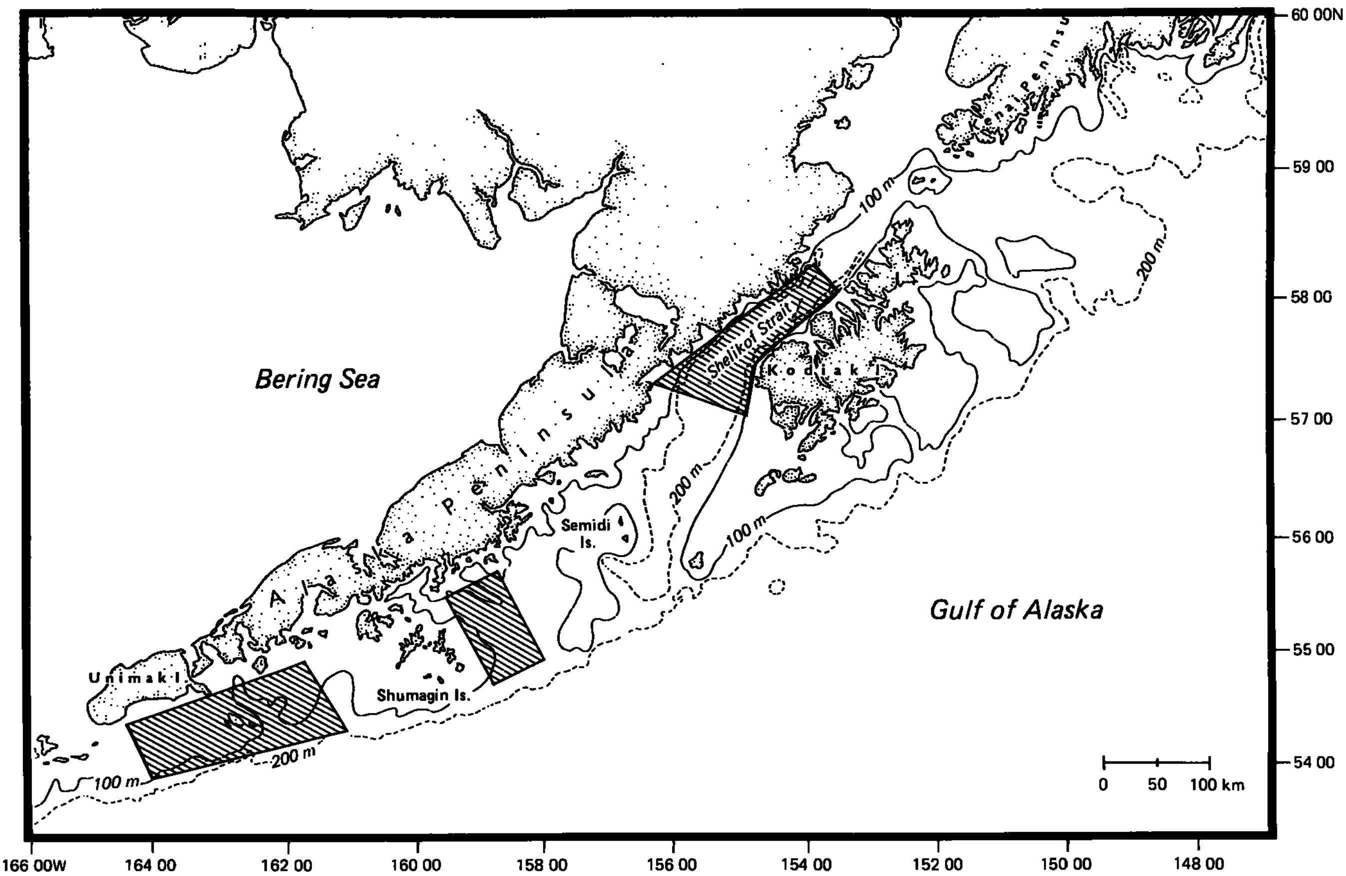

Figure 1

Western Gulf of Alaska, including Shelikof Strait, a major spawning area for walleye pollock. Shaded areas indicate regions from which samples were taken.

