Year-class formation in Pacific herring (*Clupea pallasi*) estimated from spawning-date distributions of juveniles in San Francisco Bay, California

Michael R. O'Farrell

Ralph J. Larson

Department of Biology
San Francisco State University
1600 Holloway Avenue
San Francisco, CA 94132
Present address (for M. R. O'Farrell, contact author): Department of Wildlife, Fish and Conservation Biology
University of California, Davis
One Shields Avenue
Davis, California 95616

E-mail address (for M. R. O'Farrell): mrofarrell@ucdavis.edu

Abstract—Inter and intra-annual variation in year-class strength was analyzed for San Francisco Bay Pacific herring (*Clupea pallasi*) by using otoliths of juveniles. Juvenile herring were collected from March through June in 1999 and 2000 and otoliths from subsamples of these collections were aged by daily otolith increment analysis. The composition of the year classes in 1999 and 2000 were determined by back-calculating the birth date distribution for surviving juvenile herring. In 2000, 729% more juveniles were captured than in 1999, even though an estimated 12% fewer eggs were spawned in 2000. Spawning-date distributions show that survival for the 2000 year class was exceptionally good for a short (approximately 1 month) period of spawning, resulting in a large abundance of juvenile recruits. Analysis of age at size shows that growth rate increased significantly as the spawning season progressed both in 1999 and 2000. However, only in 2000 were the bulk of surviving juveniles a product of the fast growth period. In the two years examined, year-class strength was not predicted by the estimated number of eggs spawned, but rather appeared to depend on survival of eggs or larvae (or both) through the juvenile stage. Fast growth through the larval stage may have little effect on year-class strength if mortality during the egg stage is high and few larvae are available.

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Both biological and physical sources of mortality have been suggested as important in determining year-class strength in fish populations. Food limitation at first feeding (Hjort, 1914; Cushing, 1975; Lasker, 1975; Cushing, 1996), larval retention (Iles and Sinclair, 1982; Sinclair and Iles, 1985), a juvenile critical period (Bollens et al., 1992; Thorisson, 1994), as well as predation and environmental conditions may ultimately affect recruitment. Egg development time and larval growth rate have the capacity to adjust the relative impacts of these mortality sources on individual propagules by modifying stage duration (Houde, 1989; Yoklavich and Bailey, 1990).

Juvenile fishes can be used to assess both inter- and intra-annual variation in egg and larval survival. Interannual variation in year-class strength is often inferred from measures of juvenile abundance (e.g., Baxter et al., 1999). In addition, when the total number of eggs spawned is known, juvenile abundance can be used to assess overall variation in egg and larval survival. Intra-annual variation in egg and larval survival can be estimated from the birth-date distribution of surviving juveniles, as determined from otolith daily increment analysis. Particularly when data on actual spawning-date distributions are available, the birth date distribution of survivors can be used to identify periods of spawning that contributed differentially to juvenile recruitment (Methot, 1983; Rice et al., 1987; Yoklavich and Bailey, 1990; Moksness and Fossum, 1992; Fox, 1997; Takahashi et al., 1999).

Recruitment of juvenile Pacific herring (*Clupea pallasi*) varies interannually by over an order of magnitude in San Francisco Bay (Baxter et al., 1999) and is the culmination of several processes. Schools of adult herring enter San Francisco Bay in discrete batches during the fall and winter. These schools shoal and deposit eggs and milt during spawning events that often correspond to the quarter moon phase. Spawning events can vary in duration from approximately one day to one week, and simultaneous events may occur at different spawning sites throughout the bay. Herring lay adhesive eggs intertidally and subtidally on rocks, algae, aquatic plants, pier pilings, and other substrates (Alderdice and Velsen, 1971; Hay, 1985). Eggs can experience extremely high mortality due to predation (McGurk, 1986; Bishop and Green, 2001), suboptimal temperature and salinity conditions (Alderice and Velsen, 1971; Griffin et al., 1998), as well as reduced hatching and developmental abnormalities associated with certain substrate se-

lection (Vines et al., 2000). Larvae hatch from eggs after an incubation period, and the San Francisco Bay estuary can serve as a larval nursery area until after metamorphosis into the juvenile stage (Hay, 1985).

Our objectives were 1) to identify periods in the spawning season that lead to successful (or unsuccessful) juvenile recruitment and 2) to evaluate larval and juvenile growth variation for two herring year classes. We used otoliths of juvenile herring from the 1999 and 2000 year classes to back-calculate spawning-date distributions and determine spawning times that lead to successful recruitment. Distributions of spawning were obtained from management surveys. Growth was then evaluated to determine its role in year-class formation.

