EGG SIZE VARIATION IN PACIFIC HERRING,

CLUPEA HARENGUS PALLASI (VALENCIENNES),

AND ITS EFFECTS ON LARVAL GROWTH AND SURVIVAL

by

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ABSTRACT

This thesis investigated variation in egg size with size of the female parent in Pacific herring, Clupea harengus pallasi (Valenciennes), and the effect of this variation on subsequent larval growth and survival. Egg weight was found to increase markedly with length or weight of the female; larger females had mean egg weights up to 50% greater than those observed in the smaller females. Differences in egg size had no effect on fertilization rate, incubation time, or hatching success, contrary to some of the other findings in the literature. Total weight at hatch, that is, the weight of the larvae and yolk combined, was highly correlated with original egg weight. Larvae from larger eggs generally had more yolk at hatch, grew more quickly on the yolk reserves, and took longer to reach complete yolk absorption. The net result was that small differences in size at hatch were amplified and larvae from larger eggs were substantially longer and heavier at yolk absorption than larvae of the same age from smaller eggs.

Under starvation conditions, larvae from larger eggs survived 4 to 5 days longer than larvae from smaller eggs at 9.1 °C. The magnitude of this difference was temperature dependent. When fed an Artemia diet larvae from smaller eggs and larvae from larger eggs had similar growth rates regardless of when feeding was initiated. Trends in survival with egg size were not significant except when feeding was initiated early. In this case, survival declined significantly as egg size increased. Implications of these results in terms of

fisheries management are discussed.

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INRODUCTION

Intraspecific Variation in Egg Size

Intraspecific variation in egg size has been observed in many species of fish, yet the causes and effects of this variation have been given little attention to date (Hempel, 1979). Bagenal (1971) listed the variation in egg size for 46 species of marine fishes. Differences in egg volume, expressed as the percent difference between smallest and largest eggs, ranged from as low as 4.5% in Pegusa lascaris to as high as 404% in Engraulis encrasicolus. Variation in egg size is important because it may influence the growth and survival of the resultant larvae (Blaxter and Hempel, 1963; Blaxter, 1969; Hunter, 1980).

Intraspecific differences in egg size derive principally from three sources. These are:
(1) differences between stocks such as those differences found between winter-spring spawning and summer-autumn spawning stocks of Atlantic herring (Hempel and Blaxter, 1967). These differences appear to be related to the time of year during which spawning takes place, which determines to some extent the amount of food available to the larvae (Bagenal, 1971).
(2) changes in egg size within a stock which occur over a spawning season as has been demonstrated for Atlantic mackerel, Scomber scombrus (Ware, 1977), and a variety of other species: Pleuronectes platessa, Solea solea, and Merlangus merlangus (Bagenal, 1971). During a protracted spawning period, a shift

is generally observed where larger eggs are produced in the winter or early spring and progressively smaller eggs are produced as spawning approaches the summer months. Like the differences found between stocks of Atlantic herring, this variation is thought to be adaptive since larger eggs should result in larger larvae with greater survival potential when food production is low, as is the case in the winter months (Hempel, 1979). According to Bagenal (1971), the decrease in egg size is not associated with trends in sea temperature or salinity, and he concludes that it is a biological phenomenon. Blaxter (1969) suggests that low fecundity and large egg size of winter spawning Atlantic herring are adaptations to reduced food supply and predator populations.

(3) variation in egg size reflects variation in maternal size: larger females often have larger eggs. That younger females in a stock may produce smaller eggs than older or larger individuals has been demonstrated for a number of species (table 1). The positive correlation of egg size with fish size has been found in most of the fish stocks investigated, although the relationship is less apparent in highly fecund marine species (Hempel, 1979). For example, the relationship is variable both in Atlantic cod and in Atlantic herring. Blaxter and Hempel (1966) concluded for herring that more data are needed to establish whether differences they observed were consistent. In cases where significant results were obtained the relationship was primarily dependent on the smaller egg sizes found in recruit spawners. Schopka (1971) found a relationship in North

Table 1. Previous studies that have related egg size and female size, showing the species and the nature of the relationship (n.s = non-significant at the 0.05 level).

Species	Study	Relationship
Argentine anchovy	Ciechomski, 1966	Positive
Atlantic cod	Oosthuzen and Daan, 1974	Positive,n.s.
	Grauman, 1973	Positive
	Schopka, 1971	Variable
Atlantic herring	Blaxter and Hempel, 1963	Variable
	Schopka, 1971	Positive
	Krivobok et al, 1971	Positive
	Toom, 1958	Positive
Atlantic salmon	Pope et al, 1961	Positive
Brown trout	Hardy, 1967	Positive
Carp	Hulata et al, 1974	Positive
	Anisimova, 1956	
Caspian roach	Nikolskii, 1963	Positive
Chinook salmon	Fowler, 1972	Positive
Dogfish	Templeman, 1944	Positive
Flounder	Solemdal, 1967	Variable
Largemouth bass	Laurence, 1969	Positive
Medaka	Stanley, 1977	None
Pacific herring	Jones, 1972	Positive,n.s.
Plaice	Bagenal, 1971	Positive
Queenfish	DeMartini and Fountain, 1980	Positive
Rainbow trout	Scott, 1962	None
	Gall, 1974	Positive
Sockeye salmon	Rounsefell, 1957	Positive
Steelhead	Bulkley, 1967	Positive
Surf smelt	Stanley, 1977	Positive
Texas darter	Hubbs et al, 1968	None
Tilapia	Peters, 1963	Positive

Sea cod between egg size and length of the mother, while in Icelandic cod the relationship was with age of the mother. In Baltic cod, there was no correlation of egg size with length or age. Oosthuzen and Daan (1974) found no significant relationship in North Sea cod, while Grauman (1973) found a positive relationship in Baltic stocks. In spite of these contradictory findings, the phenomenon of increasing egg size with female size is generally well established. In a few

instances it appears that egg size may decline slightly in very old spawners (Krivobak et al., 1971).

Egg Size and Larval Survival

Differences in egg weight are mainly due to differences in the quantity of yolk (Peters, 1963). Larger eggs produce larger larvae with greater yolk reserves at hatch than those from smaller eggs (Blaxter and Hempel, 1963; Bagenal,1971; Toom, 1958). Larger eggs might confer a survival advantage on the larvae in one or a combination of three ways:

(1) Larger larvae with greater yolk reserves may have a longer time to starvation and therefore may be able to survive for longer periods before encountering food.

(2) Larger larvae, once food has been encountered, may feed more efficiently due to higher swimming speeds, greater reactive distances, and a larger gape.

(3) Larger larvae may be better able to avoid predation due to higher swimming speeds and greater physical size.

The first of these three points is supported by Blaxter and Hempel (1963, 1966), who found that larger eggs did result in longer times to starvation. This was true for eggs of widely different sizes taken from different races or stocks of Atlantic herring. Within a race, differences in egg size were not as great and the larvae hatching from larger eggs did not survive longer than those from smaller eggs under starvation conditions. This was presumably due to the higher metabolic demands of the

larger larvae. Bagenal (1969), studying brown trout, Salmo trutta, found that large fry derived from large eggs survived longer without food than small fry from small eggs. The same was true of jack mackerel larvae (Theilacker, 1980). On the other hand, Stanley (1977) and Ciechomski (1966), working with medaka and Argentine anchovy respectively, found that the size of the egg had no detectable effect on survival times of larvae deprived of food.

The effects of egg size on growth and survival of fed larvae in hatchery situations have been investigated in rainbow trout (Gall, 1974) and chinook salmon (Fowler, 1972). Growth, at least in the early stages, was observed to be highly correlated with original egg size. Growth of fed carp larvae also appears to be dependent on egg weight (Hulata et al, 1976). On the other hand, Fowler (1972) found in three separate runs that total mortality was significantly higher in larvae derived from large eggs. Observations of swimming speed, reactive distance, and gape all show these parameters to be positively correlated with larval size (Hunter, 1972; Blaxter, 1969; Blaxter and Hempel, 1963). Unfortunately, the latter studies confound the effects of age and size since conclusions were drawn using larvae of different ages.

Studies of predation on fish larvae are rare. Lillelund and Lasker (1971) found that several species of marine copepods were efficient predators of anchovy larvae, but that swimming and escape ability increased as the larvae grew. Theilacker and Lasker (1974) tested the ability of Euphausia pacifica to

capture anchovy larvae. Again, the capture success was reduced when older, more active larvae were introduced. These studies also confound the effects of age and size and many of the differences between larger and smaller larvae can be attributed to learning or developmental effects.

Bagenal (1969) examined the effects of egg size on brown trout larvae under relatively natural conditions using cages embedded in a stream. The larvae were subject to natural variations in physical conditions and food availability, but not to predation. Trout fry survival was significantly greater in fry derived from larger eggs. Bagenal believed this might be due primarily to competition for space among larger and smaller larvae rather than differences in feeding capabilities or starvation times.

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Female Size and Larval Survival

If younger or smaller females produce smaller eggs which result in less viable larvae, then it is likely that the younger female spawners in a stock produce less viable larvae. This has been suggested by a number of authors (Nikolskii, 1963; Blaxter and Hempel, 1963; Stanley, 1977), but has received little interest from other investigators. Since the effect of a fishery is to lower the average age of the stock, less viable egg production in younger fish could conceivably have serious effects on recruitment beyond those due to changes in total egg production. Bridger (1960, 1961; cited by Parrish and Saville,

1965) postulated such an effect for Atlantic herring. He found a strong correlation between the spawning potential of fish 5 years or older and the number of larvae produced. When the entire stock was considered, there appeared to be no relationship. Likewise, Ponomarenko (1973), working with Atlantic cod, found that when recruit spawners are predominant in the spawning stock, the probability of the appearance of a strong year class is very slight, even if the spawning population is large. The probability of a strong year class was positively related to the proportion of the stock made up of repeat spawners. Ponomarenko concluded that smaller females produce less viable offspring. Ponomarenko and Nikolskii (1963) both suggested that the recruit spawners constitute a reserve, which can contribute in a significant way to recruitment only under very favorable conditions. Hempel and Blaxter (1967) concluded, however, that the age- or size-specific effect on larval survival in Atlantic herring was negligible based on a maximum observed egg size difference of 14% between young recruits and older spawners, and that it was unlikely that a significant maternal effect on larval survival existed. This conclusion seems premature in light of the available information.

The present study investigates the relationship between female size, egg size, and larval growth and survival in a stock of Pacific herring, Clupea harengus pallasi . The hypothesis that age or size of the female affects larval survival is reformulated as three statements:

(1) In Pacific herring, <u>Clupea</u> <u>harengus</u> <u>pallasi</u> , larger females have significantly larger eggs at spawning than do younger individuals.

(2) Under starvation conditions, larvae derived from larger eggs have a larger size, faster growth, and longer survival times than larvae from smaller eggs.

(3) Under a variety of delayed feeding regimes larvae from larger eggs have a greater capacity to withstand starvation, and higher growth and survival rates than larvae from smaller eggs.

MATERIALS AND METHODS

All experiments were carried out at the Pacific Biological Station in Nanaimo, B.C. Ripe herring were obtained from Nanoose Bay in 1980 and from Departure Bay in 1981. In both cases, the herring were obtained from seiners engaged in test sets prior to the opening of the roe fishery. Herring were dipnetted from the pursed seine net and placed in oxygenated holding tanks on board another vessel. The fish were then transported to P.B.S. and held in large circular tanks supplied with flow through seawater taken from Departure Bay.

Ripe males and females were selected from the larger group in such a way as to provide as wide a range of sizes as possible. Each fish was sampled for standard length and weight, and scales were taken for aging. A sample of eggs was taken from each female by applying gentle pressure to the abdomen, thereby forcing eggs out through the genital opening. A minimum of 50 eggs were taken from each female and fixed in 4% formalin. Additional samples were taken from five females and dry egg weights determined without preservation for comparison with fixed dry weights. Eggs were also sampled from eight different gonad positions in three females to confirm that egg size is independent of position in the gonad. Eggs were dried on glass slides at 90 degrees for 24 hours and weighed individually on a Cahn microbalance accurate to 1 μg. Dry weight is believed to be the best measure of egg size as both diameter and volume are dynamic quantities which change markedly following fertilization (Blaxter, 1969) and depend to some extent on the past osmotic

history of the female (Solemdal, 1967).

The methodology involved in fertilization and incubation of the eggs is straightforward and well described elsewhere (Alderdice and Velson, 1978). The adhesive eggs were squeezed from the female onto labelled glass slides in narrow lines. These were then fertilized with a sperm solution obtained by removing the testes from several males and mixing the contents with seawater. The glass slides with fertilized eggs were then placed in racks in the water table for incubation. Larval experiments were conducted in aquaria placed in water tables to maintain constant water temperature.

Year 1 (1980)

In year 1, forty females over as wide a range of size as possible were used as sources of ripe eggs. Each fish was sampled as noted above and approximately 2000 eggs from each female were fertilized on glass slides. The fertilization success was determined the next day by counting approximately 300 eggs under a dissecting microscope and noting the number which were unfertilized. Unfertilized eggs are easily distinguished by absence of cleavage and failure to form the perivitelline space. There is no swelling in unfertilized eggs and therefore they are significantly smaller than fertilized eggs.

The development of the larvae was monitored daily. One or two days before the initiaton of hatch the eggs from each female were placed in separate containers. The percent hatch was

estimated by counting a representative number of eggs daily following the first day of hatching. Eggs that had hatched out were detected by the presence of empty shells attached to the glass slide. When it appeared that no further hatching would occur, the slides were removed from the containers and the final hatch estimated.

On the 17th day following fertilization, or 2 days after the main hatch, 100 larvae from each female were placed in separate 1 liter containers on the water table. The containers were not aerated since Blaxter and Hempel (1963) found that larvae lived longer in unaerated jars. This set of containers was used to estimate the mortality of the larvae under starvation conditions. Dead larvae in each container were removed and counted daily. Dead larvae are white and opaque and easily detected on the bottom of the containers when held against a dark background. The total number of dead larvae was used to confirm the initial number present.

The hatching containers were adjusted to contain approximately the same number of larvae and these were sampled periodically to estimate growth and yolk utilization. Commencing on the first day of hatch, 10 larvae per day were sampled from each container, anaesthetized with MS222, and preserved in 4% formalin solution. Anaesthetization before preservation prevents excessive bending of the larvae and facilitates later measurement. Fresh dry weights were also measured on several occasions for comparison with fixed dry weights.