Laboratory experiments

Laboratory investigations were conducted using captive walleye pollock in March and April 1987. Adult prespawning walleye pollock were caught in January and February by handline in the Tacoma Narrows region of Puget Sound. Fish were transported to the laboratory and held in net pens under ambient light and temperature conditions and fed chopped herring *ad libidum* until they were nearly in spawning condition (i.e., eggs and milt were expelled with slight pressure to the abdomen). These fish were then transferred to individual 1700- or 2500-L tanks. One female and one or two males were placed in each tank and held throughout their spawning cycle. Water temperatures in the tanks were ambient and varied over the spawning season from 9.5 to 11.5°C ($\bar{x}$ 10.08°C). Ambient water temperature increased significantly (R^2=20.9%) over the experimental period. Salinity was constant at 28 ppt. A 20-cm plankton net with a hard codend was suspended in each tank to catch a sample of eggs from each spawning event. Plankton nets were checked each morning for the presence of eggs. If eggs were present in the codend, they were saved, and the water in the tanks replaced.

In 1988, pollock caught in Puget Sound were held individually in tanks to further examine the effect of female length on egg size. Eggs from the first batch from each of seven females were collected and measured in the same manner as described for the 1987 studies.

Egg diameters were measured on 15–25 unpreserved eggs, and egg dry weights were determined for 5–10 eggs from each spawning event. The remainder of the eggs were incubated separately (by female and spawning event) in 4-L jars filled with filtered seawater. The jars were placed in a water bath with running seawater at ambient water temperatures. Light levels were ambient. Water in these jars was changed several times during incubation (which lasted 6–9 days) and dead eggs were removed daily.

Six to fifteen larvae were collected on the day of hatch, anaesthetized with MS222, and their standard lengths measured. The rest of the larvae were held in the 4-L jars until yolksac absorption (defined as the point when individual larvae had used up 90–100% of their yolksacs). Standard lengths were measured (on anaesthetized larvae) and dry weights determined for 5–10 larvae at this stage.

A sample of live eggs collected from the ichthyoplankton in Shelikof Strait was transported to Seattle in April of 1987. Diameters and dry weights were determined on a subsample of these eggs and the rest were incubated. Larvae were measured at hatching and at yolksac absorption in the same manner as described above.

Table 3
Differences in mean walleye pollock egg diameter among years in April in the Shelikof Strait region of the Gulf of Alaska.

Year*	Egg diameter Mean	SE	*N*	SNK grouping**
1981	1.360	0.003	320	A
1986	1.317	0.004	250	B
1985	1.299	0.004	250	C
1984	1.298	0.003	250	C
1982	1.296	0.004	249	C

*Data not available from 1983.
**Student-Newman-Keuls multiple range test (SAS Institute 1985). A, B, C indicate significantly different groups.

Eggs collected from the Gulf of Alaska ichthyoplankton surveys for examination of yearly, seasonal, and regional differences in egg size were preserved in 3–5% formalin. No correction factor was used to correct for changes in egg size due to preservation, as all eggs used in these analyses were preserved in the same manner. The field samples taken from spawning adults and used to examine the relationship between egg size and fish size, age, and condition were also preserved in 3–5% formalin. These, however, were collected before spawning, and the diameters may not be directly comparable to sizes of spawned eggs collected from the ichthyoplankton, due to possible changes in egg size at fertilization and activation (Fleming and Ng 1987, Kjørsvik and Lonning 1983). Eggs from the laboratory were measured fresh and are therefore not directly comparable with eggs from the field studies. The comparison between sizes of Gulf of Alaska eggs and Puget Sound eggs was made only on the fresh samples collected in 1987 from both areas.

Results

Geographical, seasonal, and regional differences in egg size

Examination of 1319 walleye pollock eggs from April plankton samples (the month when most spawning occurs; Kim 1987) collected in Shelikof Strait demonstrated a significant difference in mean egg diameters among years (F = 19.862, p<0.0005). Mean egg diameter was largest (Table 3) in 1981 and smallest in 1982; there was a 4.7% difference in size between these years. Mean egg size was not statistically different in 1982, 1984, and 1985 (SNK test, Table 3). Mean egg size was intermediate in 1986.

Table 4
Differences in mean walleye pollock egg diameter over the spawning season in Shelikof Strait for 1981, 1982, and 1984.

Year	Month	Egg diameter Mean	SE	N	SNK grouping
1981	March	1.405	0.007	103	A
	April	1.360	0.003	320	B
	May	1.297	0.005	204	C
1982	March	*			
	April	1.296	0.004	249	A
	May	1.314	0.006	159	B
1984	March	1.383	0.002	792	A
	April	1.299	0.004	250	B
	May	*			

*Data not available from these months.

Table 5
Differences in mean walleye pollock egg diameter by area within the Gulf of Alaska, April 1982.