Methods

Surveys

All information on adult herring spawning events and juvenile herring specimens were obtained from ongoing monitoring and management surveys conducted by the California Department of Fish and Game (CDFG).

Data on timing, location, and magnitude of herring spawning events for the 1998–99 and 1999–2000 spawning seasons were obtained from the herring spawn survey conducted by the California Department of Fish and Game (CDFG). The survey is conducted from November through March throughout central San Francisco Bay, the area of most herring spawning (Watters et al., 2004). The central bay region is searched for herring spawning on a daily basis from a small boat, and the entire spawning region is covered at least once per week. Eggs are located visually at low tide and by rake in shallow subtidal areas. When a spawning area is located, the number of eggs per square meter is measured from a subsample of the spawning area and is expanded to an estimate of total eggs spawned (for spawning survey method details, see Spratt, 1981; Watters et al., 2004). At the end of the 1998–99 and 1999–2000 spawning seasons, information on date, location, spawning area, average eggs/m^2, total eggs, and the spawning biomass estimate was provided for the purpose of this study (Watters[1]).

Juvenile (age-0) herring were sampled monthly from 30 stations in San Francisco Bay aboard the RV *Longfin* as part of CDFG's Bay/Delta Division's Bay study (Fig. 1). Each station was visited once a month and juvenile herring were retained from catches during the months of April–June 1999 and March–June 2000. Stations were sampled by mid-water trawl with a 3.7-m^2 mouth and 1.3-cm mesh codend, towed against the current, for 12 minutes. Volume of water filtered was calculated by using a flowmeter and was used to calculate

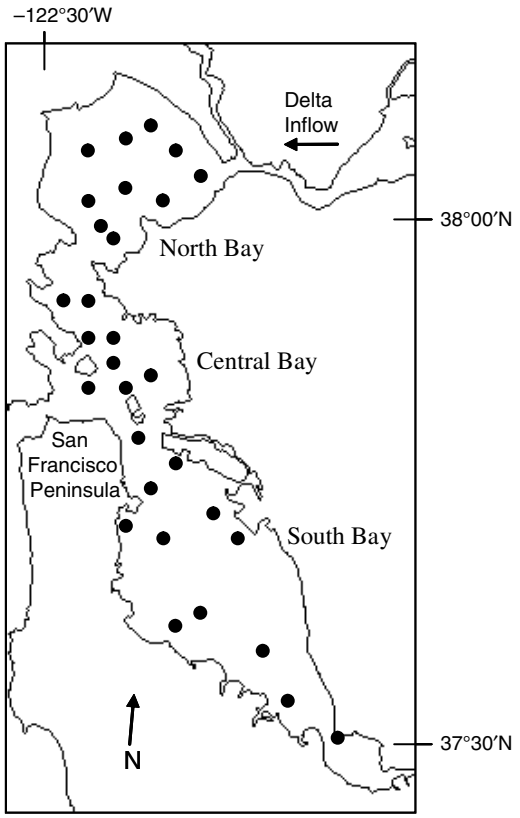

Figure 1
Midwater trawl sampling stations in San Francisco Bay.

catch per unit of effort (CPUE) for each station. Juvenile herring were measured onboard, sorted from the catch, kept on ice, and transported to the laboratory, where they were frozen. Relative recruitment in each year was calculated by summing the CPUE at each station for the months of March–June in 1999 and 2000.

Otolith preparation and analysis

Frozen juvenile herring, separated by date and station, were thawed in batches and all fish were re-measured for standard length to the nearest mm. If the catch was small at a particular station (less than approximately 10 individuals), all specimens from that station were reserved for otolith analysis. If the catch was large, a subsample of the measured catch was reserved for otolith analysis. Subsampling consisted of randomly selecting at least two specimens from each 1-mm length bin in the catch.

Both sagittal otoliths were extracted from each fish, cleaned with fresh water, and transferred to a microscope slide where they were allowed to dry. When completely dry, both otoliths were mounted on the slide, convex side up, with clear nail polish.

Otoliths were read with a compound microscope. Because otoliths were too thick to allow sufficient light transmission for increment reading, all otoliths were

[1] Watters, D. 2000. Personal commun. Calif. Dep. Fish and Game, 411 Burgess Dr., Menlo Park, CA 94025.

ground with 2000 grit sandpaper. Otoliths were alternately ground and examined under the microscope at 100× to ensure that the section was thin enough to allow sufficient light transmission, yet not over-ground so that the edges of the otolith were lost.

