Abstract.–Pacific herring *Clupea pallasi* eggs were collected from spawning grounds in Bristol Bay, Alaska, transferred to Norway for hatching, and for 63 days raised in a 2000-m^3 marine basin located at the Flødevigen Biological Station. The eggs were from the same spawning, and hatching took place over 3 days. Upon completion of hatching, 24,840 larvae (12.42 larvae/m^3) were released into the basin. Larval growth was rapid and metamorphosis was observed 28 days after hatching at a length of 25 mm. The experiment was terminated by draining the basin; 4891 juveniles were recovered. The average rate of growth was 0.66 mm/day in length and 2.89 mg/day in weight. The larval length frequency, unimodal at hatching, segregated into three modes within 2 weeks, which persisted until termination. The slowest growth rate was 0.31 mm/day and the larger herring averaged 1.48 mm/day. At first feeding, copepod nauplii were abundant but food declined later. Cannibalism was observed on day 45 and a 30-mm herring was captured that contained a 20-mm herring. Survival was higher in the basin than estimated for larvae at sea. Mortality appeared to be greatest during the first 2 weeks, and much of it may have been due to hydromedusa predation.

Observations on Growth and Survival During the Early Life History of Pacific Herring *Clupea pallasii* from Bristol Bay, Alaska, in a Marine Mesocosm

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Pacific herring *Clupea pallasii* that spawn in northern Bristol Bay are the largest herring off western North America and are genetically distinct from herring in the Gulf of Alaska and off British Columbia (Fried and Wespestad 1985, Grant and Utter 1984) (Fig. 1). Very little is known of the early life history of Bristol Bay herring. Checkley (1982) examined otoliths from age-0 juveniles for growth increments and sampled posthatching larvae at several spawning areas in western Alaska (Checkley 1983). These studies provided limited information on early growth, since the time of spawning and hatching were unknown and otolith increments were not verified to be daily rings.

To investigate the growth in length and weight of larval and post-larval Bristol Bay herring and other aspects of early life history, known-age herring were sampled from hatching to postmetamorphosis in a marine mesocosm. A mesocosm study was chosen because larval density could be regulated as well as sources of mortality, such as predators and food supply which cannot be done in a field study. Control of these variables is possible in a laboratory experiment, but Øiestad (1983) has shown that

container size may bias laboratory results. He investigated the early life history of Atlanto-Scandia herring *Clupea harengus* and the effect of ration and predation on survival in a large marine enclosure located at the Flødevigen Biological Station near Arendal, Norway. The results of his studies showed life history parameters of herring in the basin were similar to those observed in nature.

Methods

Herring eggs on rockweed (*Fucus* sp.) were collected at low tide on 24 May 1986 from a single spawning that occurred on 22 and 23 May. Water temperature at the time of spawning was 4.5°C and salinity was 30 ppt. *Fucus* fronds with light egg coverage (1–2 egg layers) were collected at random within the spawning area and packed into half-liter plastic bags filled with seawater. A total of 25 bags were filled with about 2000 eggs per bag. The bags were shipped via air in insulated containers with gel ice to the Flødevigen Biological Station. After 48 hours in transit, the eggs were unpacked and placed in hatching boxes supplied with circulating seawater at 7.7°C and salinity of 32 ppt.
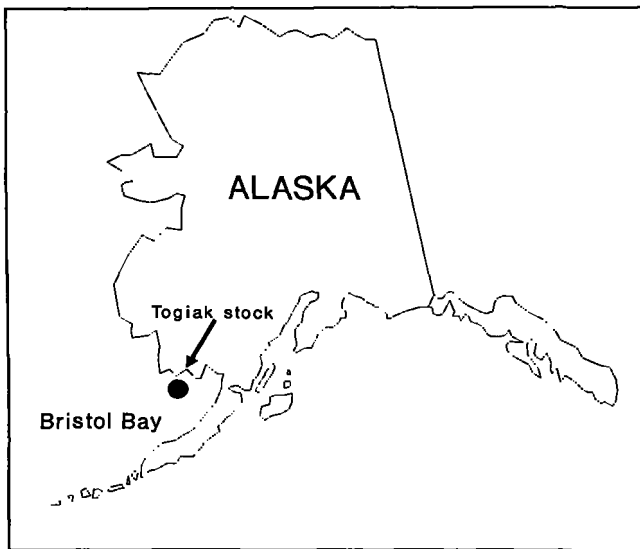
Figure 1
Location of spawning grounds of the Togiak herring stock in Bristol Bay, Alaska.

Hatching began on 10 June 1986 and was completed by 12 June. Survival to hatching was about 50%, with 25,200 larvae produced. The eggs were not treated during incubation, and heavy fungal growth was noted on the eggs. Newly hatched larvae were collected from incubation boxes in white plastic cups in groups of 5–25, counted, and transferred to 5-L cylinders placed in an 8.1°C water bath. Each cylinder held 1000 larvae.