Throughout the experiment, temperatures were monitored daily. Minor differences between containers could be eliminated by adjusting the water flow in the water table. Salinities were checked periodically and water lost to evaporation replaced with distilled water.

The preserved materials were analyzed at U.B.C. following completion of the experiments. Fixed larvae were rinsed briefly and placed on glass slides previously treated with a silicon compound, 'Siliclad', which facilitated removal of the larvae for weighing following drying. Each larvae was measured for length, from the tip of the snout to the end of the notochord, as well as length and height of the yolk. Yolk volume was calculated as an approximation to the volume of a spheroid, where;

$$V=(\pi/6)lh^2$$

This approximation has been used formerly by Blaxter and Hempel (1963) and by Howell (1980).

The yolk sac was dissected away from the body and both were dried for 24 hours at 90° C, then cooled in a desiccator and weighed on a Cahn microbalance to the nearest 1 μg. Ehrlich (1974) found that dried larvae gained an additional 1% weight during weighing due to absorption of atmospheric water.

Year 2 (1981)

In the second year of the study, growth and mortality of the larvae was examined under a variety of delayed feeding regimes. Eggs and the same information collected in year 1, including gonad weight and carcass weight, were taken from 28 females. Eggs were fertilized from 10 females representing the broadest range of available sizes. In year 2, the eggs were extruded onto nitex screens measuring 30 * 45 cm thereby greatly increasing the number of fertilized eggs per female. The fertilization procedure and the means of estimating fertilization rate, incubation time, and hatching success followed the methodology given in year 1.

The larvae were held in 18 liter aquaria with 750 larvae per aquarium. Four treatments were used: starved, first fed on day 15, first fed on day 17, and first fed on day 20. Since the mean day of hatch in year 2 was 12 days following fertilization the first feeding took place 3 days following hatching. The larvae were fed Artemia nauplii from eggs incubated at 28-29 ° C for 24 hours. Each aquarium received approximately 20,000 nauplii per day or roughly 1.1 nauplii per ml. Werner and Blaxter (1980) found for Atlantic herring that Artemia densities exceeding 0.1-0.3 per ml did not result in increased growth or survival. Likewise, Haegele and Outram (1978) found no improvement in growth or survival of Pacific herring larvae when total daily ration exceeded 7500 nauplii per day in 8 liter tanks. It is therefore assumed that larval food was in excess at all times from commencement of feeding. Artemia densities

were probably higher than 1.1 per ml as there were always nauplii remaining in the tank from the previous day's feeding. Dead Artemia and larvae were siphoned from the bottom of the tank daily and the dead larvae counted for estimatiom of larval mortality.

In order to estimate size and growth, 20 larvae per day for the first 7 days following hatch and 20 larvae every second day thereafter were collected from each tank and preserved. The subsequent analysis of preserved samples was identical to year 1. The experiment was terminated when the fed larvae reached 32 days of age.

A second set of experiments was initiated subsequent to completion of the first. It was originally planned to repeat the feeding experiment using natural plankton less than 200 μ in size as a food source. It was believed that this might overcome some of the limitations of using Artemia. Unfortunately, after 10 days of plankton tows it became apparent that sufficient plankton in the desired size range was not available and the experiment was terminated. The adequacy of Artemia as a food source for herring larvae is discussed in a subsequent section of the thesis.

RESULTS

<u>Female</u> <u>Size</u> <u>and</u> <u>Egg</u> <u>Size</u>

Egg size, expressed as dry weight, is positively correlated
with length or weight of the female. The relationships between
egg weight and female weight, and egg weight and female standard
length, are shown in figures 1 and 2 respectively. The results
of regression analyses are given in table 2. The data from both
years have been combined in the final regression since analysis
of covariance shows no significant difference between slopes or
intercepts in different years (table 3). The dry weights given
are those of eggs previously fixed in 4% formalin. Five sets of
fixed and fresh dry weights were compared. The fixed dry
weights averaged 5.1% less than fresh dry weights.

Table 2. Results of regression analyses of mean egg weight
(ug) as a function of female size, expressed both
as weight (g) and length (cm). The indicated prob-
ability is the probability that slope=0.

Variable	Source	Intercept	Slope	r^2	F	n	P
Weight	Year 1	183	.543	.594	67.2	48	.000
	Year 2	189	.507	.541	30.6	28	.000
	Total	185	.527	.571	98.5	76	.000
Length	Year 1	17	11.2	.515	49.9	49	.000
	Year 2	29	10.7	.551	31.9	28	.000
	Total	22	11.0	.528	84.0	77	.000

Although the regressions are highly significant, they only
account for about 55% of the observed variation in mean egg

Figure 1. The relationship between mean egg weight and female weight for years 1 and 2. The regression lines for each year are not significantly different and the data are combined to obtain the line of best fit shown.
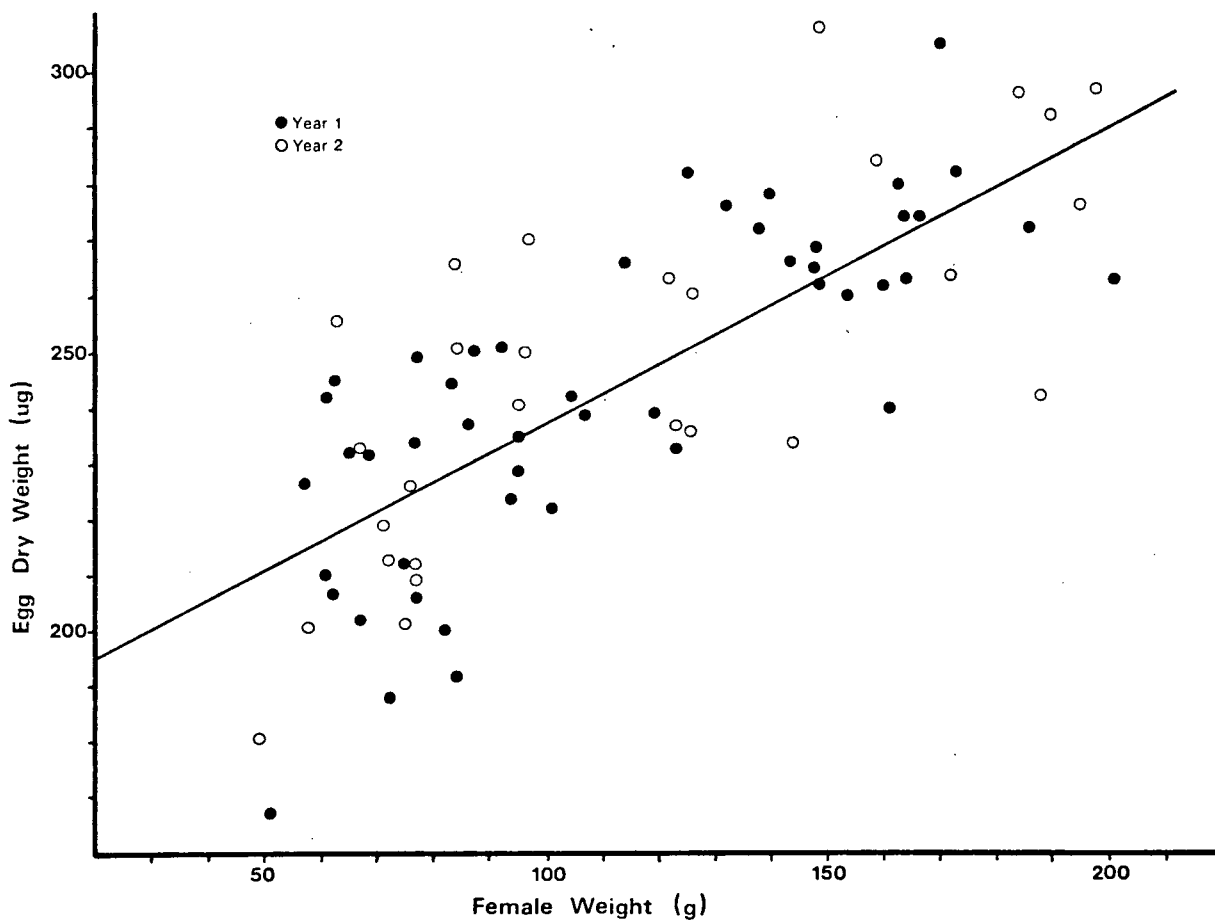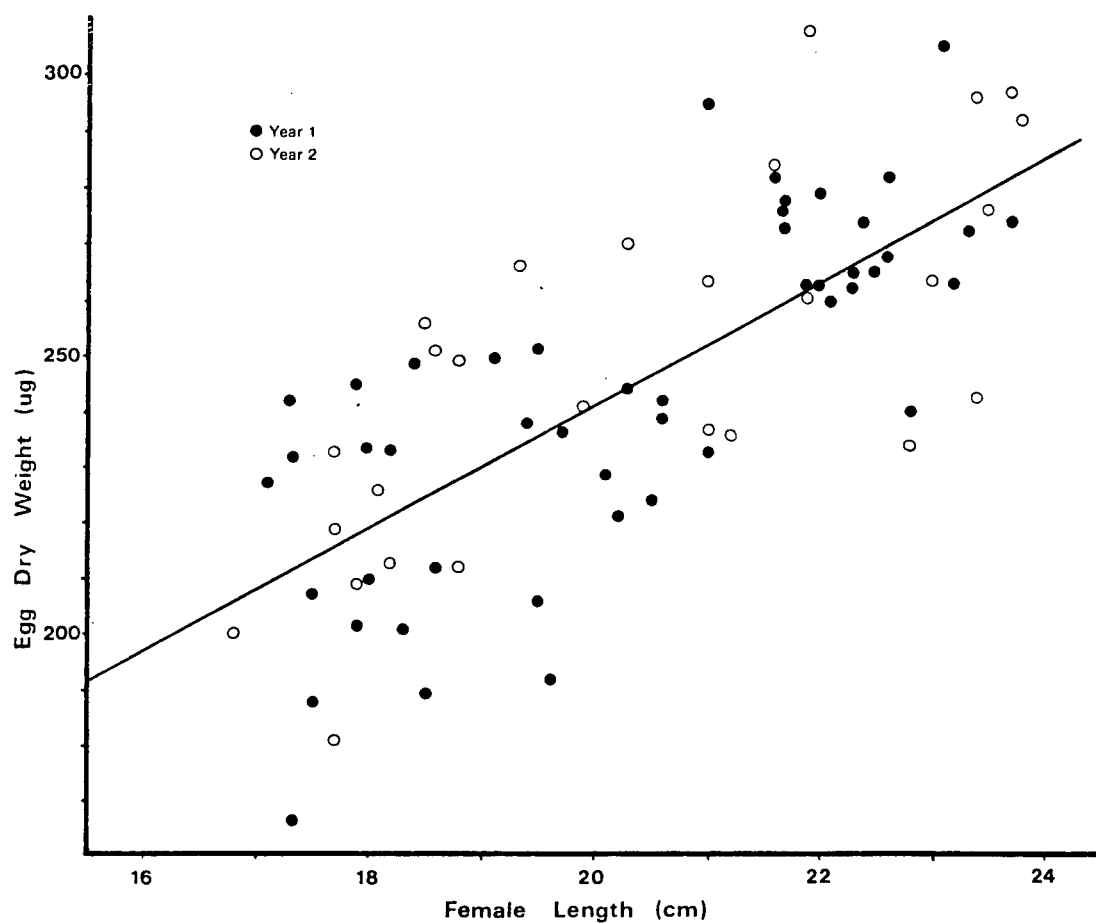
Figure 2. The relationship between mean egg weight and female length for years 1 and 2. The regression lines for each year are not significantly different and the data are combined to obtain the line of best fit shown.

Table 3. Results of analysis of covariance performed on regression lines of mean egg weight as a function of female size, expressed both as length and weight. There is no significant difference between the two years (analysis according to Snedecor and Cochran, 1967).

Variable	Hypothesis	F	dF	P
Weight	Slopes are equal	.112	1,72	>.25
	Intercepts are equal	.116	1,73	>.25
Length	slopes are equal	.027	1,73	>.25
	Intercepts are equal	.182	1,74	>.25

size. The larger scatter of points around the regression lines represent individual differences, either in feeding history and therefore the amount of energy available for reproduction, or in the way that individual fish balance fecundity and egg size.

The smallest egg weight recorded was 151 ug and the largest was 325 ug. The eggs from the largest females are up to 50% larger than those from smaller females. This difference is substantial when compared with the maximum 14% difference found between older and recruiting females in stocks of Atlantic herring (Blaxter and Hempel, 1967). Blaxter and Hempel also found that positive correlations between egg weight and female size were significant only if egg weights from new recruits were included in the data. Egg weights did not increase as markedly with female size in the larger size classes. In this study, the egg weight increases at a constant rate with the size of the female.

Recently, investigators at the Pacific Biological Station have derived egg weights for a number of Pacific herring stocks using information on gonad weight and fecundity for different

sized fish. Preliminary results indicate that all of the stocks demonstrate a positive relationship between egg size and female size (Hay, pers.comm.).

Previous work by Anokhina (1971) suggests that fat content or condition of herring might in some way influence egg size. Therefore the condition factor of the female was compared to egg size, where;

$$\text{Condition Factor} = \text{body weight}/(\text{length})^{3.23} * 10^3$$

The exponent, 3.23, was derived as the slope of the length-weight relationship when log weight was plotted against log length (r=.979). There was no significant relationship between condition factor and egg size (r^2=.003, p=.79).

Variation in egg size within individual females was considerably less than between females: the range in egg weight was about 30 μg and the standard deviation of each sample of 30 eggs varied between 5 and 8 μg. The 95% confidence intervals for the mean weight were normally within plus or minus 2.9 μg of the estimated value. There was no significant difference in egg size between samples taken from different positions in the gonad (table 4).

Table 4. Results of a two-way analysis of variance. The two
factors are gonad position, one of eight locations
in the gonads from which eggs were taken, and fish,
which of three fish the samples were taken from.