Daily increment deposition in herring begins at yolksac absorption, corresponding with the first heavy ring near the nucleus (Geffen, 1982; McGurk, 1984a; McGurk, 1987; Moksness and Wespestad, 1989). This heavy ring was located in all herring examined and increment counts were initiated there. Increment counts were made at 1000× (with an oil immersion objective) and 400× (without oil immersion) magnification along the axis of maximum resolution. All increments were counted from the first heavy ring until the last ring on the edge of the otolith.

Several days after the first reading, the same reader performed a reading on the second otolith. If the two increment counts differed by more than a value of 7, a third reading was conducted at a later date on the highest quality otolith. If the three increment counts differed from each other by more than a value of 7, otolith data from that fish were not used in further analyses. Where two readings differed by 7 or fewer increments, the final increment number for each fish was determined by averaging the two increment counts.

Daily otolith increment deposition has been demonstrated in Pacific herring larvae reared in captivity (McGurk, 1984a; Moksness and Wespestad, 1989) and in the field (McGurk, 1987). In our study, otolith increments were assumed to be deposited daily and the validity of this assumption is treated in the "Results" and "Discussion" sections. Precision of otolith increment counts was determined by computing the average percent error for each otolith examined (Beamish and Fournier, 1981).

Spawning-date distributions

Spawning-date distributions were constructed from specimens retained for otolith analysis in 1999 and 2000. Distributions were calculated 1) by adding a constant of 14 days to the otolith increment count and 2) by subtracting that value (otolith increments+14) from the Julian date of capture. Because Pacific herring begin daily increment deposition at yolksac absorption, the constant of 14 days was added to the increment value to account for egg incubation and the yolksac larval period. Taylor (1971) reported a 9-day egg incubation period for a British Columbia Pacific herring stock between 13.4°C and 13.8°C. For San Francisco Bay spawned herring, Griffin et al. (1998) found developmental rate to be influenced by salinity; the greatest hatching rate occurred 10 days after fertilization at a salinity of 14 ppt. Yolksac absorption occurs in Pacific herring 4–7 days after hatching (McGurk, 1987; Griffin et al., 2004, and references therein). The final value of 14 days for egg incubation and yolksac absorption used in our study was determined 1) from laboratory-derived values reported for British Columbia (Taylor, 1971; McGurk, 1987) and San Francisco Bay (Griffin et al., 1998) herring populations and 2) by visually matching back-calculated spawning-date distributions with the observed spawning-date distribution from the CDFG spawn-deposition survey.

The back-calculated spawning-date distributions determined from specimens used for otolith analysis were extrapolated to include as many herring as possible caught in the juvenile surveys of 1999 and 2000. Length-frequency distributions were converted to spawning-date distributions by using age-length keys. Separate age-length keys were constructed for each survey in both 1999 and 2000. In some cases, the monthly survey was split into two legs separated by several days. When the monthly survey was split into legs, separate age-length keys were constructed for each leg.

It was not possible to fit all herring caught between the months of March and June into age-length keys because some samples were inadvertently discarded after measurement in the field. If the range of lengths in the discarded samples extended beyond the sizes of samples aged, a complete age-length key could not be constructed. To avoid ascribing a possibly inaccurate age to a fish outside the size range of the age-length key, those fish were not included in the spawning-date distribution. Table 1 displays the number of herring caught in each leg, the number of otoliths used to construct the age-length key for that survey leg, and the total number and proportion of juveniles caught that are represented in the spawning-date distribution. The number of juveniles caught was greater than the number of juveniles in the spawning-date distribution for all but one survey leg. This discrepancy was due to discarded fish (in the field) with lengths not within the range of the age-length key constructed from the subsampled individuals.

Mortality estimate corrections are often superimposed upon spawning-date or hatching-date distributions to account for different size juveniles captured (Methot, 1983). Presumably a larger juvenile is older, and thus has been exposed to mortality factors for a longer period of time than has a smaller juvenile. The lack of a correction for juvenile mortality can lead to an underrepresentation of larger juveniles in the distribution. Because of the noncontinuous mid-water trawl sampling schedule, mortality rates could not be estimated from the data used in our study. As a result, mortality corrections were calculated by using an instantaneous mortality rate value of 0.016/d, corresponding to the greater of two mortality rates calculated from juvenile Pacific herring in Prince William Sound, Alaska (Stokesbury et al., 2002).