On 13 June, 24,840 larvae were released into a large outdoor basin (2000 m³ volume, 600 m² surface area, maximum depth 4.0 m) filled with seawater pumped from Flødevigen Bay. Phytoplankton and zooplankton abundance was high when the larvae were introduced to the basin. A detailed description of the basin is presented in Moksness (1982).

Larvae were retained in the laboratory to examine starvation-induced mortality. Four batches of 100 larvae were placed in 5-L cylinders supplied with filtered seawater. Temperature was maintained at 8°C by placing the cylinders in a water bath. A batch was terminated every 7 days and the larvae recovered and preserved with buffered 4% formalin.

The larvae in the basin were sampled daily using a two-chambered plankton net of 500-μm mesh and a total sampling area of 0.3 m². The net was drawn diagonally across the basin at a depth of 2 m. The total volume sampled was 7.5 m³. Larvae and invertebrates captured in the plankton nets were preserved in buffered 4% formalin for later analysis.

Weekly estimates of zooplankton density were obtained from pump samples taken from depths of 0.5, 1, 2, and 3 m. Water was pumped from each depth for a short period prior to filtering a 30-second sample through a 90-μm plankton net. Samples were preserved in 4% formalin and examined later using a binocular microscope and counting chamber. Temperature, salinity, and oxygen saturation were measured at each depth on the day pump samples were obtained.

Preserved larvae were examined using a binocular microscope vernier eyepiece; they were measured, examined for food contents, and weighed. Length was measured from the snout to the tip of the notochord in larvae, and to the hypural plate in postlarvae. To test for shrinkage due to preservation, a sample of 21 newly hatched larvae were anesthetized, measured, and then preserved in 4% formalin. After 10 days the larvae were measured. The live length, 7.70 mm (SD 0.42), and the preserved length, 7.74 mm (SD 0.35), were not different. Under the preservation conditions employed, shrinkage of about 8% would be expected based on results presented by Hay (1982).

For food examinations, the entire gut was removed from post-yolk sac larvae. After the stomach differentiated, it was removed for food content analysis. After gut or stomach removal, larvae were placed on Teflon strips and dried at 60°C for 24 hours and then weighed using an electronic balance.

Results

Environmental parameters

The Flødevigen Biological Station is located at 58°24'N which is approximately the same latitude as the herring spawning ground in Bristol Bay (59°00'N), so herring in the basin experienced the same daylength as they would in Bristol Bay. The temperature in the basin averaged 11.75°C when the larvae were introduced on day-0, 3 days after hatching (Fig. 2a). Initially the basin was at a nearly uniform temperature varying from 11.9°C at the surface to 11.6°C at 3.5 m. After the larvae were introduced, temperatures in the basin began to rise owing to a prolonged period of sun and above-average air temperature. On day-12, surface temperature reached 18.8°C and then declined to range between 14 and 16°C for the remainder of the experiment. Temperatures below 2 m increased but not as sharply as surface waters (Fig. 2a). For the duration of the experiment, temperatures averaged 15.2, 15.1, and 15.8°C at 1, 2, and 3+ m, respectively. Temperature data recorded on the same dates offshore of the Bristol Bay spawning grounds at a depth of 2 m show that the temperatures in the basin averaged 4.5°C higher (15.26°C vs. 10.7°C).

Salinity during the experiment ranged from 30.6 to 32.7 ppt (Fig. 2b). The lowest salinity values were recorded at the start of the experiment followed by a slight increase throughout the experiment. The increase in salinity was attributed to evaporation and in flow of a small amount of denser water pumped into the basin to offset losses from evaporation and leakage.

Oxygen levels were checked periodically during the experiment. The lowest levels were recorded on day-12 at 70% saturation. At other times oxygen saturation was near 100%.

Zooplankton

Calanoid copepod adults and nauplii were the primary component of the zooplankton in the basin, constituting 26% and 68% of the number of organisms in pump samples, respectively (Fig. 3a). Adult copepod abundance was greatest when the herring larvae were introduced into the basin; it then declined rapidly (Fig. 4a). Copepod nauplii were also at greatest abundance in the beginning and declined over time from a peak of over 100/L to less than 1/L (Fig. 4b).

The other plankton species taken in pump and net samples were present at much lower densities (Fig 4c). The non-copepod zooplankton were primarily harpacticoid copepods, *Littorina littorea* veligers, crab (*Cancer pagurus*) zoea, and cladocera (*Bosmina* sp., *Evadne* sp., and *Podon* sp.). *Ephyra* sp. hydromedusa were abundant in the first days of sampling and then declined rapidly.