Source of Variation	SS	DF	MS
Total	1,296,362	719	
Cells	1,255,203	23	
gonad position	820	7	117
fish number	1,252,345	2	626,172
interaction	2,038	14	146
Error	41,159	696	59

H: Egg size does not vary between different locations in
the gonad.
F=1.98 DF=7,696   P > .05
H accepted

H: Egg size does not vary between fish.
F=10,600 DF=2,696 P << .001
H rejected

Egg Size Effects

Fertilization rate

Fertilization rate is not affected by egg size (figure 3) or by the size of the female. In year 1, the overall rate of fertilization was 91.6%; the lowest value observed was 85.4% and the highest was 97.1%. In year 2, the overall fertilization rate was 81.3% and more variable. The lowest value recorded was 70.6% and the highest was 92.2%.
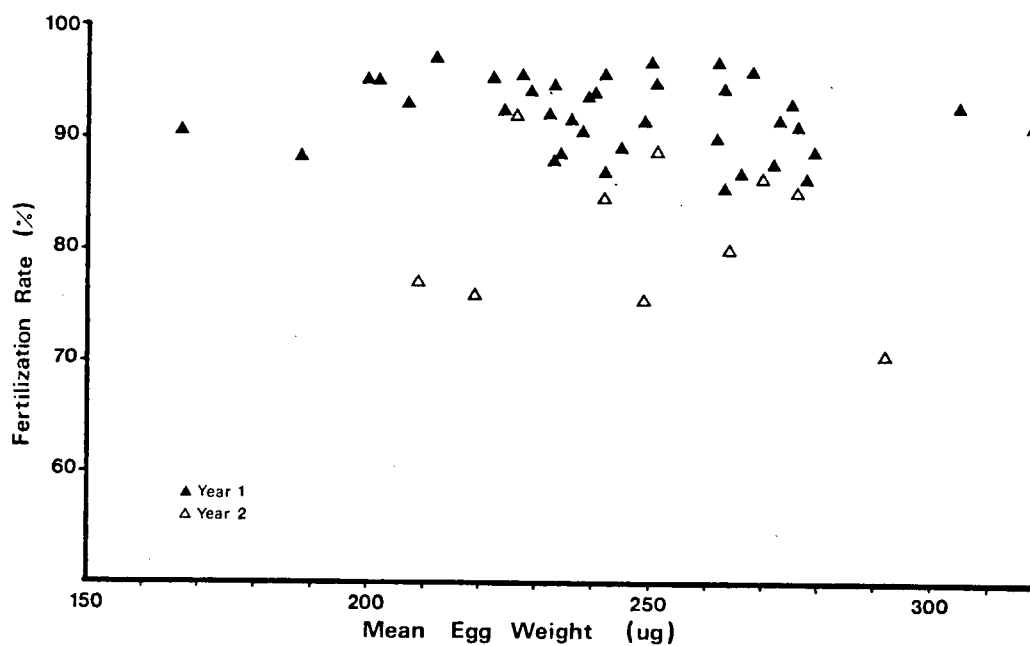
Figure 3.   Percent fertilization and egg weight.   There does
   not   appear   to   be   a   relationship   between   the   two.
   Fertilization rate is slightly lower overall in the second
   year.

Incubation Time

Hatching of the larvae occured over a period of 3 to 4 days
in a pattern similar to that described by Alderdice and Velson
(1971). Hatching took place during the dark hours and the
number of larvae hatched was estimated each morning. The
incubation time is here defined as the mean day of hatch.
Blaxter and Hemple (1963) defined incubation time as the time
from fertilization to 50% hatch. The two methods give similar
results.

Incubation time between years varied since the water system
temperature was slightly higher in year 2. During the first
year the seawater system averaged 9.1 C and the total incubation
time was 15.5 days; in the second year the seawater system
averaged 9.9 C and the total incubation time was 12.4 days.
These values correspond with those found by Alderdice and Velson
(1971) for Pacific herring incubated at various temperatures,
although the incubation time during the second year is somewhat
lower than might be expected.

The incubation time did not depend in any way on size of
the egg and it is apparent that minor temperature differences
would have a much more dramatic effect than egg size (figure 4).
It should be noted that incubation times measured in the
laboratory may have little correspondance with those observed in
the sea. In the lab the eggs are in calm water baths, while in
the sea they are exposed to a variety of conditions such as air
drying and wave turbulence. Handling or vibration of herring
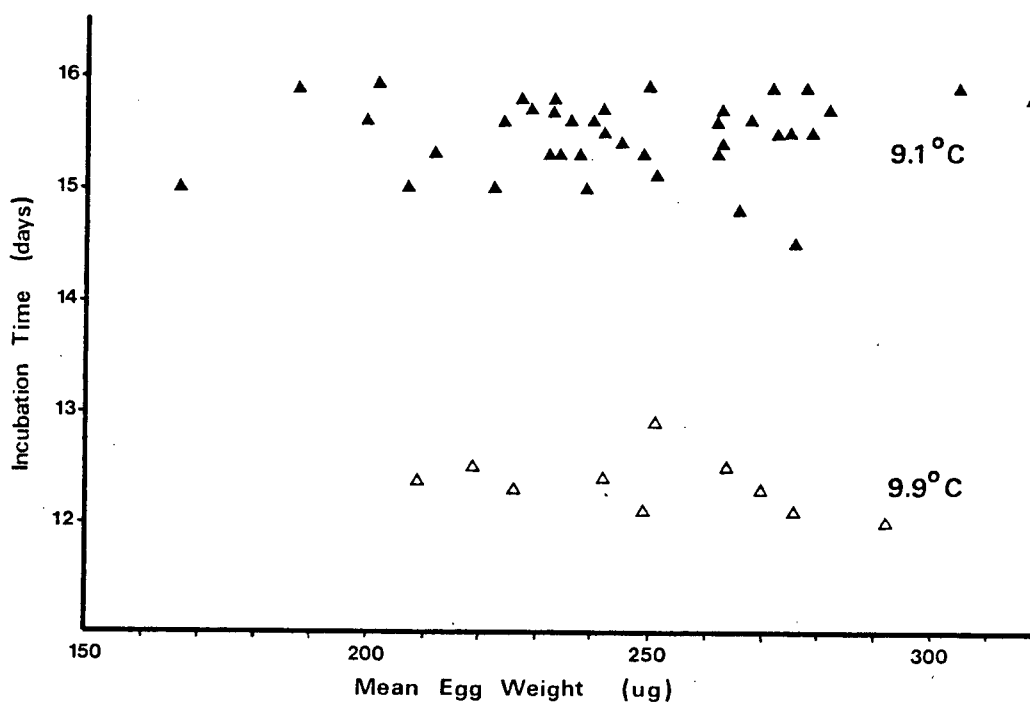eggs definitely causes hatching to occur earlier than might be

Figure 4. Incubation time and mean egg weight. There is no relationship between the two quantities. Two sets of data are shown for two different incubation temperatures; Year 1, 9.1 C; Year 2, 9.9 C.

expected otherwise (Marliave, 1975; Hay, pers.comm.). Since this is the usual case under natural conditions, hatching in the sea likely occurs earlier than in the lab.

Hatching Success

Hatching success is the percentage of eggs initially fertilized that hatch out. Knowing the initial number of eggs fertilized, this quantity was estimated by counting the number of dead embryos remaining inside the egg cases after hatching was complete. Hatching success was determined for year 1 only.

The average hatch rate was 70% with values ranging from 35.2% to 93.6%. There was no relationship between hatching success and egg size (figure 5). Jones (1972) found some indication of a relationship between these two quantities; eggs from smaller females had a lower survival rate from fertilization to hatch.

Size and Condition at Hatch

During the first year of the study, larvae were preserved in 4% formalin solution prepared using distilled water. This salinity of preservative results in minimum shrinkage of larvae in terms of length (Hay, 1982). Samples of larvae were measured fresh and after fixation. In 25 fixed samples, the average shrinkage in length was 3.7%. Changes in dry weight were much larger, though relatively constant. In 5 samples, the fixed dry weight averaged 35.6% lower than fresh dry weight of larvae from
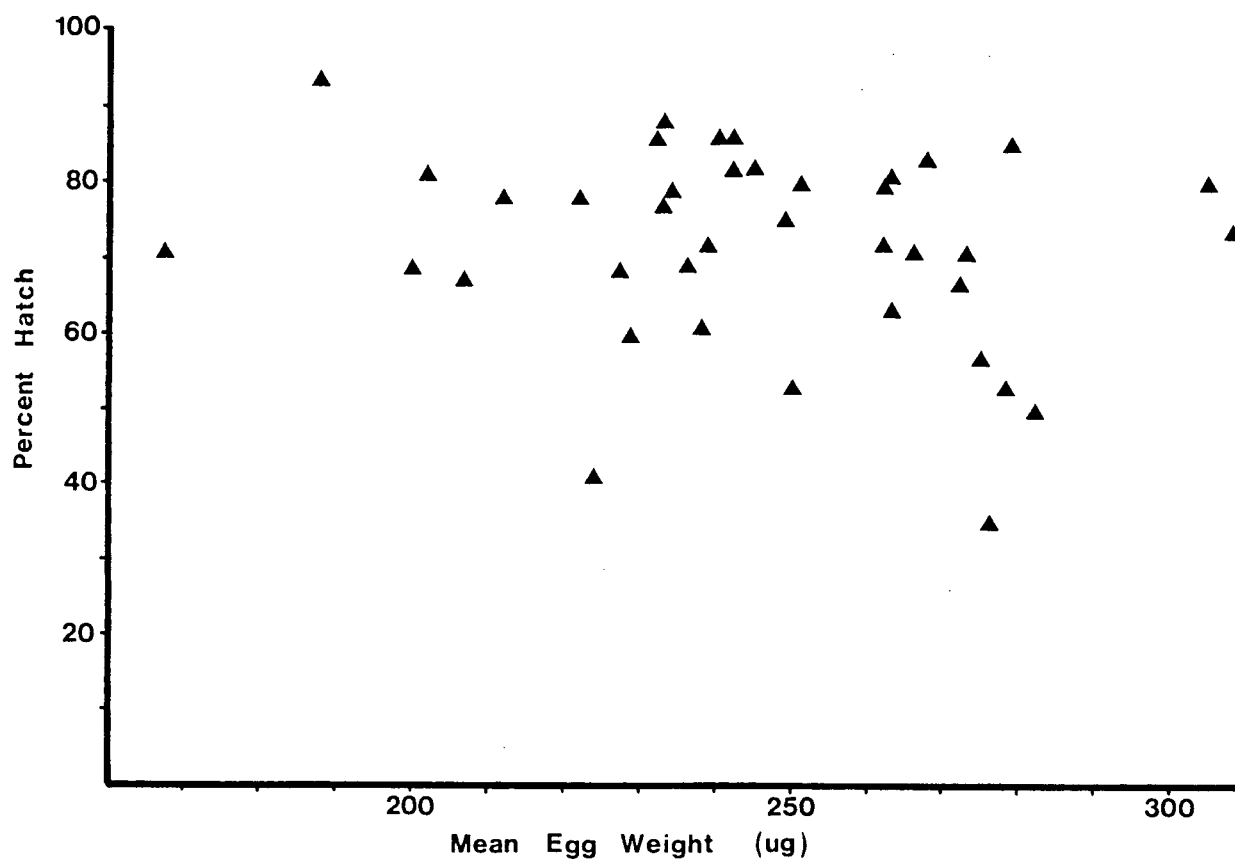
Figure 5.   Total percent hatch and mean egg weight for year 1
    only.   There is   no   relationship   between   the   two
    quantities.

the same group. During the second year, an attempt was made to reduce this weight difference by using a formalin solution of 15 ppt salinity, which Blaxter and Hempel (1966) reported would result in a weight difference of -0.4 to 0.5%. In the present study, the observed weight loss was 22% which prompted a series of experiments examining weight loss during fixation in formalin solutions of different concentrations and salinities. The results of these experiments are summarized in Hay and Kingston (in press). Briefly, as salinity increases, weight loss decreases and shrinkage in length increases. The weights of yolk and larvae presented in this study are fixed dry weights. Theilacker and Dorsey (1980) also found that formalin preservation caused a 30% decrease in dry weight of larval sardine and preservation in ethyl alcohol decreased dry weights of Pacific mackerel by 50%.

Yolk volumes are often estimated in larval studies owing to the difficulty of obtaining actual yolk weights. Both quantities were measured in this study and compared. Yolk volume appears to be a reliable estimator of yolk weight (figure 6) since the degree of correlation between the two parameters is high (r^2=.949). The exact nature of the relationship varies with the salinity of the fixative.

Several parameters were measured for larvae on the day of hatch; taken to be the 15th day in year 1 and the 12th day in year 2. Length, total weight, larval body weight, and yolk weight were measured. Yolk weight/ body weight ratio was calculated as well as the condition factor used by Blaxter
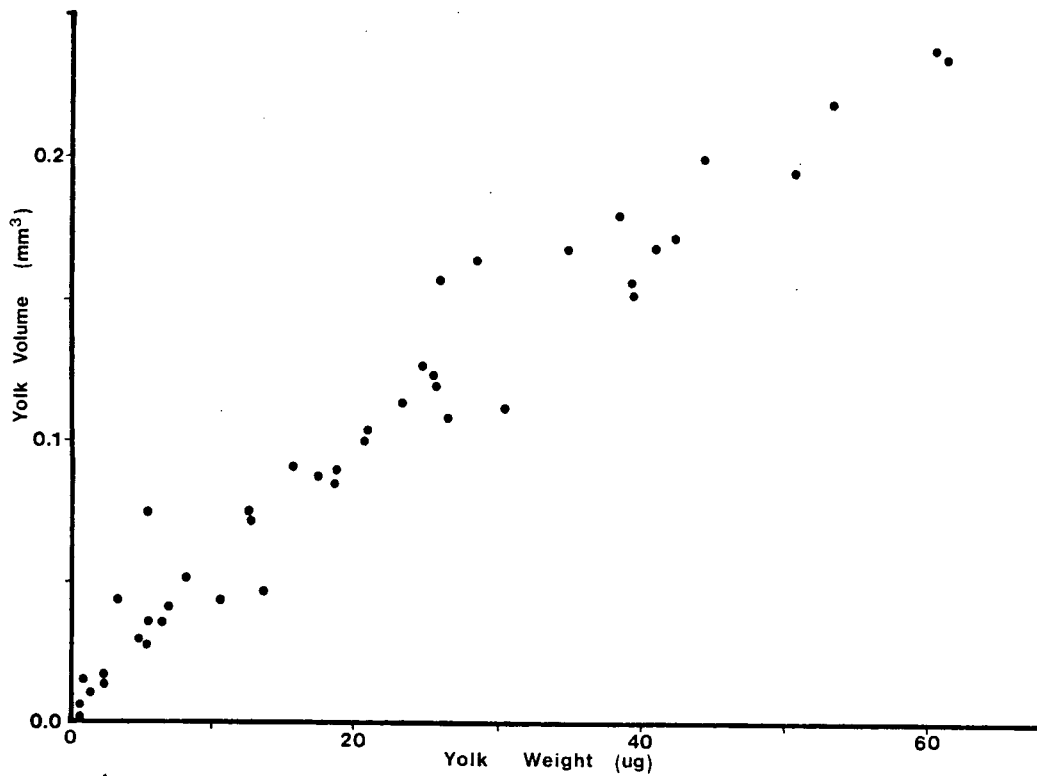
Figure 6.   The relationship between the mean yolk volume,
    measured as the volume of a spheroid, and the mean yolk
    weight.   The data are from year 2 of the study for larvae
    fixed in 15 ppt salinity, 4% formalin.