Spawning-date distributions were corrected for mortality by calculating abundance at age 100 days (N_{100}). For fishes aged at less than 100 days:

$$N_{100} = N_a e^{-0.016(100-a)}, \quad (1)$$

where a is the age of the fish in days.

Table 1

Summary of the catch, number of *Clupea pallasi* otoliths examined from the catch, number and percent available for use in the spawning-date distributions, and catch per unit of effort (CPUE) for the midwater trawl survey in 1999 and 2000. ΣCPUE represents summed CPUE for all stations in each survey leg. Juveniles were not used in analysis if they were inadvertently discarded in the field and if a complete age-length key could not be constructed.

Survey dates	Area surveyed	Juveniles caught	Otoliths examined	Used in analysis	Percent used	ΣCPUE
1999						
Mar 99	entire bay	0	0	0	0	0
21 Apr 99	central and north	41	0	0	0%	1653
26–28 Apr 99	south and north	66	53	60	91%	2360
18–19 May 99	north	19	4	2	11%	771
24–27 May 99	north, central, and south	280	251	273	98%	12,856
9–10 Jun 99	north and central	91	25	45	49%	3457
15 Jun 99	south	61	0	0	0%	2551
Total		558	333	380	68%	23,648
2000						
8–9 Mar 00	north and central	11	0	0	0%	637
13–14 Mar 00	south	7	7	6	86%	294
4–5 Apr 00	north	25	25	25	100%	1053
10–11 Apr 00	central and south	302	115	284	94%	14,712
10 May 00	north	898	77	740	82%	38,270
22–24 May 00	central and south	2244	77	2237	100%	102,516
6–7 Jun 00	central and south	569	74	569	100%	25,352
13 Jun 00	north	13	0	0	0%	539
Total		4069	375	3861	95%	183,373

For fishes aged greater than 100 days:

$$N_{100} = \frac{N_a}{e^{-0.016(a-100)}}. \quad (2)$$

Combining the results of Equations 1 and 2 produced the mortality-corrected spawning-date distributions.

Growth

To evaluate correlates of both inter- and intra-annual variation in survival to the juvenile stage, we wanted to compare growth rates of herring up to the juvenile stage. However, because it was apparent that growth rates may have differed for specimens spawned at different times of the year, either a linear or nonlinear growth curve fitted to size-at-age data would be erroneous (O'Farrell, 2001). Larger (older) and smaller (younger) individuals would have experienced different growth histories; therefore a plot of size versus age for any sample of fish would not reflect the growth history of any one cohort. Furthermore, consecutive samples rarely contained individuals from any given cohort because older juveniles appeared to leave San Francisco Bay. Finally, we did not have data on size at age of larvae; therefore growth curves would be incomplete.

Instead, we used age at size to compare growth within and between years. To do this, we computed the number of otolith increments (days after yolksac absorption) present in fish between 40 mm and 50 mm standard length. This size group was chosen to analyze growth because it was well represented in both in the 1998–99 and 1999–2000 spawning seasons. The mean and stan-

Table 2

Summary statistics and distribution of juvenile *Clupea harengus* lengths within the 40–50 mm size bin for sampling events where size-at-age data were used. Other sampling events were not included in growth analyses because they did not contain juvenile herring between the sizes of 40 mm and 50 mm.

Survey leg	*n*	Mean (mm)	SD (mm)
26–27 Apr 99	15	43.80	2.54
24–27 May 99	162	45.02	2.63
9 Jun 99	10	42.20	2.82
5 Apr 00	16	46.25	3.00
10–11 Apr 00	23	46.43	2.94
10 May 00	9	43.67	3.04
22–24 May 00	36	44.81	3.19
6–7 Jun 00	36	46.56	2.82

dard deviation of the length distribution within the 40–50 mm bin for each sampling event is provided in Table 2. Thus, the amount of time (measured by otolith increments) needed for fish to grow to the 40 mm–50 mm size group was used to compare growth. Differences in age at length were evaluated and compared with observed variation in juvenile abundance.

Results

Egg and juvenile abundance

Both the magnitude and timing of estimated egg deposition differed little between the 1998–99 and 1999–2000 spawning seasons (Fig. 2). Total egg deposition was estimated to be 9.66×10^{11} eggs for 1998–1999 and 8.59×10^{11} eggs for 1999–2000 (Watters[2]). Peak egg deposition in both spawning years occurred in January (Fig. 2).