Area	Egg diameter Mean	SE	N	SNK grouping
Shelikof Strait	1.397	0.003	348	A
Semidi Is. to the Shumagin Is.	1.361	0.004	348	B
West of the Shumagin Is.	1.296	0.005	249	C

Table 6
Correlation coefficients (r) between walleye pollock egg diameter and egg dry weight, and female length, age, body weight, and liver weight.

	Length	Age	Body weight	Liver weight
Egg diameter	0.210	0.245	0.080	0.171
Egg dry weight	0.294	0.297	0.125	0.070

A significant difference in mean egg diameters was also observed over the course of the spawning season (March–May) in Shelikof Strait (Table 4) in 1981 (F = 23.389, p<0.0005), 1982 (F = 16.3387, 0.01<p<0.025), and 1984 (F = 54.105, p<0.0005*). In 1981 and 1984 egg sizes decreased over the course of the spawning season by about 7% per month (Table 4, 0.02<p<0.05). In 1982, mean egg diameter apparently increased from April to May by 1.4%.

Unpreserved walleye pollock eggs collected from the plankton in the Gulf of Alaska (in April 1987) were larger in diameter ($\bar{x}$ 1.36 mm, range 1.30–1.41) and dry weight ($\bar{x}$ 0.120 mg, range 0.097–0.139) than fresh eggs from Puget Sound (diameter $\bar{x}$ 1.19 mm, 1.03–1.27; dry weight $\bar{x}$ 0.077, 0.052–0.092), which were spawned naturally in laboratory tanks in April 1987. Mean egg diameters from various parts of the spawning range within the Gulf of Alaska were also compared from collections in April 1982 (Table 5). Egg sizes differed among all of the areas examined (F = 18.854, p<0.0005). Egg sizes showed a decrease of 7.2% from Shelikof Strait westward to Unimak Pass.

Relationship between egg size and female characteristics

The mean diameter of hydrated eggs taken from Shelikof Strait females in 1986 was 1.41 mm (range 1.29–1.57). The mean dry weight of these eggs was 0.119 mg (range 0.095–0.148). Variation in egg diameter and egg dry weight among fish was more significant (p <0.001) than variation within fish. Correlation coefficients between egg diameter or egg dry weight and female length, age, body weight, and liver weight are presented in Table 6.

The multiple regressions of egg diameter and dry weight against fish length, age, body weight, and liver weight were nonsignificant (R^2 = 0.361, 0.10<p<0.25, and R^2 = 0.321, p>0.25, respectively). A stepwise regression eliminated all variables as nonsignificant (p>0.05). No interactions or nonlinear relationships among variables were found. Fourteen females (29.5–47.0 cm FL) were held in the laboratory to investigate the female length-egg size relationship. As in previous regression analyses, no relationship was seen between female length and egg diameter for these fish (Fig. 2, r = 0.006).

Spawning characteristics and the relationship of egg size to larval size

The number of egg batches spawned per female in the laboratory in 1987 ranged from 2 to 21 over 3–26 days (Table 7). Excluding the two females which died prematurely, the average number of batches was 14.4 (range 9–21), and the average duration of spawning was 21.4 days (range 18–26). The average interval between batches for all fish was 2.1 days (range 1–5). The relationship between egg diameter and egg dry weight was linear (p<0.0005, R^2 = 0.630).

*Satterthwaite approximation not used in this test as the criteria were not met. A simple approximation test (Sokal and Rohlf 1981) was used in this case.

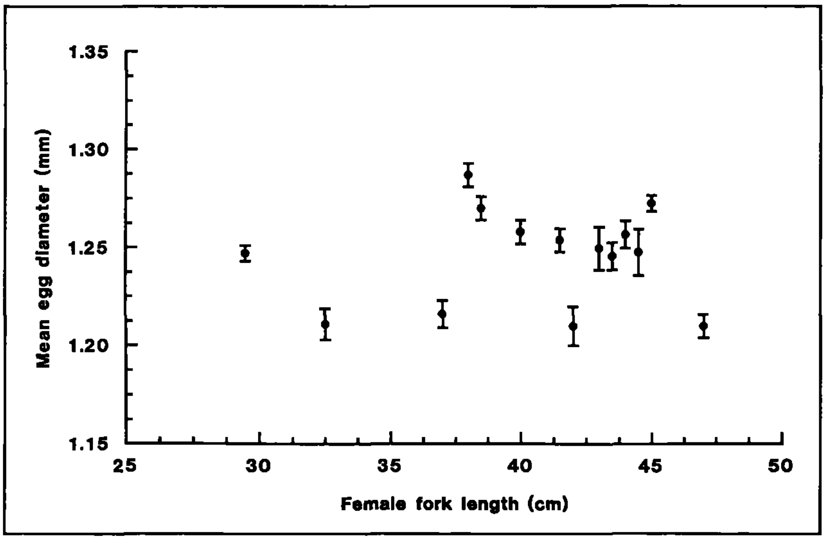

Figure 2
Relationship between female fork length and mean egg diameter in walleye pollock. Each dot represents the mean egg diameter from the first batch of eggs spawned from one female in the laboratory. Bars indicate standard error of the mean.