Feeding

Herring larvae in the basin fed primarily on copepod eggs, nauplii, and adults (Fig. 3b). Other items found in the diet were *L. littorea* veligers, crab zoea, and chiromomid larvae which occurred in the basin sediments. Food items were found in the gut within a few days of release into the basin. Within the first 5 days of release, 12% of the larvae contained food items (Table 1).
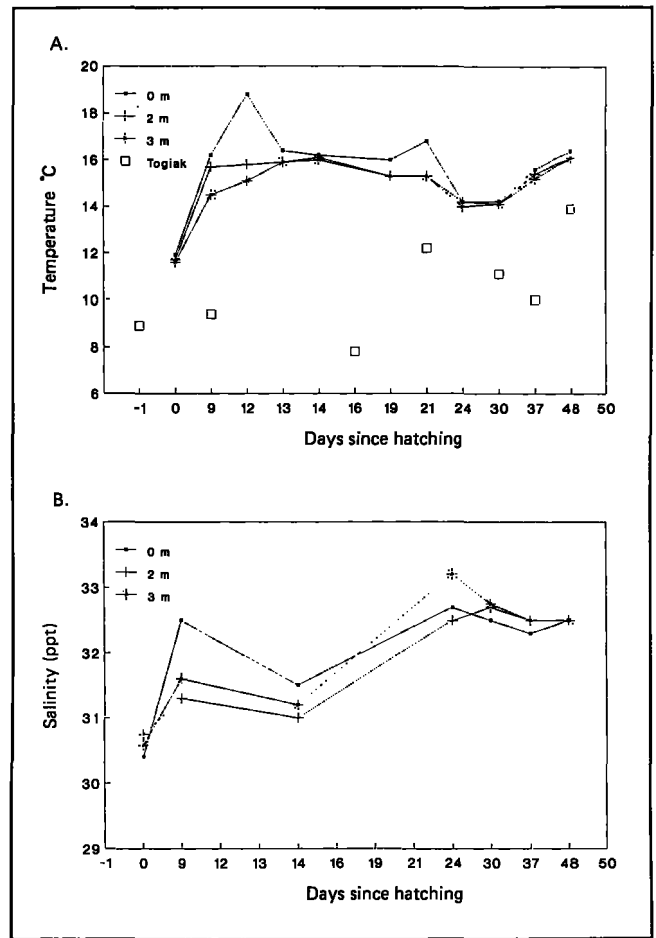

Figure 2

(A) Water temperature in the 2000-m³ basin, Fl⌀devigen Biological Station, Norway, at 0, 2, and 3 m compared with observed temperature at 2 m in Togiak Bay, Alaska. (B) Salinity (ppt) in the 2000-m³ basin at 0, 2, and 3 m.

The items observed in the gut during the first week were primarily copepod nauplii and eggs. The proportion of larvae with food doubled in the second week; eggs and nauplii continued to be major items, but small copepods were also found (Table 1). From day-13 to
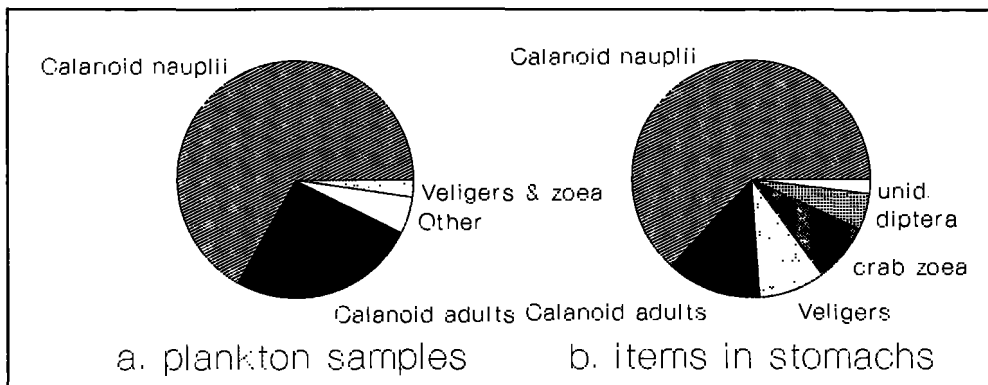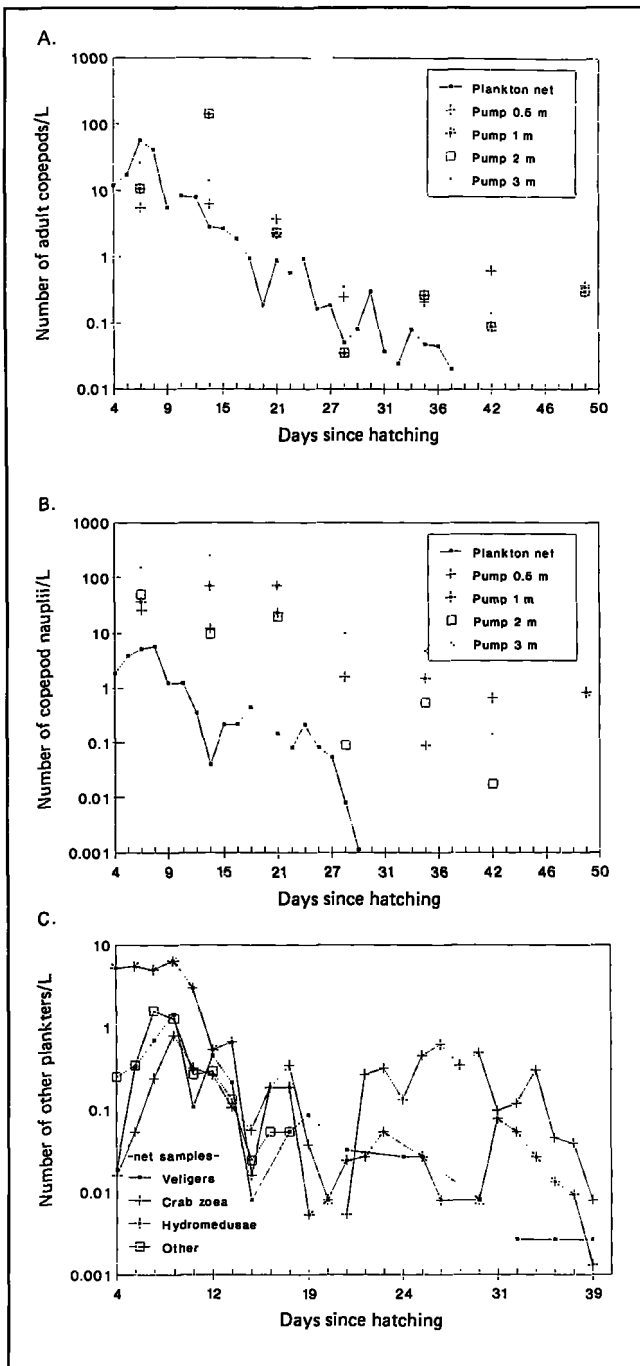