Abundance of juvenile herring resulting from these two spawning seasons differed greatly. The cumulative estimated relative recruitment ($\Sigma CPUE$) of juvenile herring was 7.75 times greater in 2000 than 1999 (Table 1).

General patterns of juvenile herring distribution were similar in 1999 and 2000. Juvenile herring recruited to the sampling gear in March and April and were widely distributed throughout the bay (Fig. 3). Peak abundances occurred in May for both 1999 and 2000, and juveniles were caught throughout the study area. By June, abundances decreased and herring became more concentrated in the central Bay region, presumably aggregating in this area prior to exiting San Francisco Bay for the coastal ocean (Fig. 3).

[2] Watters, D. 2000. Unpubl. data. Calif. Dep of Fish and Game, 411 Burgess Dr., Menlo Park, CA 94025.

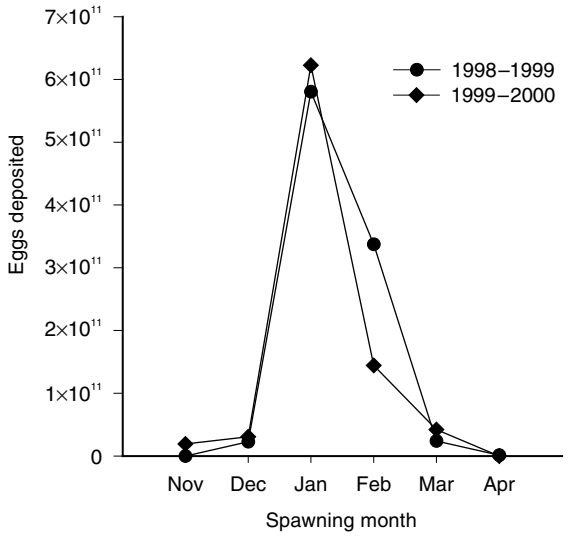

Figure 2

Total egg deposition by Pacific herring (*Clupea pallasi*), summed by spawning month for the 1998–99 and 1999–2000 spawning seasons. Data provided by the California Department of Fish and Game, Menlo Park.

Spawning-date distributions

The temporal distribution of successful spawning-dates differed between the 1999 and 2000 year classes (Fig. 4, A and B). In 1999, the earliest spawning-date that resulted in juvenile recruitment was 30 November 1998. The greatest numbers of juvenile recruits were a product of the middle of the spawning season, from approximately early January 1999 though early February 1999, and the highest recruitment occurred from spawnings between 10 January and 14 January 1999 (Fig. 4A). An additional spike of recruitment was observed from spawning events at the end of the season (early March). The period of highest recruitment came at the same time as the highest spawning intensity. Spawning events early in the spawning season (November–December) appeared to produce few juveniles (Fig. 4A).

In 2000, juveniles recruited from much earlier spawning events. Back-calculated spawning dates indicated that spawning may have occurred as early as 13 October 1999 (Fig. 4B). Both the March 2000 and April 2000 juvenile surveys contained herring with back-calculated spawning dates that ranged from mid to late October, indicating that a spawning event occurred extremely early in the spawning season and was undetected by the spawn-deposition survey (which commences in November). Although early spawnings appeared to produce some recruitment success, a near lack of success was noted for many of the mid-season spawnings that occurred from mid-November through mid-January 2000 (Fig. 4B). This period of poor survival was then followed by the period of highest recruitment; spawning dates ranged from mid-January to early March and peak recruitment resulted from February spawning (Fig. 4B).

Juvenile mortality corrections superimposed upon the spawning-date distributions had little effect on the general results. An instantaneous juvenile mortality rate of 0.016/d produced minor adjustments on the percent recruitment resulting from particular spawning periods in both years (Fig. 4, A and B). This mortality correction did not alter the general spawning periods that resulted in juvenile recruitment. Increasing the instantaneous juvenile mortality rate to 0.05/d (O'Farrell, unpubl. data) also had negligible effects on the general results of the spawning-date distributions.