(1965), where;

$$\text{Condition Factor} = \text{body weight}/\text{length}^3 * 10$$

The relationship between these parameters at hatch and original egg weight are shown in figures 7 through 10 and the appropriate statistical analyses are summarized in table 5. A strong

Table 5. Results of regression analyses of several parameters at the time of hatching as a function of the initial egg weight. The analysis is performed separately for each year. Day of hatch is the 15th day following fertilization in year 1 and the 12th day in year 2. The probabilities given are probability that the slope of regression line equals zero.

Variable	Source	Intercept	Slope	r^2	F	n	P
Length	Year 1	7.9	.0018	.048	.799	18	.385
	Year 2	5.7	.0069	.341	4.14	10	.076
Total Weight	Year 1	13.0	.313	.697	36.9	18	.000
	Year 2	-1.5	.532	.914	84.8	10	.000
Yolk Weight	Year 1	-5.7	.111	.225	4.35	17	.054
	Year 2	-21.7	.269	.433	6.10	10	.039
Larval Weight	Year 1	23.8	.185	.462	12.87	17	.003
	Year 2	19.1	.267	.483	7.48	10	.039
Condition Factor	Year 1	0.65	.002	.233	4.53	17	.050
	Year 2	1.91	.001	.021	.17	10	.687
Yolk/ larvae	Year 1	.082	.001	.073	1.18	17	.295
	Year 2	.183	.001	.069	0.59	10	.463

positive correlation is apparent between the total weight at hatch and egg weight (figure 8) and the relationship is highly significant. Yolk weight and larval body weight at hatching are
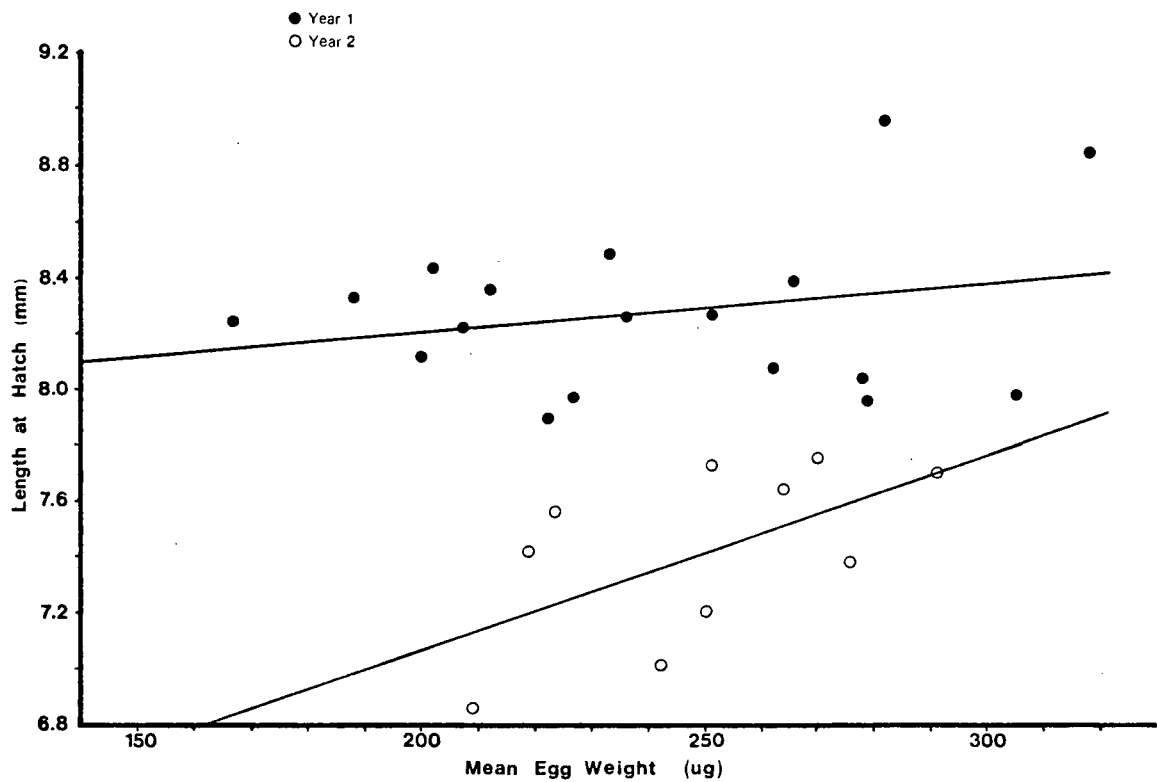
Figure 7. The relationship between mean length at hatch and original egg weight for both years. The lines of best fit are shown even though the regressionsare not significant. The lower lengths in year 2 may reflect the earlier hatch in that year.
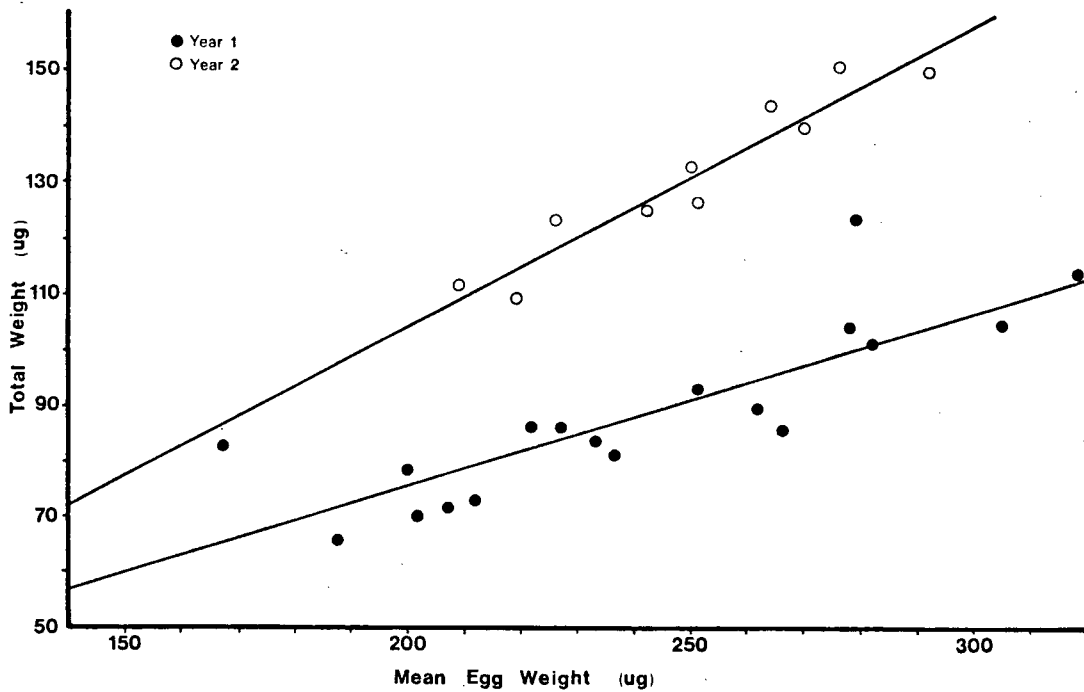
Figure 8. The relatonship between total weight, that is, larval body weight and yolk weight combined, and original egg weight. The regressions are highly significant. Higher values in year 2 are due to earlier hatch and a higher salinity of preservative.

Figure 9.   The relationships between larval weight at hatch and mean egg weight, and yolk weight at hatch and mean egg weight.   Solid triangles are data points from the first year of the study, open triangles are from the second year.
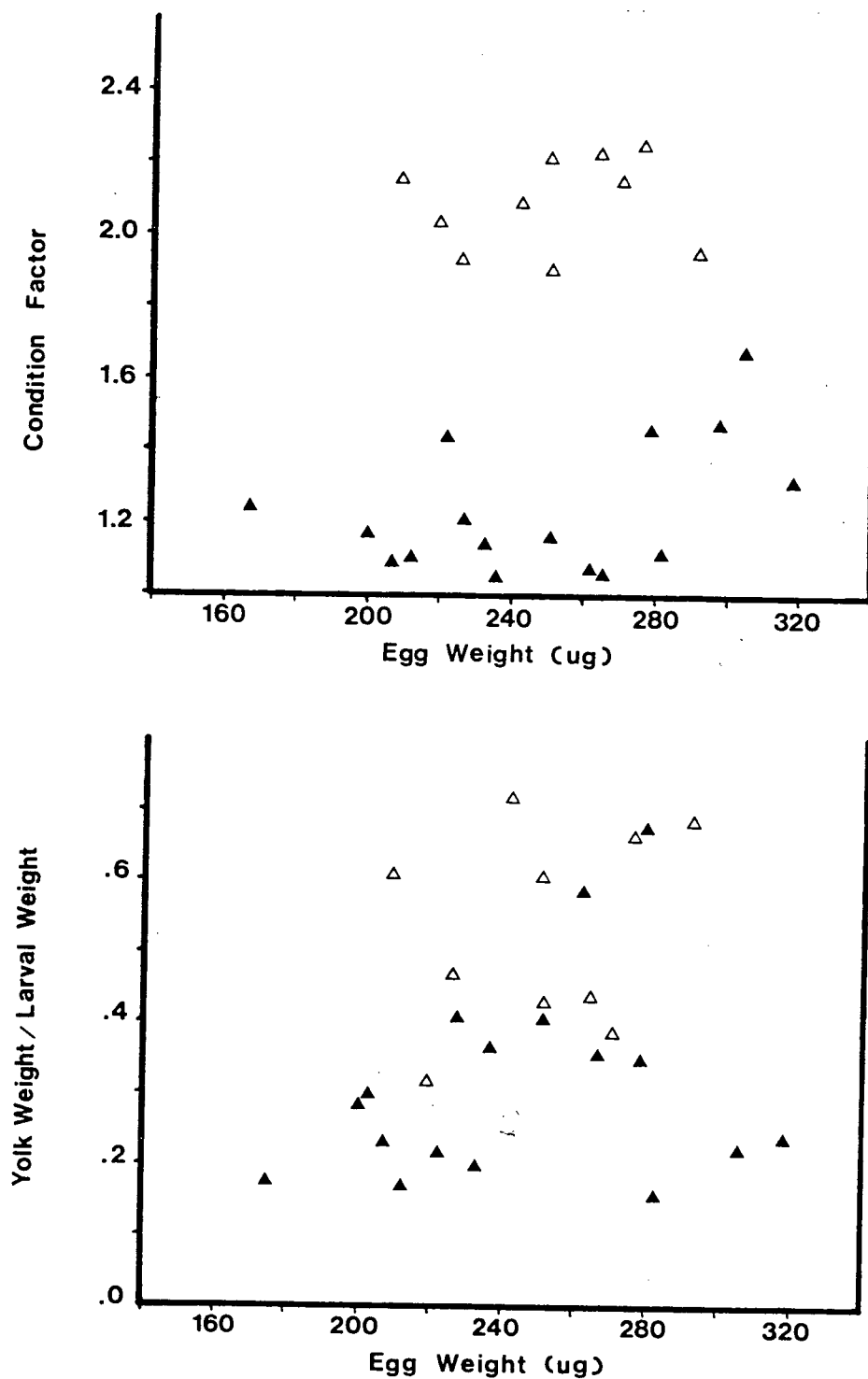
Figure 10. The relationships between condition factor at hatch and egg weight, and the yolk/larval weight ratio at hatch and egg weight. Solid triangles are data from year 1, open triangles from year 2.

also significantly correlated with egg weight, although the relationship is not as clear as that for yolk and larval weight combined. This is likely due to slightly different rates of development between different sets of eggs. Although the total weight is dependent on original egg weight, different proportions of the initial yolk mass may be utilized resulting in corresponding variations in larval body weight. If yolk weight is included as an independent variable in the regression of body weight as a function of egg weight, the r^2 almost doubles. The body weight at hatch is therefore dependent on egg weight and on the amount of yolk which has been utilized to the point of hatch.

Length, condition factor, and yolk weight/larval weight ratio are not significantly related to egg weight at the time of hatch, altough the regression of length on egg weight is almost significant in year 2. These results differ from those found by Blaxter and Hempel (1963, 1966) for different stocks of Atlantic herring, where length and yolk weight/ larval weight ratio were related to original egg weight.

Rate and efficiency of yolk utilization

The rate of yolk utilization was estimated both as a decrease in weight and decrease in volume per day. The slope of the regression of yolk volume and weight on age in days was taken as the best estimate of yolk utilization rate. Rates estimated from volumes are considered more accurate since a greater number of observations were available. The average rate

in year 1 was .036 mm³/day and ranged from .018 to as high as .088 mm³/day. The overall rate in year 2 was .040 mm³/day and ranged from .023 to .074 mm³/day. The slightly higher average rate in year 2 is to be expected given the higher temperatures in that year.

The relationship between yolk utilization rate and the initial egg weight is shown in figure 11. It is evident from the figure that larger larvae from larger eggs consume their yolk at a higher rate than smaller larvae from smaller eggs. This is due to the greater metabolic requirements of the larger larvae. Even so, larvae from the larger eggs generally take longer to complete yolk absorption, as shown in figure 12. This generalization is less evident in the second year of the study. Under conditions of higher temperature, larger larvae may not exhibit longer times to complete yolk absorption,as was reported by Theilacker (1980) for jack mackerel larvae.

Blaxter (1969) defines yolk conversion efficiency as;

$$\text{Efficiency} = \frac{\text{dry weight increment of body}}{\text{dry weight decrement of yolk}} *100$$

This definition assumes that yolk is not stored internally in the body as is the case in plaice (Shelbourne, 1957). It is the percentage of the yolk that ends up as larval tissue. This quantity has been calculated in other studies from dry weight (Blaxter and Hempel, 1966) and from caloric contents of yolk and larvae (Lasker, 1962). In the present study, the efficiency was estimated as the slope of the regression between larval weight and yolk weight for all pairs of observations (figure 13). The

Figure 11. The relationship between the rate of yolk utilization and mean egg weight. Larger larvae from larger eggs absorb their yolk at a higher rate than smaller larvae from smaller eggs. Solid circles are data from year 1, open circles are data from year 2.