a. plankton samples   b. items in stomachs

Figure 3

Comparison of (a) species composition in plankton samples and (b) food items consumed by Pacific herring larvae.

day-21 the herring captured did not contain food items. This may have been due to regurgitation during capture, or the larvae may not have been feeding immediately prior to capture. The absence of food is likely a combination of the shock of capture and preservation, two processes which have been shown to cause significant voiding of the gut (Rosenthal 1969, Hay 1981).

By day-22 the stomach had begun to differentiate, and greater than 75% of the larvae had food items in the stomach from this time forward. The frequency of copepod eggs and nauplii occurrence decreased and adult copepods increased; also, other items appeared in the diet, primarily veligers and crab zoea.

On day-43 cannibalism was observed in the basin. On that date a school ($N = 10$) of 60–80 mm herring was observed attacking schools ($N = 10$–60) of smaller herring. Immediately afterward, dip net samples were attempted and two herring, one 57 mm and the other 32 mm, were obtained. The 32-mm herring was found to contain a 20-mm herring.

Comparison of feeding relative to abundance, using the Ivlev (1961) electivity index, shows that adult copepods were increasingly selected as the herring grew and that copepod nauplii were less utilized (Table 2). Veligers and crab zoea were not utilized initially but were strongly selected after the larvae had grown large enough to consume these species.

Growth

The average length of newly hatched larvae was 7.61 mm (SD 0.53), average dry weight 190 µg (SD 38.5) and yolk volume 0.16 mm³ (SD 0.09) (Table 3). Measurements were taken of herring hatched each day and no significant differences were found between days (F test, $\alpha = 0.05$).

Figure 4
(A) Number of calanoid copepods/L, (B) number of calanoid copepod nauplii/L, and (C) number of hydromedusae and other plankton/L in net samples in the 2000-m³ basin, Flødevigen Biological Station, Norway.

Table 1
Proportion of Pacific herring from Bristol Bay, Alaska, containing food and percentage of major food items consumed during five time-periods.

Day	Percent with food	Copepods		Veligers	Diptera	Crab zoea	Unidentified
		Nauplii	Adults				
2–5	12	95	5	0	0	0	0
8–12	23	84	17	0	0	0	0
13–21	0						
22–27	77	66	12	13	1	9	0
29–33	81	47	13	9	15	11	4

Table 2

Electivity index (Ivlev 1961) of Pacific herring larvae from Bristol Bay, Alaska, for items found in plankton and stomach samples by time periods.

Days	2–5	8–12	13–21	22–27	29–33
Copepods					
adults	−0.61	0.04	—	0.64	0.50
nauplii	0.10	0.01	—	0.19	−0.13
Veligers	−1	−1	—	0.71	0.77
Crab zoea	−1	−1	—	0.82	0.53

Table 3

Average length, weight, and yolk volume at hatching of Pacific herring larvae from Bristol Bay, Alaska. Standard deviation in parentheses.