Data for both 1999 and 2000 are not totally complete. The spawning-date distribution for 1999 was based on a total of 380 herring, whereas 558 herring were caught between the months of March and June. Similarly, the 2000 spawning-date distribution was based on a total of 3861 herring, whereas 4069 herring were caught during the same months (Table 1). Fish were omitted from

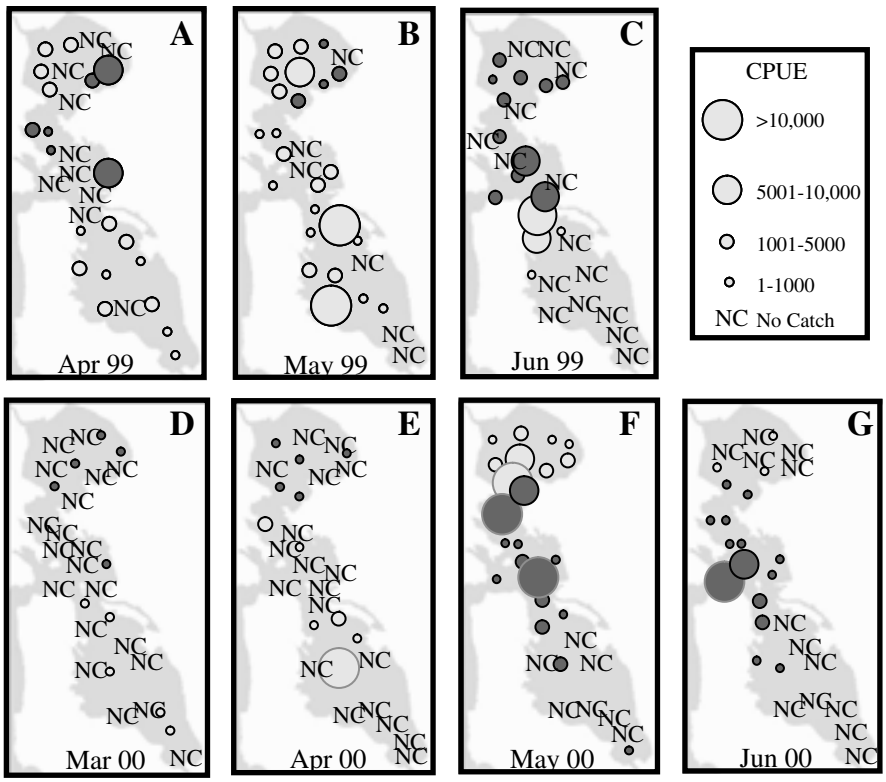

Figure 3

Juvenile herring (*Clupea pallasi*) CPUE distribution by station and month for 1999 and 2000. April 1999 (**A**) dark bubbles represent the 21 April survey leg and light bubbles represent the 28–28 April survey leg. May 1999 (**B**) dark bubbles represent the 18–19 May survey leg and light bubbles represent the 24–27 May survey leg. June 1999 (**C**) dark bubbles represent the 9–10 June survey leg and light bubbles represent the 15 June survey leg. March 2000 (**D**) dark bubbles represent the 8–9 March survey leg and light bubbles represent the 13–14 March survey leg. April 2000 (**E**) dark bubbles represent the 4–5 April survey leg and light bubbles represent the 10–11 April survey leg. May 2000 (**F**) dark bubbles represent the 22–24 May survey leg and light bubbles represent the 10 May survey leg. June 2000 (G) dark bubbles represent the 6–7 June survey leg and light bubbles represent 13 June survey leg.

the spawning-date distribution because some samples were discarded and otoliths were unavailable. Because of evidence for intrayear growth-rate variation, other age-at-length data were not used to infer spawning dates for these fish. The standard length data for the fish not included in this analysis were used for all other analyses in our study.

Precision of multiple otolith readings was calculated for all otoliths examined. Average percent error (Beamish and Fournier, 1981) was 3.60% in 1999 and 1.64% in 2000, indicating that aging precision was less than 4 days for 100-day old herring in both years.

Growth

Different patterns of age at length (40–50 mm) were observed in 1999 and 2000. In 1999, specimens between 40 mm and 50 mm were captured in three survey legs. A significant decrease in the number of otolith increments for juveniles 40 mm–50 mm standard length was detected in 1999 (Fig. 5A; Kruskal-Wallis test; H=27.93, P<0.0001). Nonparametric multiple comparisons indicated that there was a nonsignificant difference in otolith increment counts for herring caught in the April 1999 and the May 1999 surveys, but herring from these surveys had significantly higher median otolith increment counts than those from the June 1999 survey. In this later survey, juvenile herring were caught that were a product of spawning events occurring late in the spawning season. Figure 5C displays the median and range of spawning dates of the specimens aged for Figure 5A. Juvenile herring that were a product of spawning between 27 February 1999 and 7 March 1999 reached a 40–50 mm size range significantly faster than