Figure 12.   The relationship between yolk size and egg weight
     as it changes over time in year 1.   Numbers in the
     upper left hand corners of the boxes are the number of
     days from fertilization.   It is apparent from the
     figure that larvae from smaller eggs have a shorter
     period to complete yolk absorption.

Figure 13. The relationship between larval weight and yolk
weight. An example from year 2 to demonstrate how
efficiency is calculated in this study. The line shown is
the GM functional regression line as defined by Ricker
(1973). Its slope is equivelent to the ratio of the dry
weight increment of the body/ dry weight decrement of yolk.
Therefore, the slope * 100 = efficiency as defined by
Blaxter (1969). The Y-intercept represents the point at
which the yolk weight equals zero, which is equivelent to
the weight at complete yolk absorption.

slope represents the gain in larval tissue per unit loss of yolk weight. The slope in this case is that of the GM functional regression line as specified by Ricker (1973) since the functional relationship between the two variables is desired. This regression line also gives the best estimate of larval weight at complete yolk absorption from the Y-intercept, or the weight of the larvae when the weight of the yolk becomes zero. Similarly, the length of the larvae at the completion of yolk absorption can be estimated as the Y-intercept of the regression of length on yolk volume.

Conversion efficiency, and length and weight at yolk absorption were estimated as outlined above. There appears to be no relationship between efficiency and egg size (figure 14; table 6), contrary to the findings of Blaxter and Hempel (1966). The efficiencies in both years are similar and average aproximately 70%. This compares with 77 to 79% for sardine larvae, Sardinops caerula (Lasker, 1962), 46.9 to 67.9% for sole, Solea solea (Fluchter and Pandian, 1968), and 50 to 60% for Atlantic herring (Blaxter and Hempel, 1966). Length and weight at yolk absorption are both strongly and positively correlated to egg size (figures 15 and 16; table 6). Larvae from the larger eggs are up to 30% heavier and 15% longer than larvae from smaller eggs at the time of complete yolk absorption.

Figure 14.   The relationship between yolk conversion efficiency
    and egg size.   There is no correlation (see table 6).
    Solid circles are year 1 data, open circles are year 2
    data.

Figure 15. The relationship between larval weight at complete yolk absorption and egg weight. The regression is highly significant. Solid boxes are year 1 data, open boxes are year 2 data.

Figure 16. The relatonship between larval length at complete yolk absorption and egg weight. The regression is highly significant (see table 6). Solid boxes are year 1 data, open boxes are year 2 data.

Table 6. Relationships between yolk conversion efficiency, length and weight at yolk absorption, and original egg weight. The probability given is the probability that the slope of the regression line equals zero.

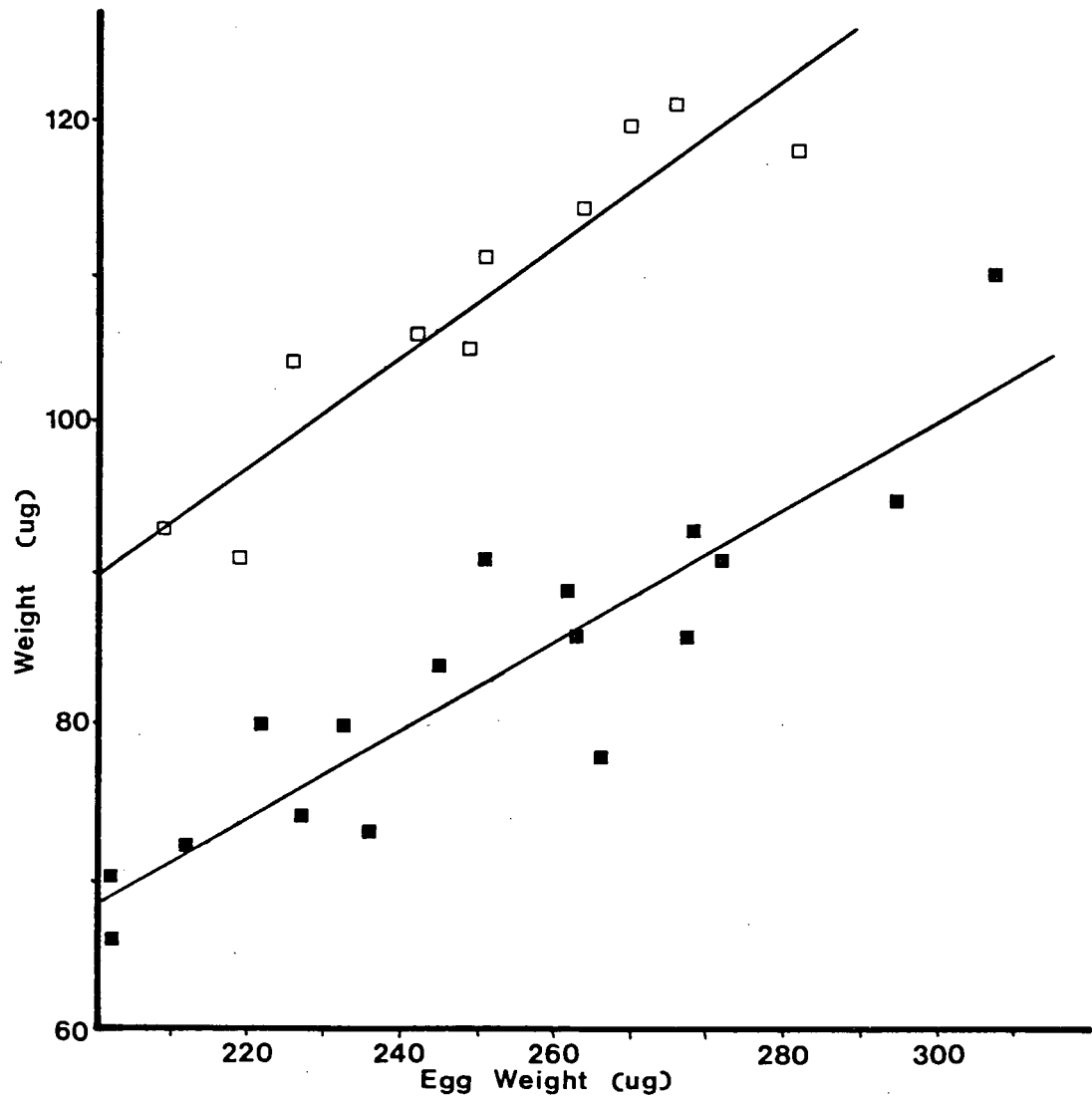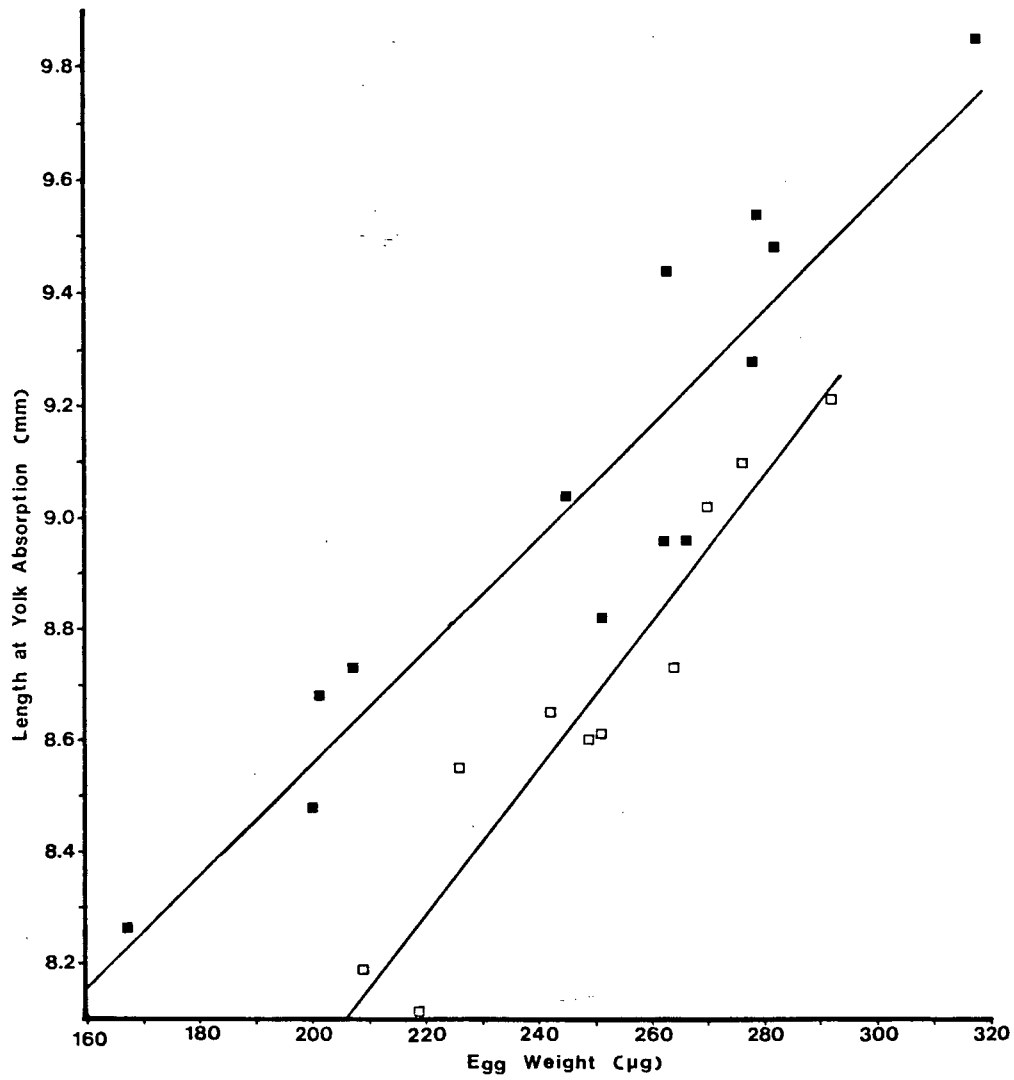| Variable	Year	Intercept	Slope	r^2	F	n	P
Length	1	6.5	.0102	.87	72.9	13	.000
	2	5.4	.0130	.90	74.9	10	.000
Weight	1	9.9	.292	.82	69.7	13	.000
	2	16.9	.365	.87	54.5	10	.000
Conversion	1	1.1	-.0014	.09	1.1	13	.312
Efficiency	2	1.1	-.0016	.28	3.1	10	.115

Growth

Starved Larvae

Under conditions of starvation, the growth of larvae is variable depending on original egg size. Figures 17 and 18 show growth in length and weight for a variety of egg sizes in year 1. Data from year 2 show identical trends. Minor differences in length become magnified as the larvae from the larger eggs grow faster and for a longer period of time since the yolk reserves last slightly longer. The maximum length observed is highly correlated with egg size (year 1, r^2=.82, P=.000; year 2, r^2=.66, P=.008). Larvae from the smallest egg size, 167 ug, showed almost no growth in terms of length. The growth curves shown here are characteristic of starved larvae. Growth is rapid until complete yolk absorption, at which point length becomes more or less constant and may even decline.

Figure 18 shows the accompanying changes in larval weight for the same four groups of starved larvae. Weight increases