Date	N	Length (mm)	Weight (μg)	Yolk volume (mm³)
11 June	50	7.46 (0.68)	180.48 (52.01)	0.19 (0.10)
12 June	25	7.74 (0.35)	218.00 (30.48)	0.17 (0.12)
13 June	24	7.77 (0.43)	181.33 (19.58)	0.09 (0.03)
Total		7.61 (0.53)	190.07 (38.52)	0.16 (0.09)

Figure 5

(A) Length-frequency and (B) weight-frequency distribution at hatching of Pacific herring larvae from Bristol Bay, Alaska.

The length of newly hatched herring was normally distributed with length ranging from 6 to 9 mm (Fig. 5a). The distribution of weight was skewed slightly, and dry weight ranged from 91 to 300 μg (Fig. 5b).

The length at hatching of these larvae is similar to that reported from other Pacific herring stocks: British Columbia 4–8 mm (Stevenson 1962), 8.5–9 (Alderdice and Hourston 1985); California 8 mm (Talbot and Johnson 1972.)

The growth rate from hatching to experiment termination 63 days later averaged 0.66 mm/day and ranged from 0.31 mm/day for the smallest to 1.48 mm/day for the largest. Daily growth increased from 0.1 mm/day on day-3 to 0.64 on day-21 and then decreased (Fig. 6a).

A Gompertz growth curve

$$L_t = L_\infty\, e^{-k - e^{bt}},$$

was fitted to the length-at-age data, where

L_∞ = Length infinity
k = Brody growth coefficient
b = regression constant
t = age in days.

The resulting parameters were L_∞ = 202.3 mm (SD 86.34), k = 3.299 (SD 0.389), and b = 0.013 (SD 0.03). The fit of observed length to the model is shown in Figure 6b. The poor fit is due to the lack of observa-
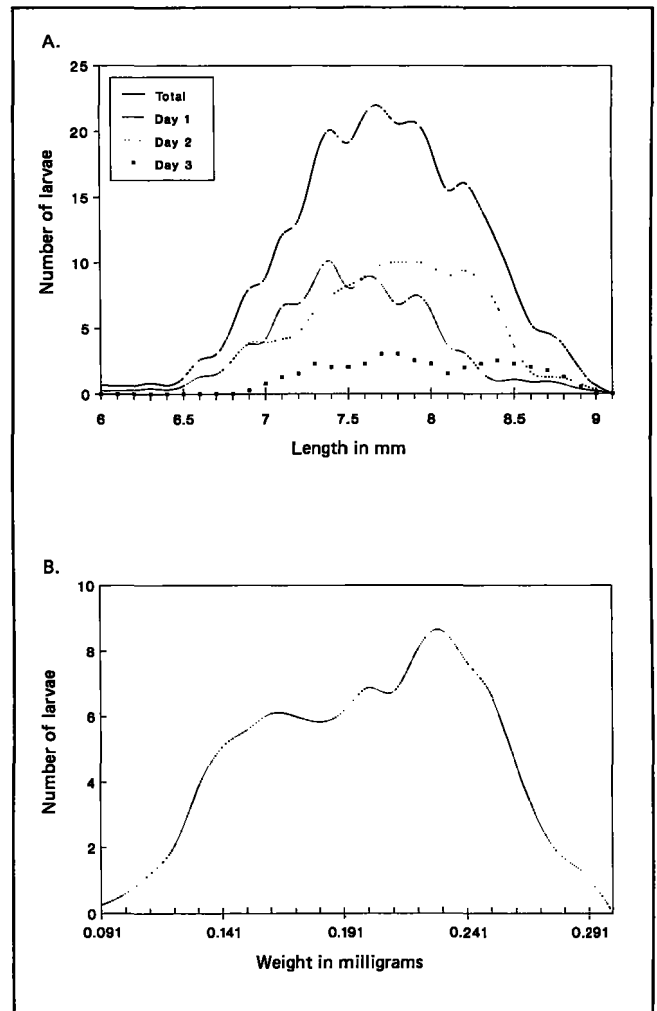
tions beyond the inflection point. Based on the length of age-0 herring captured in the Bering Sea in September, L_∞ should be between 80 and 90 mm and k proportionately lower.