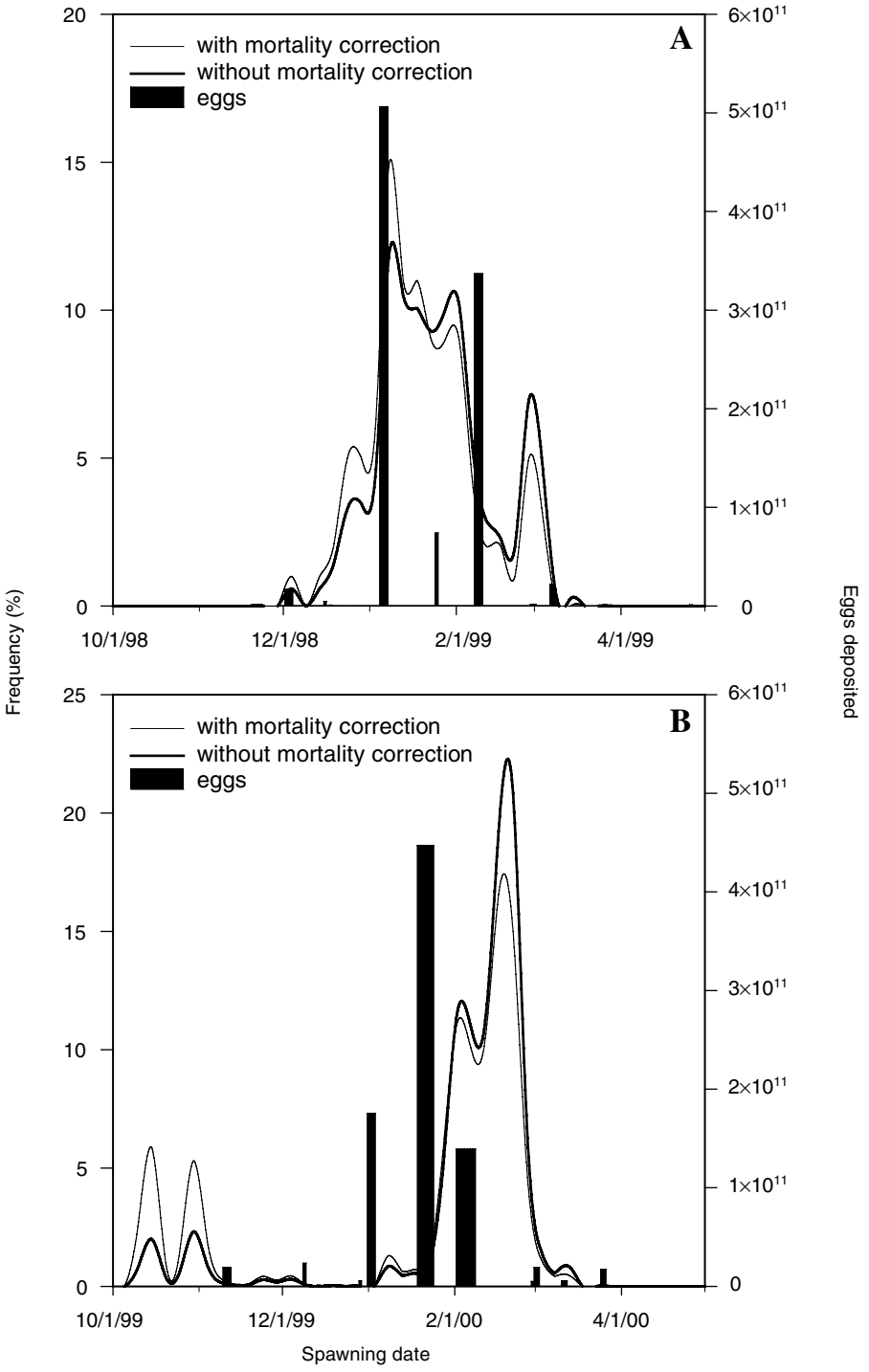

Figure 4

Spawning-date distributions for juvenile herring (*Clupea pallasi*) caught in (**A**) 1999 and (**B**) 2000. Vertical bars represent dates and magnitude of observed spawning (eggs deposited), heavy lines represent the spawning-date distribution of juveniles without the mortality correction, and light lines represent the spawning-date distribution corrected for juvenile mortality at an instantaneous rate of 0.016/d. Distributions are smoothed with a cubic spline interpolation. Data on observed spawning were provided by D. Watters, CDFG (see Footnote 2 in the text).