Figure 17.   Changes in length with age for larvae from a
    variety of egg sizes.   The mean egg weight is shown in
    brackets following each growth curve.   Arrows indicate
    complete yolk absorption.
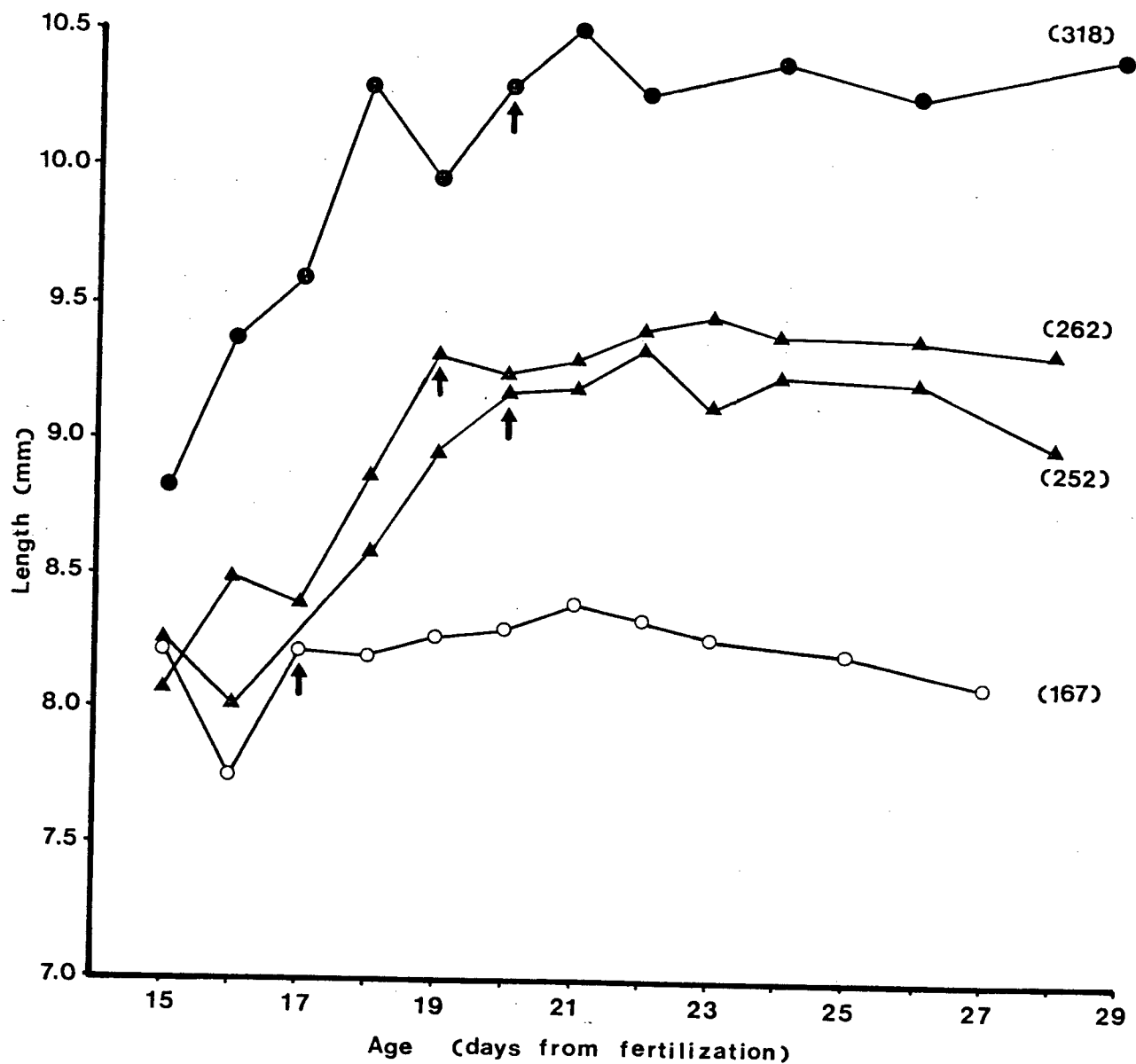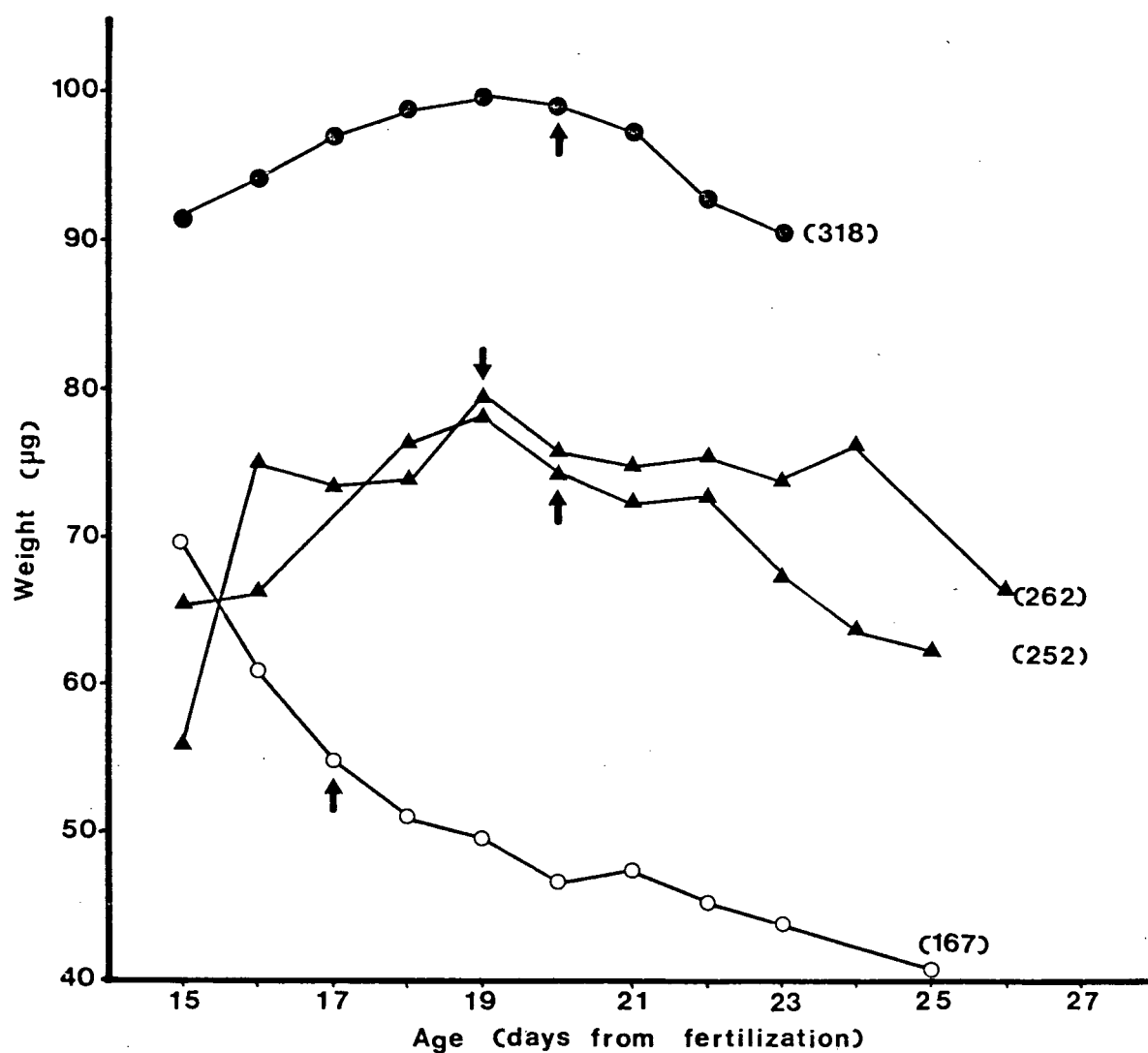
Figure 18.   Changes in larval dry weight (yolks   removed)   with
             age   for larvae from a variety of egg sizes.   The mean egg
             weight is shown in brackets following each curve.   Arrows
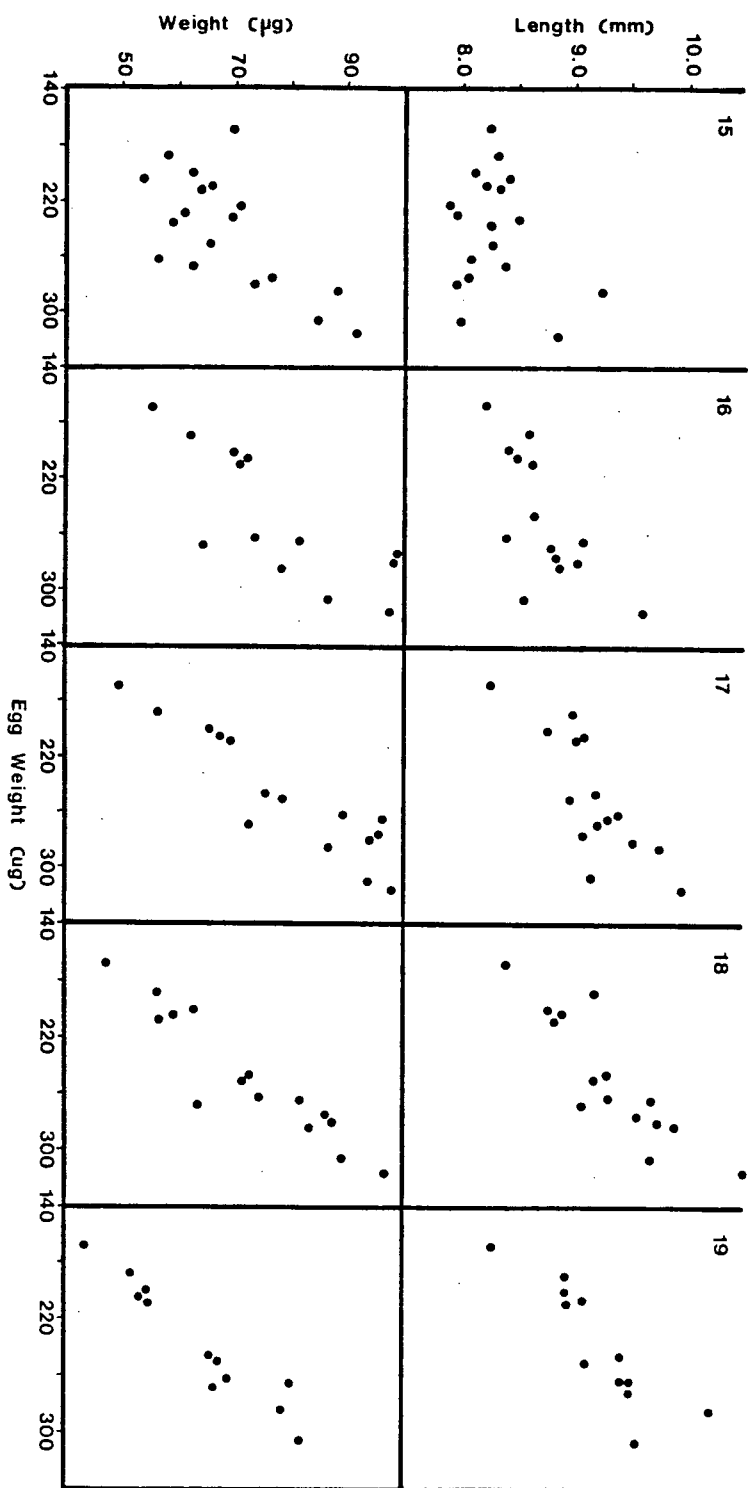   indicate complete yolk absorption.

until the yolk is completely absorbed and then declines rapidly with an accompanying decline in condition of the larvae. In the case of the larvae from the 167 ug eggs, there is a continuous decline in weight following hatch. It is likely that metabolic requirements exceed the energy available from the yolk and no increment in larval tissue is observed. As with length, the maximum observed weight is highly correlated with egg size (year 1, $r^2=.77$, P=.000; year 2, $r^2=.87$, p=.000).

Figure 19 emphasizes these relationships and demonstrates how they change with time for year 1. Again, data from the second year show identical patterns. Initially, the relationships of larval length and weight with egg weight are not clear, especially in the case of length. However the correlation becomes more pronounced with time. One might speculate that the sooner food becomes available, the less marked is the feeding advantage enjoyed by larger larvae from larger eggs. In year 1, larvae from larger eggs were almost twice as heavy as larvae of the same age from smaller eggs at the point when larval size differences were maximum. This occured when larger larvae were just completing yolk absorption while smaller larvae had completed yolk absorption a day or two earlier and had already begun to decline in weight.

Fed Larvae

During the second set of experiments, larvae were exposed to four different feeding regimes: first fed on day 15, or three days after hatch when yolk absorption was incomplete; first fed

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Figure 19.   The relationships between larval length and
     weight, and egg size at various times in the experiment
     for year 1.   Numbers in the upper left hand corners of
     the boxes are the number of days from fertilization.
     When differences are greatest, larvae from larger eggs
     may be up to 90% heavier and 20% longer than larvae of
     the same age from smaller eggs.

on day 17, when complete yolk absorption had occured; first fed on day 20, delayed feeding; and finally, no feeding or starvation. Figures 20 and 21 show combined results and how length and weight change over time under the above feeding conditions. As expected, the largest larvae were those fed earliest on day 15. Larvae fed as late as day 20 still appeared capable of feeding and increasing in size, although at the termination of the experiment they were much smaller than larvae fed earlier. In certain individual cases, the final size at the end of the experiment was greater for those larvae first fed 17 days after fertilization than for those first fed on the 15th day. The initial lag in growth after initiation of feeding is probably due to low capture success when larvae are first presented with food. Atlantic herring larvae were successful in capturing only 6% of the food particles at which a strike was made during initial feeding trials, but feeding success increased rapidly in subsequent trials (Blaxter and Staines, 1971).

Figure 22 shows the average growth during the experiment in mm/day for the four treatments. There appears to be no relationship between egg size and growth rate of the larvae. Smaller larvae must be at least as successful in feeding as larger larvae, even when feeding is delayed to 20 days following fertilization. Growth rates in larvae first fed on day 15 were comparable with Haegele and Outram's (1978) figures for larval Pacific herring growth of .089 to .179 mm/day, depending on type and concentration of food. The final lengths of the larvae in