Weight-at-age was more variable than length-at-age (Fig. 6c). Average weight increased in weight from 0.19 mg at hatching to 182 mg on day-63, or an average daily growth rate of 2.89 mg/day. The specific growth rate,

$$\ln(wt)_i - \ln(wt)_0/t_i - t_0$$

where $\ln(wt)$ = $\log_e$ weight,
t_i = day i,
t_0 = day 0,

exhibited a decrease as yolk was depleted and then increased to a peak on day-21, which was followed by a decline similar to daily growth in length (Fig. 6a).
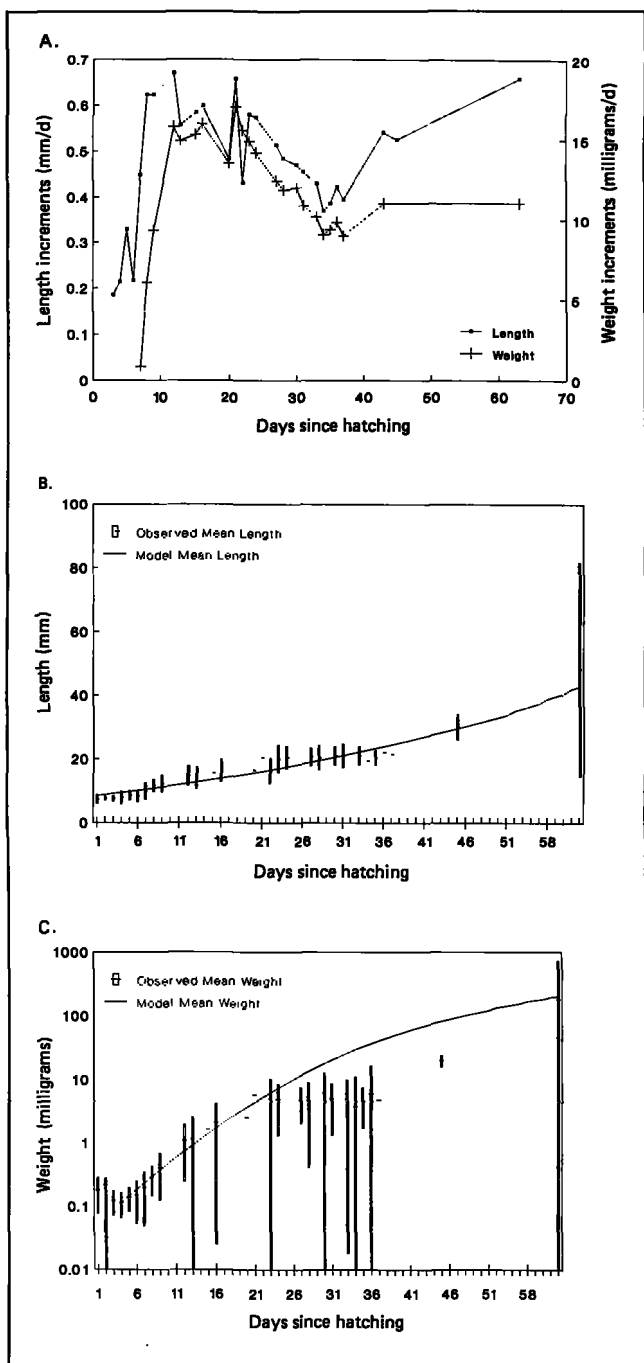
Figure 6
(A) Growth increments in length (mm/d) and weight (mg/d) for Pacific herring from Bristol Bay, Alaska, in a 2000-m³ basin at Flødevigen Biological Station, Norway. (B) Observed length-at-age and 95% confidence interval, and length-at-age estimated by a Gompertz model (solid line), of Pacific herring in the basin. (C) Observed weight-at-age (mg) and 95% confidence interval, with a Gompertz model growth estimate, of Pacific herring from Bristol Bay, Alaska, in the 2000-m³ basin at Flødevigen Biological Station, Norway.
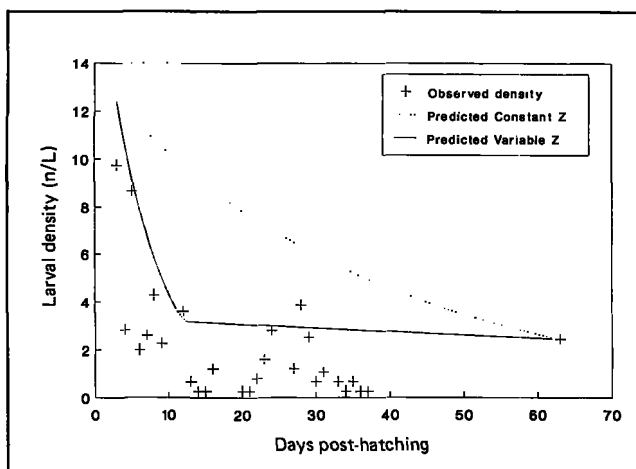

Figure 7
Estimated survival of Pacific herring from Bristol Bay, Alaska, in the 2000-m³ basin at Flødevigen Biological Station, Norway, from yolksac stage to termination on day-63, based on plankton net samples fit to constant and variable mortality (Z) models.

The great variability in weight made it difficult to fit a growth model by nonlinear least-squares. A modified Gompertz model (Zweifel and Lasker 1976) was examined iteratively by fixing one parameter and varying the others. The Gompertz model and observed weights are shown in Figure 6c. It can be seen that the model describes growth well to day-25, but then observed growth deviates from predicted growth. The point of deviation is at the time metamorphosis commences, when the more robust fish may have begun to avoid the sampling net. Ware (1975) points out that net avoidance often results in underestimation of growth rate.