Table 7
Frequency and duration of spawning of captive walleye pollock from Puget Sound in 1987.

Female	Number of batches	Duration of spawning (d)	Interval (d) between batches: Mean	Interval (d) between batches: Range	Condition of ovary at death
1	9	20	2.2	1-5	>90% spent*
2	2	5	5.0		<10% spent**
3	13	18	1.4	1-2	spent*
4	15	23	1.5	1-3	spent*
5	2	3	3.0		<10% spent**
6	14	20	1.4	1-2	spent*
7	21	26	1.2	1-2	spent*
Mean	14.4***	21.4***	2.1		

*Sacrificed within 1 week of cessation of spawning.
**Died after 2 batches.
***Spent fish only.

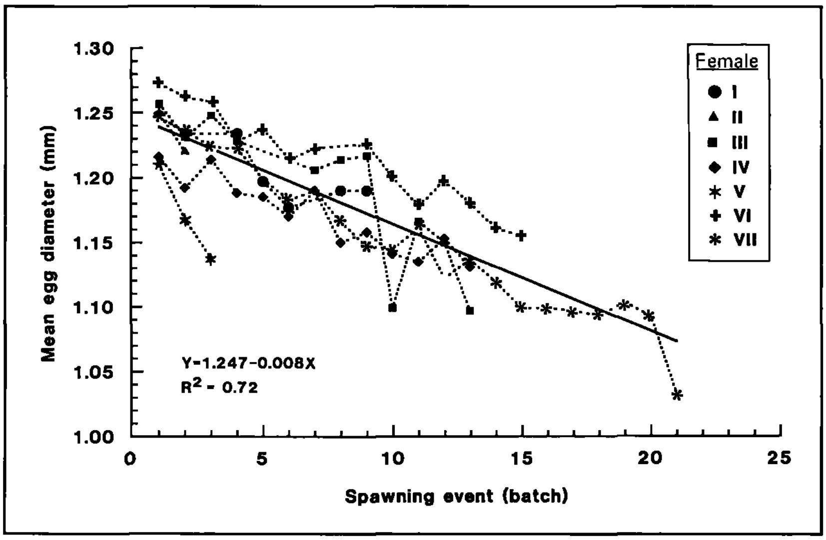

Figure 3
Change in mean egg diameter over the batch spawning cycle of female walleye pollock. Solid line indicates fitted regression line. Each symbol represents a separate female held in the laboratory over the spawning cycle.

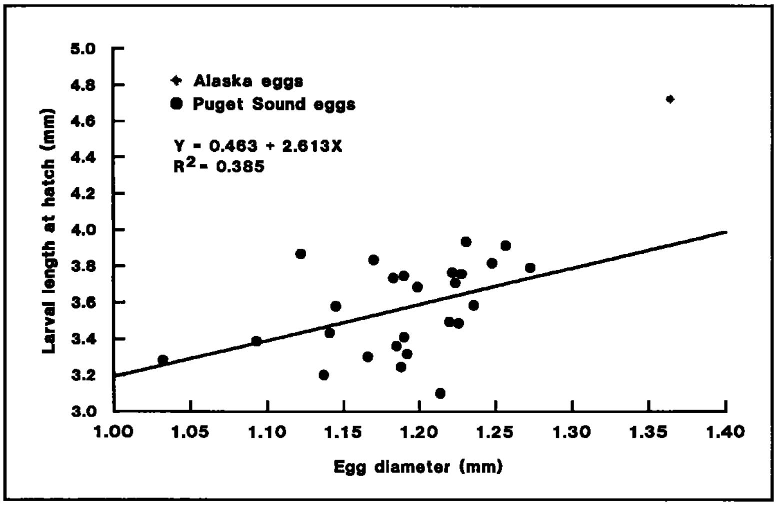

Figure 4A

Relationship between mean diameter of a batch of walleye pollock eggs spawned in the laboratory, and the mean standard length of larvae hatched from that batch.