Figure 20. Average growth in length of larvae where feeding
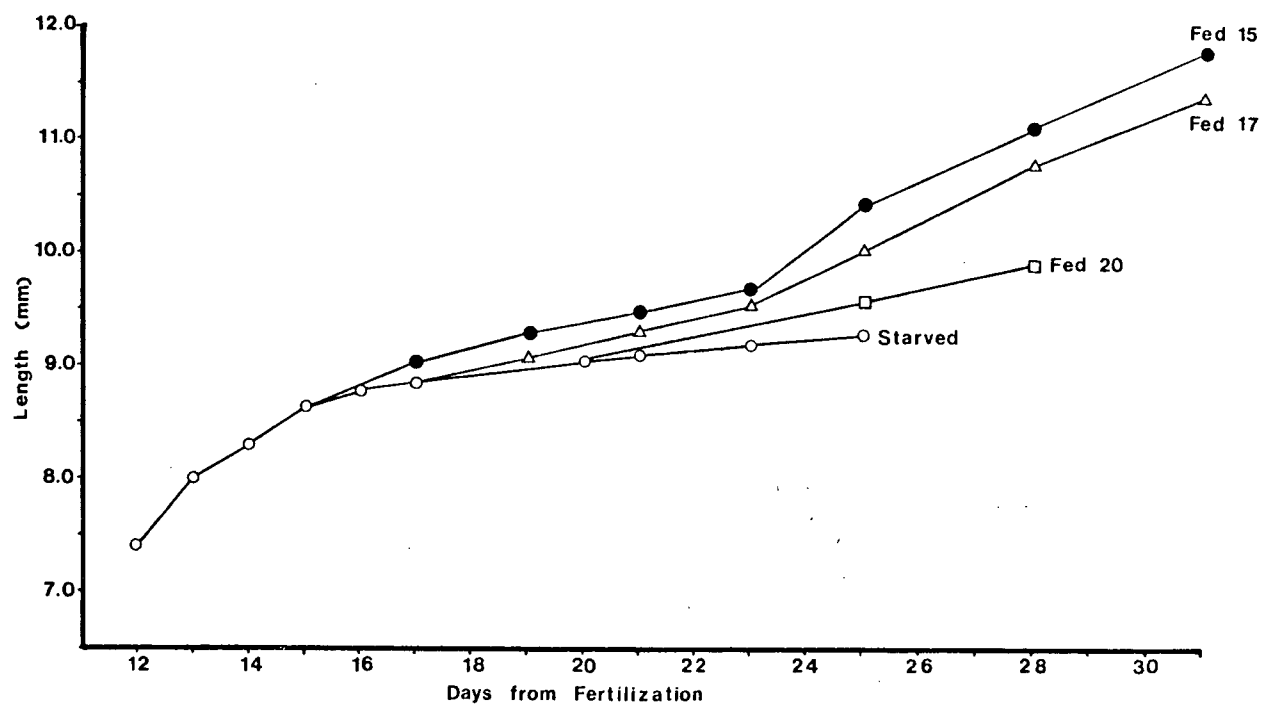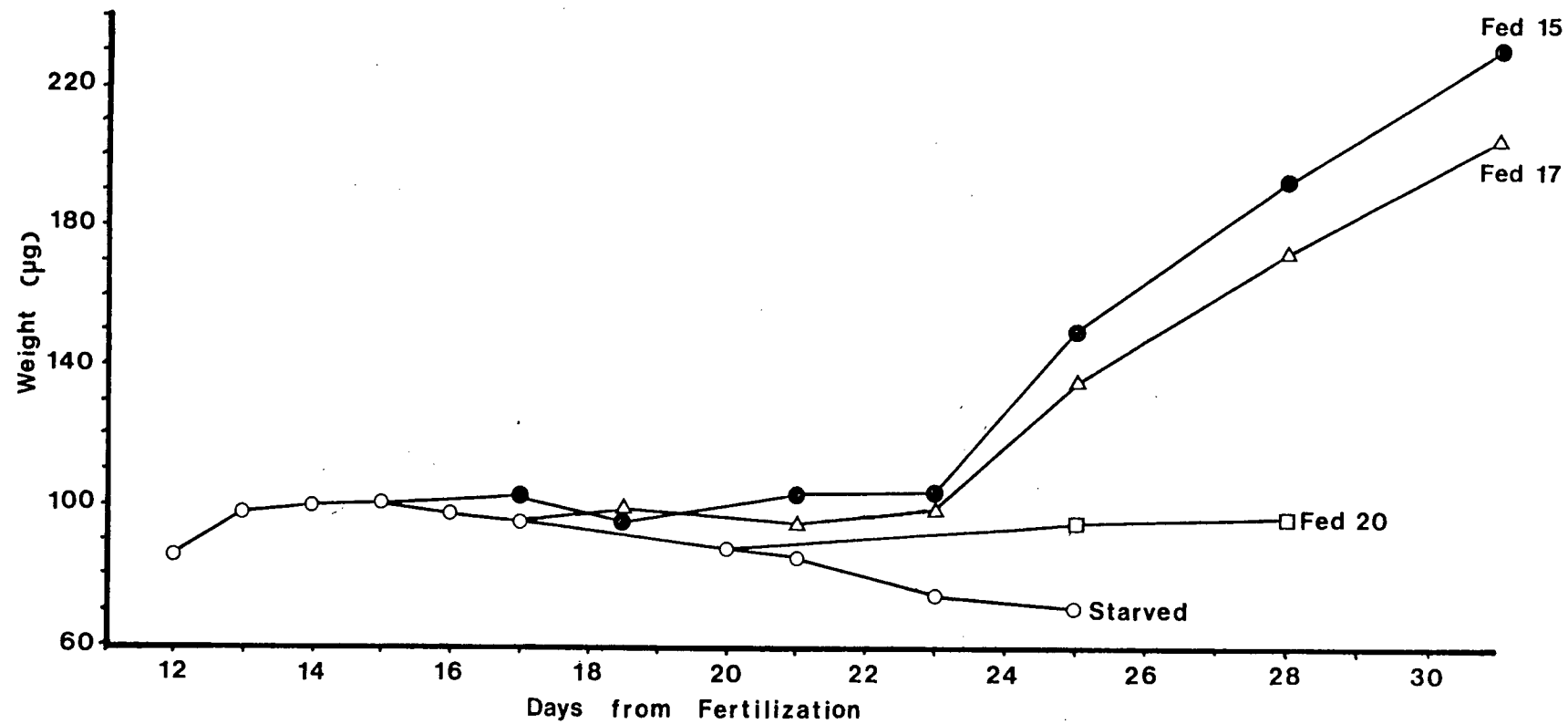is initiated on different days.

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Figure 21.   Average growth in weight of larvae where feeding
        is initiated on different days.

relation to egg size for the different treatments is shown in figure 23. The marked differences observed for starved larvae are not apparent in larvae first fed on day 15 and are less evident in larvae first fed on day 17. Minor variations in growth rates eventually allow some of the smaller larvae to catch up and some of the larger larvae to fall behind. Thus, when feeding is initiated on a full ration Artemia diet, larvae from larger eggs do not seem to have an advantage, in terms of growth rate, over larvae from smaller eggs even when feeding is delayed up to 20 days following fertilization (8 days following hatch).

In addition to the above, 20 larvae from each egg size were placed in separate containers for 2 hour periods and allowed to feed on high concentrations of Artemia. After this 2 hours had elapsed, the larvae were removed and the number of nauplii in each larval gut counted. There was no difference in feeding success of larvae from different sized eggs. However, the extreme variability of the data makes it difficult to draw any firm conclusion.

Mortality

Starved Larvae

Mean starvation times are strongly and positively correlated with original egg weight (r^2=.595, P=.000) (figure 24). Survival curves for larvae grouped according to egg size exhibit the typical pattern of mortality in herring larvae and the
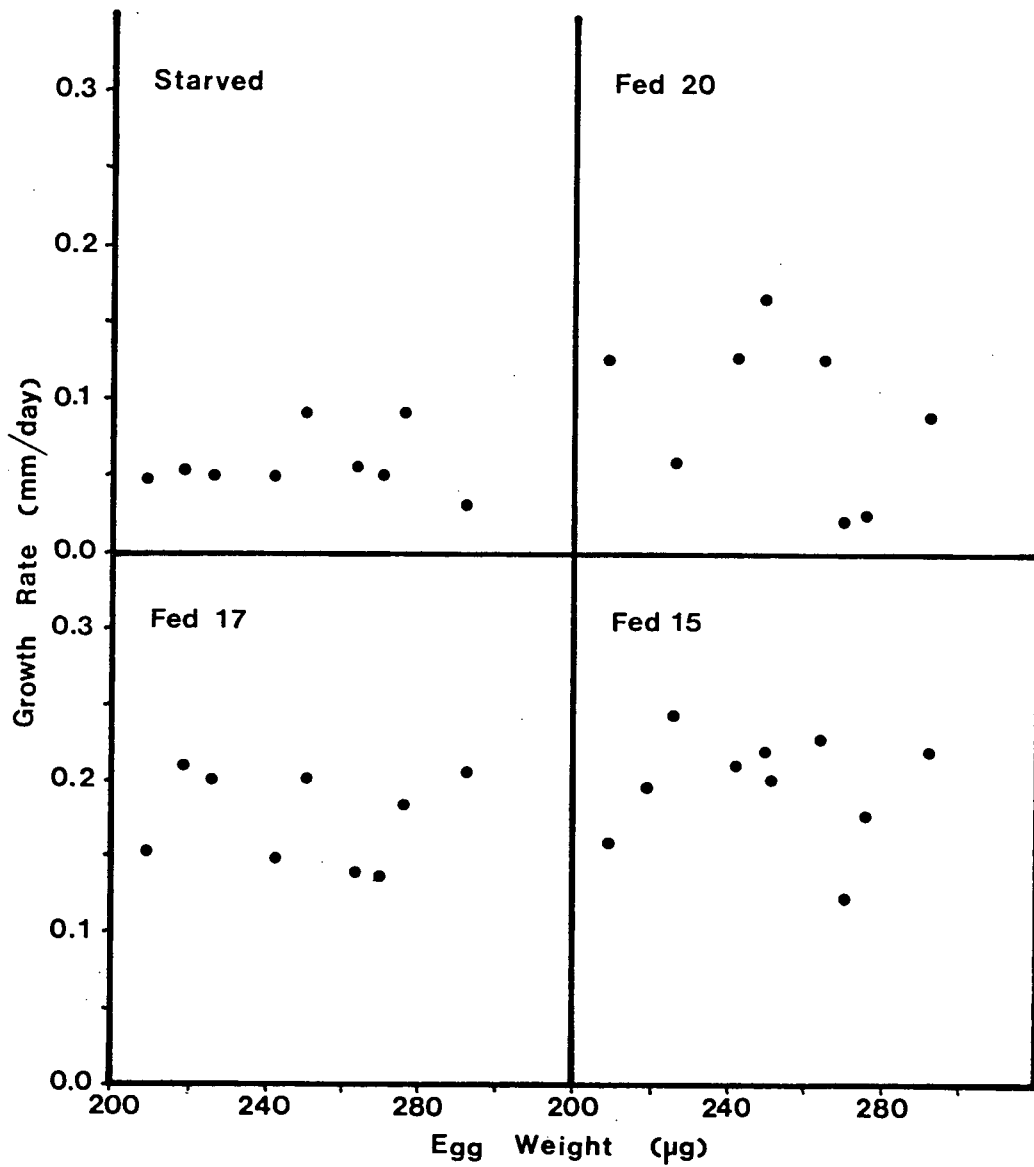
Figure 22. Growth rates of larvae in relation to egg size. Treatment is shown in the upper left corner of each box.

Figure 23.   Final lengths of larvae in relation to egg size.
Treatment is shown in the upper left corner of each box.

Figure 24.   The relationship between mean day of starvation and egg size.   Starvation time is strongly correlated with egg size.

relative differences between egg sizes (Figure 25). Larvae from the largest eggs last for approximately 3 days longer than larvae from the smallest eggs.

Aside from dependence on initial yolk reserves, starvation time is strongly affected by temperature (Figure 26). The three starvation experiments were run under slightly different temperatures due to increases in the temperature of the seawater system. An increase in temperature of 1 degree causes a corresponding decrease in survival time of approximately four days. Thus, increases in temperature in the sea would significantly decrease the amount of time available for a larvae to find food.

Fed Larvae

The percent survival for each egg size and each of the three feeding treatments are given in figure 27. The relationship between percent survival and egg size is significant for the larvae first fed on the 15th day following fertilization (r^2=.520, P=.018). The correlation is a negative one; survival decreasing slightly with increasing egg size. In the case of larvae fed initially on the 17th day following fertilization, the relationship is positive, but not statistically significant (r^2=.205, p=.221).

Figure 25.   Survival of larvae grouped according to egg weight.

Figure 26. Combined survival curves for runs at three different temperatures. An increase of 1 degree decreases time to starvation by approximately 4 days.

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Figure 27.   Percent survival to the 32nd day following
        fertilization as a function of egg size for the three
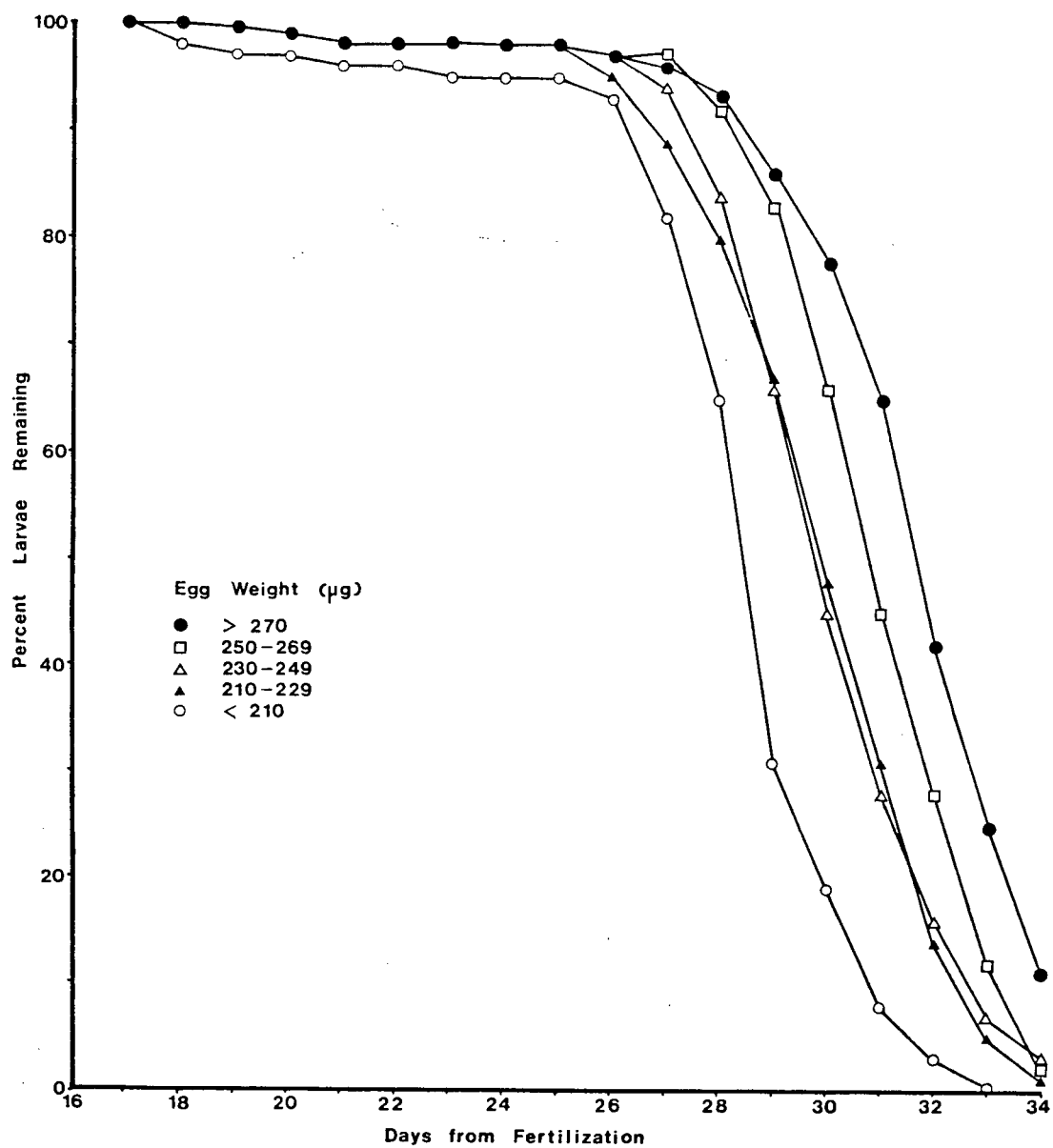   different feeding regimes.

DISCUSSION

General

In the stock of Pacific herring investigated in this study, eggs from larger females were up to 50% heavier than eggs from smaller individuals. This female size-egg size relationship has been confirmed for other stocks of Pacific herring (Hay; unpublished data). Egg size is not related to condition factor of the female. In any of the female size categories, the range of mean egg sizes is quite large suggesting that other factors are important in determining final egg weight. Perhaps individual feeding histories or variations in the way individual fish balance fecundity and egg size accounts for the observed variation.