Survival

Of the 24,840 larvae released into the basin, 4891 were recovered when the basin was drained on day-63. The overall survival rate in the basin was 19.69%, total instantaneous mortality (Z) = 1.625. The daily mortality rate was 2.7%.

Comparison of the estimated density (fish/m³), based on decay of the initial population by the daily mortality rate, with the density of larvae estimated from plankton net samples shows that net samples underestimated larval abundance in the basin if the rate of decline was constant (Fig. 7). The net samples suggest that mortality was initially high following release and then declined. A two-part mortality curve is shown in Figure 7 which estimates daily mortality to be 15.08% during day-3 to day-12 followed by a rate of 0.05% for the remainder of the experiment.

Table 4

Summary of larval survival of Pacific herring from Bristol Bay, Alaska, held without food. Standard deviation in parentheses.

Day	No. alive	Sample size	Mean length (mm)	Mean weight (μg)	Mean yolk volume (mm³)	Condition factor (K)
1	100	25	7.0 (0.1)	175 (29)	0.101 (0.04)	52.2 (0.07)
8	88	25	9.4 (0.2)	147 (27)	0.004 (0.01)	18.0 (0.03)
13	93	25	9.1 (0.1)	119 (26)	0	15.7 (0.02)
19	52	25	9.0 (0.3)	109 (20)	0	15.5 (0.03)

Table 5

Growth rates reported for Pacific herring *Clupea pallasii* larvae.

Growth rate (mm/d)	Days	Temperature (°C)	Location	Source
0.48–0.52	15	8.9–9.1	BC1	Alderdice and Hourston 1985
0.40–0.80	30?		BC2	Stevenson 1962
0.39–0.79	30	8.0–14.0	WA	Keegen et al. 1986
0.33	60	9.0–12.0	CA	Talbot and Johnson 1972
0.78–0.94	87		BB	Checkley 1982
0.60	100	11.0–16.0	JN	Mority 1985

BC1 Strait of Georgia, British Columbia; BC2 Barkley South, British Columbia; WA Northern Puget Sound, Washington; CA laboratory, San Francisco Bay, California; BB Bristol Bay, Alaska; JN Hokkaido, Japan.

Herring held in the laboratory and deprived of food died 21 days after hatching. Larval survival was high until day-19 at which time the number alive had decreased to 52% (Table 4). Mortality proceeded rapidly at this point, and total mortality was observed in the remaining batch on day-21 of the experiment.

Length increased in starved herring during the first week from an average of 7.0 mm to 9.4 mm and then remained essentially unchanged for the remainder of the experiment (Table 4). Weight, on the other hand, decreased from 175 μg on day-1 to 147 μg near the end of the yolksac stage and to 109 μg on day-19 (Table 4).

Discussion

The development of Bristol Bay herring larvae in the basin was similar to that reported for other stocks. The average growth of 0.66 mm/day was near the upper end of the range reported from British Columbia and Washington but greater than that observed in aquaria experiments in California (Table 5). Direct comparison is difficult because of the differences in duration of observation periods, but it is likely that the 0.33 mm/day reported for San Francisco Bay herring is low due to a diet of *Artemia* nauplii, which have been shown to produce poorer growth than natural plankton (Blaxter and Hunter 1982).

Comparison of our results with otolith ring data (Checkley 1982) indicates that the growth observed in the basin is similar to at-sea growth. The otolith-ring age estimates were 0.78 mm/day and 0.94 mm/day for herring of 82 mm average length and 108 mm maximum length. These are likely slight overestimates of growth rates since there is a lag time between hatching and ring formation related to yolksac absorption (Messieh et al. 1987, Moksness and Wespestad 1989).

McGurk (1984) concluded that growth in laboratory experiments is always lower than at-sea growth. The similarity between growth rates observed in the basin and rates estimated from at-sea otoliths suggests that the basin environment resembled natural conditions. Stevenson (1962), Keegen et al. (1986), and McGurk (1984) reported higher growth rates for batches of larvae developing at higher temperature.

Blaxter and Hunter (1982) relate that the growth rate of herring is primarily governed by temperature and food abundance. In Bristol Bay, summer surface-water temperatures are warmest nearshore (10°C and greater) and decrease (7°C or less) a short distance offshore (Ingraham 1981). That herring growth in the basin was similar to growth observed in field samples

suggests that, in Bristol Bay, herring larvae are re-
tained in the nearshore zone during the larval period
to experience a temperature regime similar to that
observed in the basin. Herring larvae transported out
of coastal waters would develop in much colder water
and exhibit a reduced rate of growth.