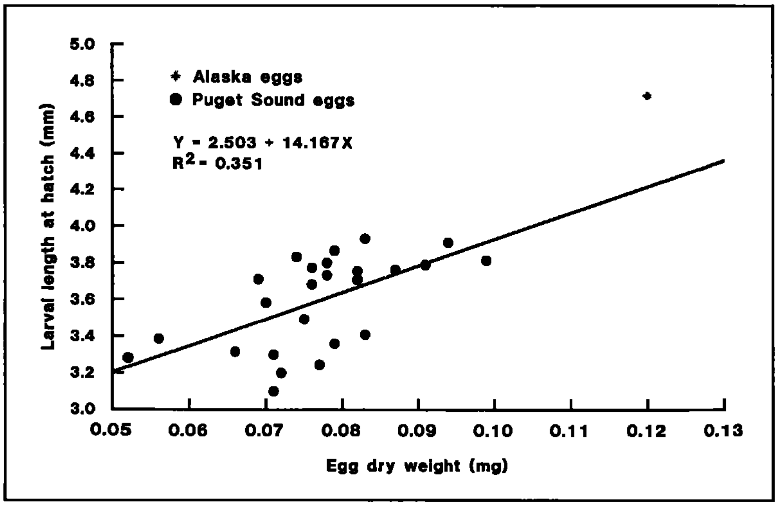

Figure 4B

Relationship between mean dry weight of a batch of walleye pollock eggs spawned in the laboratory, and the mean standard length of larvae hatched from that batch.

Mean egg diameter per batch of eggs spawned declined over the spawning cycle of an individual for all females (Fig. 3). The average decline in egg diameter over the batch spawning cycle (for females that completed spawning) was 0.14 mm, or 11.5% of the initial egg diameter.

Thirty-three batches of eggs were incubated and hatched. Larval standard length at hatch was positively correlated with egg diameter (Fig. 4A) and egg dry weight (Fig. 4B). The regressions of larval length at hatch on egg diameter and dry weight were both significant ($0.001<p<0.0025$, $R^2=0.385$, and $0.001<p<0.0025$, $R^2=0.351$, respectively).

Eighteen batches of larvae were raised to yolk-sac absorption and measured. The relationship between egg size and larval size at yolksac absorption was more variable than at hatch. Both egg diameter and dry weight were significantly correlated with larval length at yolksac absorption ($0.025<p<0.05$ and $0.005<p<0.01$, respectively; Fig. 5A, B).

Egg diameter varied positively with larval dry weight at yolksac absorption (Fig. 6A, $0.0025<p<0.005$, $R^2 = 0.462$), as did egg dry weight and larval dry weight at yolksac absorption (Fig. 6B, $p<0.0005$, $R^2 = 0.852$).

Discussion

Characteristics of spawning

The laboratory work from this study supports Sakurai's (1982) evidence that the batch spawning process in walleye pollock (which are partially synchronous spawners; Hinckley 1987) extends over a period of about a month, at least in the laboratory. Sakurai's walleye pollock, however, spawned approximately every 3 days, whereas walleye pollock in this study spawned about every 2 days. This probably reflects the effect of higher water temperatures in this study ($\bar{x}$ 10.1°C, versus 3.5–7.6°C in Sakurai's study). Higher temperatures have been shown to decrease the inter-

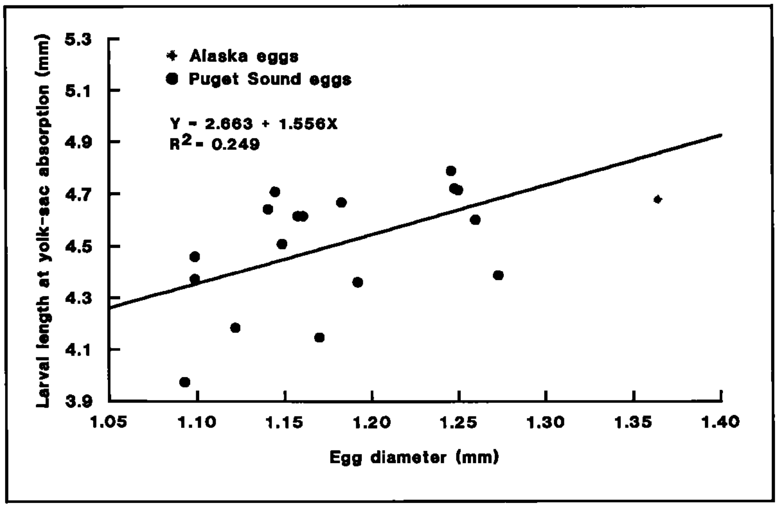

Figure 5A
Relationship between mean diameter of a batch of walleye pollock eggs spawned in the laboratory, and the mean standard length of larvae at yolksac absorption.