Egg size does not affect fertilization rate, incubation time, or hatching success. Assuming that spawning is more or less synchronous within a stock of herring, then for a given number of eggs the number of larvae produced and the time that they will hatch is independent of egg size. Therefore, any effect on viability must be related to differences in larval characteristics at hatch and the effects of these differences on events subsequent to hatching. Ware (1975) derived a relationship in which incubation time increases with egg size. A correlation was shown between egg size and temperature such that at lower temperatures it was advantageous for fish to produce larger eggs. Ware did not, however, imply that egg size had a direct effect on incubation time. Since then, several

authors have concluded that incubation time is dependent on egg size in the same way that it is dependent on temperature (Theilacker and Dorsey, 1980; Hunter, 1980). These conclusions appear to be based on a misinterpretation of Ware's results. Blaxter and Hempel (1963) and Ciechomski (1966), working with Atlantic herring and Argentine anchovy respectively, also found that incubation time was independent of the size of the egg.

The combined weight of the larva and the yolk at hatch is strongly dependent on original egg weight. Larger egg size therefore provides for greater body weight at hatch, greater yolk reserve at hatch or, in most cases, both of these advantages.

Following the hatch, any differences between larval body weight or length increase rapidly. Disparities that were not large or absent in the case of length, become magnified. Since larger larvae tend to take longer to reach the point of complete yolk absorption they can grow for a longer time on their yolk reserves. In addition, yolk conversion efficiency is independent of egg size, at least in the period following hatch. This means that the final size of the larvae at yolk absorption, in terms of length as well as weight, is strongly dependent on the original weight of the egg. The point of complete yolk absorption is more critical ecologically than the time of hatch as it marks the time when the larvae must shift from endogenous to exogenous feeding. The success or failure of this process is believed by many to exert a major influence on the eventual size of the year class entering the fishery (Hjort, 1926; Theilacker

and Dorsey, 1980). After this period of maximum larval length and weight, if food is not available, the length remains constant or decreases slightly, while the weight declines at a constant and relatively rapid rate as the larval tissue is itself catabolized. The condition of the larvae also falls accordingly. Throughout this starvation period, however, larvae from larger eggs maintain their advantage in terms of length and weight.

The larvae from the larger eggs also demonstrate a greater resistance to starvation than larvae from smaller eggs, surviving for up to three days longer without food. Thielacker (1980), working with jack mackerel larvae, found that larvae from larger eggs starved more slowly and lived for one day longer without food than larvae from smaller eggs. More important than the point of starvation is the point at which the larva is functionally incapable of feeding. This point is termed the "point of no return" or PNR by Blaxter and Hempel (1963). In Atlantic herring larvae, the PNR occurs at about 75% of the time from hatch to starvation regardless of egg size (Blaxter and Hempel, 1963). Assuming a PNR of approximately 75% of starvation time, larvae from larger eggs might be functionally capable of feeding up to 25 days following fertilization (10 days following hatch), while larvae from smaller eggs would be incapable of feeding 23 days after fertilization (8 days following hatch). These figures are only valid for the temperature regime under which the above experiments were run. At higher temperatures the starvation

times would be shorter and the time differentials between PNR's for larger versus smaller larvae would be decreased. At lower temperatures, the reverse would be true. Thus, there might exist a 'time window' or limited period of time where smaller larvae are incapable of feeding while larvae from larger eggs are capable of feeding, growing, and, ultimately, surviving.

This study also investigated the effect of egg size on the subsequent ability of the larvae to feed and grow after varying periods of starvation. It seems reasonable to assume that larvae from smaller eggs would be at a disadvantage once food became available due to slower swimming speeds, shorter reactive distances, and smaller gapes. This disadvantage should be reflected in different growth rates of larvae from small and large eggs under identical feeding conditions. On the other hand, larvae from small eggs absorb their yolk more quickly and may be ready to feed earlier than larvae from larger eggs. This would prove advantageous if food became available soon after hatching occured.

The growth rates observed for fed larvae were quite variable and independent of both the initial size of the larvae and initial egg weight. The final sizes of larvae first fed 15 days after fertilization were not related to egg weight. This result would likely hold for the other treatments as well if the experiments had been extended for a longer period. Even in larvae fed as late as the 20th day following fertilization, or 8 days following hatching, smaller larvae grew as well or even better than larvae from the larger eggs. It may be that an even

later day of first feeding, one which fell within the PNR 'window' discussed above, would be necessary to demonstrate differences in the ability of the larvae to recover and grow. In rainbow trout, fingerlings from older females grew 20% faster than those from two year old females under identical feeding conditions (Gall, 1974).

The fact that Artemia nauplii were exclusively used as a food source may have a significant bearing on the results obtained. The ability of fish larvae to grow and survive is very much dependent on the type of food particle available. Results obtained using Artemia may differ from results obtained using other food sources due to differences in particle size, swimming capability of the prey, and visibility. Artemia is a large, highly pigmented, and therefore highly visible prey item. It is also a slower prey than the nauplii and copepodites that herring larvae prey on in the natural environment (Rosenthal and Hempel, 1970). Both the vulnerability of Artemia and the high prey densities in the aquaria may have provided the larvae from the smaller eggs with optimum conditions for feeding and growth. Haegele and Outram (1978), in their experiments with Pacific herring larvae, obtained the highest initial survival rates with Artemia nauplii, a fact which they attributed to the high visibility and low mobility of the prey. Rosenthal and Hempel (1980) also recorded the best feeding success of Atlantic herring larvae in a pure plankton of Artemia larvae. Use of natural plankton by Haegele and Outram led to a much higher initial mortality rate as the larvae learned more slowly to

capture the less visible and highly mobile prey.

Repeat experiments were planned in year 2 using natural plankton as a food source, but sufficient plankton in the appropriate size interval was not available at the required time. Therefore general conclusions concerning relative feeding capabilities of different sized larvae are difficult to make. It appears that given optimum conditions, smaller larvae from smaller eggs can grow as quickly or more quickly than larger larvae from larger eggs, even when feeding has been considerably delayed.

Initial feeding on the fifteenth day following fertilization led to a significantly higher mortality among larvae from larger eggs. Fowler (1972) found similar results for chinook salmon. In three separate experiments, mortality in larger egged larvae was higher than in smaller larvae from smaller eggs fed on a standard hatchery diet. In this study, the smaller larvae had absorbed all of their yolk by the fifteenth day following fertilization while larvae from larger eggs still had some yolk remaining. It seems feasible that premature exposure to food could lead to less successful feeding in larvae with incomplete yolk absorption than that observed in larvae which have absorbed all of their yolk. In this way, the larvae with incomplete yolk absorption would obtain a lower return for a given amount of energy expended. This possibly explains higher survival rates observed in larvae from smaller eggs which are exposed to food at an early stage in development. It might be expected that differences in early feeding ability

would also show up in growth rates. Since this is not the case, it seems likely that the earlier feeding affects not the feeding rate and therefore growth rate, but the proportion of the larvae that actually make the transition from endogenous to exogenous feeding. If the larvae is successful in making the transition, then feeding success and growth rate is similar between different sized larvae.

Variability in the survival rates in the other two feeding treatments make it very difficult to draw conclusions, though survival rate appears to increase with egg size in larvae first fed 17 days following fertilization.

Larval Survival

As previously stated, survival and growth may be affected by (1) susceptibility to predation, (2) starvation time, and (3) feeding ability once food has been located.

The degree to which larger larvae may be more successful in avoiding predation than smaller larvae of the same age was not studied in this thesis. The number of potential predators of herring larvae is quite large and includes other fish species, both adults and juveniles, as well as a invertebrate plankters such as ctenophores, euphausiids, copepods, and amphipods. There is some evidence that mortality rate due to predation is dependent on particle size (Ware, 1975). As size increases, predation mortality may also decrease simply due to a decline in the number of potential predators. Larger larvae may be stronger and slightly faster than smaller larvae which would

confer an advantage against some of the smaller invertebrate predators in terms of their ability to stay away or break free when caught. Lillelund and Lasker (1971), working with copepod predators, and Theilacker and Lasker (1974), working with euphasiids, found that larger anchovy larvae were caught and eaten less frequently han smaller larvae. Larger larvae are also considerably more capable of avoiding plankton nets (Hempel, 1979). In contrast, it has been demonstrated that some fish predators may actively select the larger of a group of food items (Ware, 1972). Therefore, larger larvae may be more vulnerable to certain predators.

Larvae under conditions where food is abundant quickly grow to a point where initial size differences are obscured. Therefore, if egg size does affect the predation rate experienced by the larvae, it is likely to be an effect of short duration. This is not to say that it may not have important consequences, however, it is not possible to address this point further with the evidence available to date.

The second consideration is the starvation time, or the amount of time the larvae has in which to encounter food. Larvae from larger eggs do have longer times to starvation and probably longer times to PNR. Plankton on which the larvae feed may be distributed in the sea as a uniform mixture or as discrete patches which vary in density and distance of separation depending on biological and physical oceanographic factors. Since the latter prey distribution is most likely, it is probable that the larvae's early survival depends upon

locating a food patch of sufficient size and density. Many studies have shown that average densities of food in the sea are not adequate to meet theoretical requirements obtained from models or from laboratory experiments. This leads to the hypothesis that larvae are dependent on small scale patchiness of food (Hunter, 1980). Lasker (1975) has found very extensive patches of <u>Gymnodinium</u> off the coast of California capable of sustaining larval anchovy. The starvation of marine fish larvae after yolk absorption is believed by many to be one of the principle causes of larval fish mortality (Theilacker, 1980). If this is indeed the case, then it seems likely that larvae from larger eggs may have some advantage in that they have a longer time in which to encounter food.

Once larvae have encountered food, there may also be differences in the feeding efficiency of larvae from large and small eggs. From results obtained in this study, smaller larvae seem as capable of feeding on <u>Artemia</u> nauplii at high densities as larger siblings and initial size differences quickly become obscured as the larvae grow. It is not possible to say what might happen under conditions of lower food density or different food items. Larger larvae are likely to have at least a slight advantage in terms of feeding.

It follows that during years of high food producton, with small between patch distances and high food densities, any discrepancies between larvae from large and small eggs would quickly disappear and larger larvae would have little survival advantage. In years of low food production, or when spawning is

out of phase with food production, the advantage of larger larvae from larger eggs might become magnified. If this line of reasoning is correct, then it may be that smaller eggs serve as a reserve and only make significant contributions to recruitment when conditions for larval survival are optimal as postulated by Nikolskii (1963) and Ponomarenko (1973). On the other hand, if conditions are very favorable, smaller larvae from smaller eggs might even be able to feed earlier than larger larvae due to earlier yolk absorption and thus experience higher survival. There is some indication that such is the case from the results obtained here.

Implications for Fisheries Management

Hjort (1926) first proposed what is now refered to as the 'critical period' concept. He believed that the availability of food at the time of transition from endogenous to exogenous feeding determined larval survival and year class size. May (1974) offers a good review of the critical period concept. Since Hjort's time the critical period has come to mean any point during the fish's life history where the potential exists for alteration of year class size. Most authors believe that for marine species, the most important effect on year class size occurs when mortality is highest, which is very early in the larval stage. According to Rosenthal and Hempel(1970), the causes of inadequate recruitment and fluctuations in year class strength are to be found during the first year of life. They also suggest that shortage of planktonic food during an early

critical stage just after the resorption of the yolk sac results in poor recruitment in herring. It seems reasonable to consider this early stage as at least one of the points where year class size is influenced.

Given that egg size influences early survival and growth, and that early survival affects recruitment, any correlation of egg size with female size becomes important in terms of the contribution of different sized individuals to the size of the year class. Since the effect of most fisheries is to lower the average age and size of individuals in the stock, recruitment may be affected by an overall decrease in viability of the larvae produced, even if the total quantity of eggs remains high. This idea has been presented by a number of authors, especially in the Soviet literature (Nikolskii, 1963; Pomonarenko, 1973), and elsewhere (Bridger, 1960, 1961; Cushing and Bridger, 1964; Blaxter and Hempel, 1963; Stanley, 1977). The idea was largely dismissed by Blaxter and Hempel on the basis of their experimental results. They found a maximum increase in egg size from recruits to older Atlantic herring of 14% and concluded that differences of this magnitude are not important. They may have reached different conclusions, however, if they had observed larger egg size differences such as those seen in this study.

It is unlikely that the existence of this phenomenon will be confirmed or denied by further laboratory experimentation. Work to date has demonstrated that the possibility of an effect exists and should perhaps be given consideration. The most

productive direction in terms of further uncovering the relationship is probably that used by a number of investigators in the past (Bridger, 1960, 1961; Ponomarenko, 1973) where age or size composition of the stock is taken into account as a factor in the stock recruitment relationship. In this way it might be possible to determine the effect of the proportion of larger individuals in the stock on the probability of the production of a large year class. Another possibility would be to conduct a study under more natural conditions such as Bagenal (1969) did for brown trout. The application of this latter approach to the marine situation, however, would be much more difficult.

Ecological Relationships

If smaller eggs are less viable than larger eggs, then why do smaller fish produce smaller eggs? At a given level of reproductive effort, the gonadal mass may be divided up in a way such that egg size and fecundity are inversely related. In other words, smaller fish could produce larger eggs as do the older individuals of the stock, but only at the expense of a lowered fecundity.

Factors determining egg size within a species are largely unknown. Svardson (1949) extended Lack's (1948) ideas concerning litter size in birds and mammals to fish. As he pointed out, if there were no relationship between egg size and larval survival, selection would favor higher fecundity and smaller egg size. A mechanism which counterbalances this

tendency towards greater numbers of smaller eggs is necessary. For this reason, Svardson believed that larger egg size resulted in increased larval survival. Since that time, investigators have tended to regard high egg numbers as compensation for heavy predation. At the same time, individual eggs must be large enough, that is have sufficient yolk, to give the larvae a reasonable chance of avoiding starvation. Since fecundity and egg size are negatively correlated, the opposing forces of starvation and predation are thought to operate together to determine the optimum division of the reproductive potential in terms of size and numbers of eggs (Hempel and Blaxter, 1966; Hunter, 1980).

This leads directly to the question as to why the optimum egg size appears to increase with increasing fish size within a species. It is possible that as the gonad weight increases, or the amount of energy available for reproduction increases, the optimum allocation in terms of egg size might change simply due to the rapid increase in fecundity. At some point, it seems reasonable that it become less advantageous for the individual to produce more eggs and instead to increase the size or survival value of an individual egg. Put another way, optimum egg number and size might shift slightly in response to available reproductive mass. The optimum division would be the one that maximized the numbers of offspring which reached reproductive age. Even though smaller eggs might individually have a slightly lower probability of surviving, a greater number of eggs of this smaller size would be produced, allowing a

higher mortality rate.

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