The mortality of larvae in the basin was high during
the first 2 weeks of the experiment, with daily mor-
tality estimated to be as high as 14%. This is about one-
half that estimated for a wild population observed over
a 20-day period in which daily mortality was 32%
(Stevenson 1962). The higher survival in the basin is
consistent with the results of Moksness and Øiestad
(1987), who estimated daily mortality to be higher (4%)
for the first 30 days and then much reduced (0.8%) to
day-100 for Atlantic herring in the same basin.

The higher initial mortality of Pacific herring in the
basin may be due to predation. Hydromedusae known
to consume herring were abundant during the first
week Pacific herring were in the basin. In the experi-
ment with Atlantic herring, the occurrence of hydro-
medusae was much later, beyond day-40. Arai and Hay
(1982) estimated that hydromedusae predation in Bri-
tish Columbia could account for a daily larval loss
of 9%.

Starvation may not have been a significant source
of mortality because the abundance of copepod larvae,
the preferred food of herring larvae, was much higher
at the time of first feeding of Pacific herring than was
estimated at the same point for Atlantic herring
(Moksness and Øiestad 1987). Kiørboe et al. (1985)
report that herring are able to successfully initiate
feeding at prey densities much lower than usually pres-
ent in the sea at the time of first feeding.

Cannibalism may have been an important source of
mortality in late-stage larvae. Blaxter and Hunter
(1982) report that cannibalism has been observed in
situations in which a size hierarchy has developed,
although they believe this is a rare occurrence based
on the scarcity of reports of cannibalism in aquarium
studies. However, the observation of attacks on smaller
herring in this study suggests that cannibalism was not
a rare event in the basin population. Cannibalism may
have been related to the reduced abundance of zoo-
plankton at the time it was observed. However, fish
larvae may be a normal component of the diet of post-
larval herring since capelin Mallotus villosus larvae
were rapidly consumed by newly metamorphosed her-
ring in an earlier basin study (Moksness and Øiestad
1987). Also, Hourston et al. (1981) reported that age-1
Pacific herring, 71–91 mm standard length, readily con-
sumed larval herring when placed together in a 197-L
tank.

An interesting aspect of herring growth in the basin
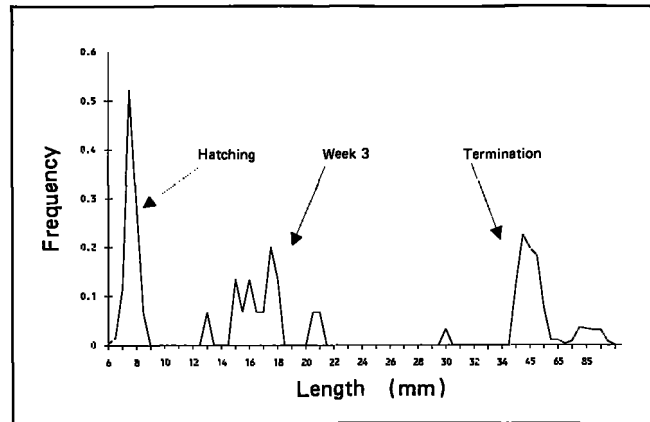was the development of three distinctive length modes

Figure 8
Length-frequency distribution of Pacific herring from Bristol Bay,
Alaska, in the 2000-m³ basin at Flødevigen Biological Station, Nor-
way, at hatching, week-3, and study termination on day-63.

from an essentially unimodal population at hatching
(Fig. 8). The cause of distinct size modes in this experi-
ment is unknown, but it may be related to success at
first feeding or be genetically based, because size dif-
ferences developed early.

Blaxter and Hunter (1982) report that strong size
hierarchy has been observed in some aquarium studies
of herring, which they speculate may involve crowding
or food competition; however, in a previous study of
Atlantic herring larvae in a 4400 m³ basin a size hier-
archy did not develop (Øiestad and Moksness 1981).
McGurk (1984) found that length and weight of larvae
of the same hatch differed at 30 days posthatch as a
result of withholding food from 0 to 14 days. This sug-
gests that modes may be a reflection of feeding suc-
cess. Moksness et al. (1989) observed that in ocean
catfish differences in feeding success at first feeding
was expressed as differential growth that persisted
throughout the larval period.

Although most of the literature suggests that differ-
ential growth is related to early feeding success genetic
factors may also influence larval growth and survival.
Christopher et al. (1988), in a study of capelin Mallotus
villosus larvae from known females crossed with a
single male, found that the amount of yolk varied
among the females and that growth and survival was
correlated with yolk quantity.

Whatever the cause, one would tend to conclude that
the modes were distinct "cohorts" from different
hatchings if observed in the wild. The significance of
these results is that a method such as otolith daily ring
counts is required to validate larval age and the use
of length-frequency analysis to determine the occur-
rence of cohorts may lead to erroneous assumptions.
If differential growth among a brood is a common

occurrence in nature, it may complicate analyses and results of larval cohort studies such as those of Lambert (1984).

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