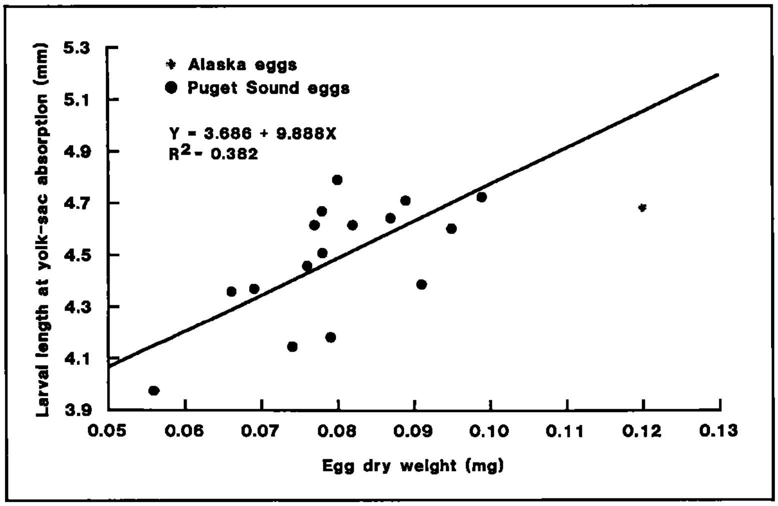

Figure 5B
Relationship between mean dry weight of a batch of walleye pollock eggs spawned in the laboratory, and the mean standard length of larvae at yolksac absorption.

val between batches of eggs spawned in Atlantic cod *Gadus morhua* (Kjesbu 1988).

Egg size variation within and among females

The laboratory studies showed that egg diameter in walleye pollock declined significantly over the spawning period of an individual. This was also shown by Sakurai (1982) for walleye pollock (over a limited portion of the spawning cycle) and for other gadoids by Hislop et al. 1978 and Moksness and Vestergård 1982 (*Melanogrammus aeglefinus*), by Grauman 1965 and Solemdal 1970 (*Gadus morhua*), and Hislop 1975 (*Merlangius merlangus*). The amount of decrease seen in walleye pollock, about 12%, was comparable with that seen in *Gadus morhua* by Kjesbu (1988) (7–15%) and with that in *Merlangius merlangus* by Hislop (1975) (9–14%). This decline may represent an adaptation by the parent stock to conditions faced by the larvae, as discussed later in this section.

Egg size in walleye pollock does not appear to be correlated with female length. The measurement of eggs from the first batch spawned (a method also used by Kjesbu (1988) for *Gadus morhua*) removes variation in egg size caused by the decline in egg size over the course of the spawning cycle, a problem which may have confused the results of other studies of the relationship between egg size and female size. Egg size in walleye pollock did not appear to correlate with female age or condition. Wet weights of body, gonad, and liver are not particularly sensitive indicators of condition in fish, however, and use of these measures may have obscured a correlation between these indices and egg size.

There are many contradictory studies on the egg size-female size relationship. Sakurai (1982, *Theragra chalcogramma*), Marsh (1984, *Etheostoma spectabilis*), Zilstra (1973, *Clupea harengus*), Solemdal (1970, *Gadus morhua*) and Ossthuizen and Daan (1974, *G. morhua*), and others did not find egg size-female size or age

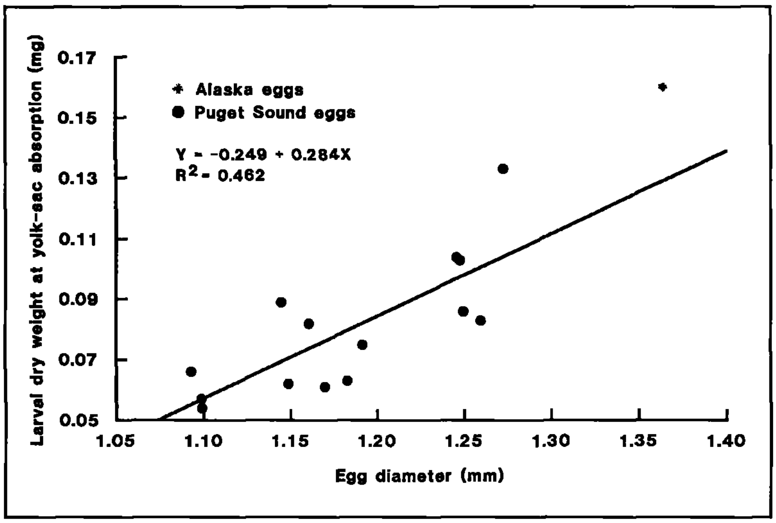

Figure 6A
Relationship between mean diameter of a batch of walleye pollock eggs spawned in the laboratory, and the mean dry weight of larvae at yolksac absorption.

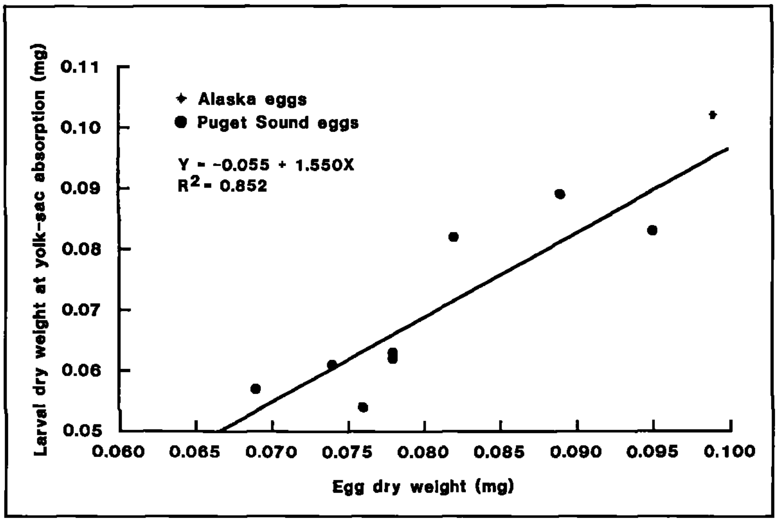

Figure 6B
Relationship between mean dry weight of a batch of walleye pollock eggs spawned in the laboratory, and the mean dry weight of larvae at yolksac absorption.

relationships in their studies. On the other hand, there are numerous studies in which egg size-female size relationships have been seen, such as Blaxter and Hempel (1963, *Clupea harengus*), Hislop et al. (1978, *Melanogrammus aeglefinus*), Grauman (1964, *Gadus morhua*), Kjesbu (1988, *G. morhua*), and many on salmonids. Some studies on the same species contradict one another with regards to this relationship. For those species showing a seasonal decline in egg size, an egg size-female size relationship may have been obscured in studies where this was not taken into account.

Within- and among-population variation in egg size

The population of walleye pollock spawning in Shelikof Strait shows significant seasonal and annual differences in egg size. The seasonal decline in egg size probably covaries with the decline over the spawning cycle. Annual differences in egg size during the peak spawning month (April) in Shelikof Strait appear to be significant. These yearly differences are apparently not attributable to changes in the size or age composition of the spawning stock, as no relationship between these factors and egg size is apparent.

It is possible that differences in the date of peak spawning in different years could change the mean egg size in the first week of April (when eggs measured for this study were collected). There is evidence that the mean date of peak spawning was later in 1986 and 1987 than in some earlier years (Yoklavich and Bailey 1990). The apparent difference in mean April egg size seen in this study could therefore be a reflection of the variability in time between peak spawning and egg collection and the decline in egg size over the spawning season, rather than a true interannual difference.

There appears to be a positive correlation between egg size and latitude in walleye pollock (Table 1). This correlation was also noted by Gorbunova (1954). In this study, this correlation was seen both among widely separated areas such as Puget Sound and the Gulf of Alaska, and within the Gulf of Alaska itself. Latitudinal clines in egg size have been seen by Demir (1963), Chiechomski (1973), and others, and have been discussed by Rass (1941), Marshall (1953), and Thresher (1988). As noted by Thresher, "Latitudinal variation in life histories of marine organisms typically are attributed to selection acting on local populations along a latitudinal environmental gradient..."

Several studies have noted an inverse relationship between egg size and temperature (Southward and Demir 1974, Ware 1977, Marsh 1984, Houghton et al. 1985, Imai and Tanaka 1987). Imai and Tanaka (1987), working with Japanese anchovy *Engraulis japonica*, found yearly changes in egg size which correlated with temperature, and were able, experimentally, to alter egg size during the spawning cycle of anchovy held in the laboratory by changing water temperature. Ware (1977) noted that peak spawning of *Scomber scombrus* occurs later if water temperatures warm more slowly than usual in the spring.

Temperature may be the latitudinal environmental gradient along which selection for egg size acts on local populations. The relationship between latitude and egg size appears to be correlated to temperature in the different spawning regions over the range of walleye pollock (Table 1). In the laboratory experiments on spawning done for this study, ambient water temperature increased over the spawning period, while egg size declined significantly for each female over this period. Mean monthly egg size and mean monthly water temperature at the depth where eggs are spawned (150 m to the bottom) within Shelikof Strait, however, show no apparent inverse correlation. There was also no inverse correlation between mean egg size in April and mean April water temperature at the depth of spawning over the years examined (J.D. Schumacher, Pacific Mar. Environ. Lab., Seattle, WA 98115-0070, unpubl. data). It may be that temperature acts on the parent stock at some earlier date, for example while the stock is migrating to the spawning grounds. Data are insufficient to investigate this question.

Consequences of egg size variation for larval survival

A correlation between egg size and larval size has also been noted in other species (*Clupea harengus*, Blaxter and Hempel 1963; *Salvelinus alpinus*, Wallace and Aasjord 1984; *Etheostoma spectabile*, Marsh 1986; *Gadus morhua*, Solemdal 1970, Knutsen and Tilseth 1985). Only a few studies have reported no correlation (Zonova 1973, Reagan and Conley 1977, Lagomarsino et al. 1988).

Egg size has been correlated with other larval factors. Growth rate, for example, has been seen to increase with increased egg size (Blaxter and Hempel 1963, Bagenal 1969, Wallace and Aasjord 1984, Moodie et al. 1989). This may be related to increased feeding success due to larger mouth sizes or increased search area (from increased reactive distance or swimming speed). Mouth size has been positively correlated with egg size (Blaxter and Hempel 1963, Shirota 1970, Knutsen and Tilseth 1985). Larvae with larger mouths are able to take larger or more varied sizes of prey items. Length of time from hatch to starvation (due to increased endogenous yolk reserves; Blaxter and Hempel 1963, Bagenal 1969, Theilacker 1981, Marsh 1986, Wallace and Aasjord 1984), and survival (Blaxter and Hempel 1963, Bagenal 1969, Pitman 1979, Small 1979, Moodie et al. 1989) have also been positively correlated with egg size. If larval survival is affected by larval size at hatch (Miller et al. 1988) and other factors, then variation in egg size in walleye pollock may cause differences in larval mortality rates.

It has been proposed that changes in egg size may be an adaptation to the timing of the production cycle, to ensure that larvae are produced that are able to take advantage of the available food supply (Cushing 1967; Hempel and Blaxter 1967; Bagenal 1971; Jones and Hall 1974; Ware 1975, 1977). The reproduction of zooplankton (such as copepods, e.g., *Pseudocalanus* and *Oithona* spp., whose naupliar stages constitute the most common food of first-feeding walleye pollock larvae in the Bering Sea and the Gulf of Alaska; Clarke 1978, 1984; Nishiyama and Hirano 1983; Kendall et al. 1987) is temperature and food related (Checkley 1980a, b; Durbin et al. 1983; Runge 1985; Corkett and McLaren 1978; Landry 1976). This implies that temperature would provide information on the timing of zooplankton reproduction, and therefore on the size of the available larval food supply (Ware 1977). Information on the changes in species and size composition of larval food sources in the western Gulf of Alaska is not presently available. The observed trends in egg size would be explained in terms of larval food supplies if the abundance of prey items increased and the size of food particles decreased and became more uniform as the season progressed.

The observed trends in egg size may also be a result of an adaptation to relieve predation pressure on eggs and larvae. Seasonal changes in egg size could result in changes in the predator-prey size ratio for eggs and larvae, affecting predation rates (Bailey and Houde 1989). This may not be important if egg predators are mainly planktivorous fishes. With zooplankton predators, however, small changes (10–20%) in egg diameter may affect their ability to handle or consume eggs. Also, if the abundance of egg predators increases, or they co-occur more frequently with eggs, then smaller but more numerous eggs (assuming a tradeoff between egg size and fecundity; Svardson 1949, Bagenal 1978) may be an adaptation to offset higher rates of predation later in the season.

Miller et al. (1988) have shown that predation rates are negatively correlated with larval size, possibly due to differences in predator mouth size, encounter rates of larvae and their predators, or the ability of larvae to escape predators. Trends in egg size and the resulting differences in larval size at hatch may, therefore, also be an adaptation to relieve predation on larvae, if the size, species composition, and co-occurrence of predators and larvae changes seasonally.

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