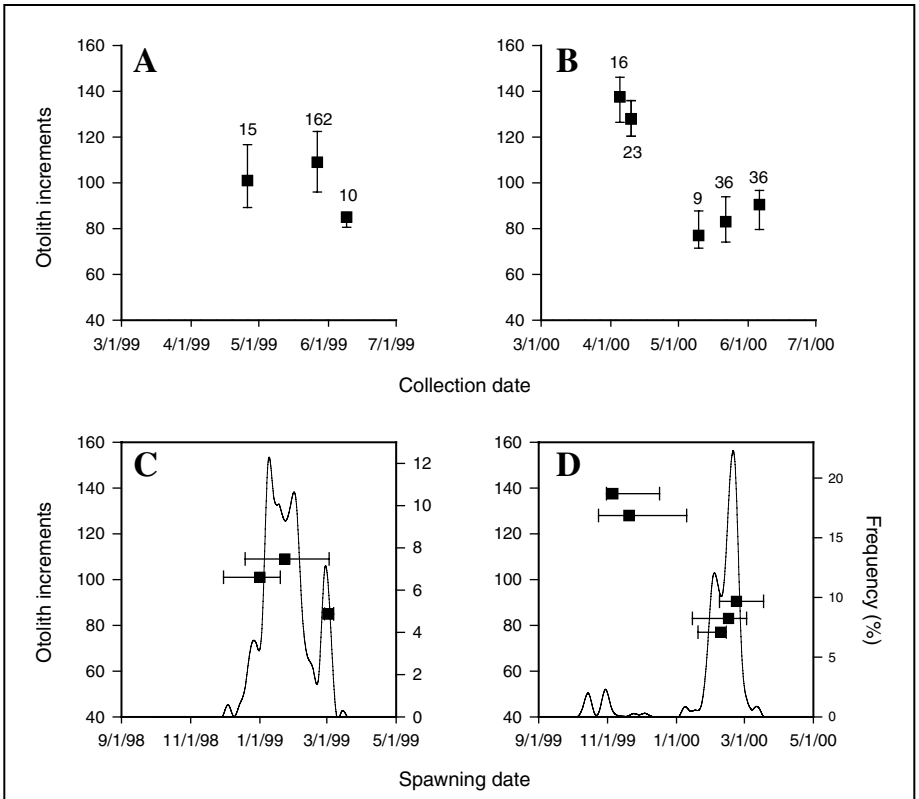

Figure 5

The upper panels display otolith increments present in 40 mm–50 mm juvenile herring (*Clupea pallasi*) arranged by capture date for (**A**) 1999 and (**B**) 2000. Boxes represent median number of otolith increments, bars indicate ±1 SD, and the number above each point is the sample size. The lower panel displays growth histories for juvenile herring originating from various periods within the spawning season for (**C**) 1999 and (**D**) 2000. Boxes represent median spawning-dates and bars represent range of spawning dates at that growth rate. The spawning-date distribution (uncorrected for juvenile mortality) is superimposed upon C and D to ascertain how changes in growth are reflected in survival to the juvenile stage.

specimens recruiting from earlier spawning periods. The period of greatest recruitment occurred during the slower growth period in 1999 (Fig. 5C).

In 2000, 40 mm–50 mm juvenile herring were caught in five survey legs conducted during three months (April, May, and June). The data are displayed by survey leg; pooling the data by month, however, does not change the result. Median increment counts differed significantly for the 2000 surveys (Fig. 5B; H=76.39, P<0.0001). Otolith increment counts for 40 mm–50 mm specimens did not differ for the 5 April 2000 and 10–11 April 2000 surveys. However, the age at length for these surveys was significantly greater than for the three later survey legs (10 May 2000, 22–24 May 2000, and 6 June 2000), which did not significantly differ from each other. Herring caught in the three later surveys grew significantly faster than herring caught in the two earlier surveys. The significant decrease in age at length indicates that juvenile herring that were a product of spawning between 15 January 2000 and 18 March 2000 grew faster than specimens recruiting from earlier spawning events. The majority of juvenile recruits in 2000 were a product of the fast growth period (Fig. 5D).

Accuracy of growth-rate estimates determined from growth increments on otoliths

The above analyses depended upon the assumption that increments were deposited daily in the otoliths examined. Two lines of evidence point to the validity of this assumption. First, back-calculated spawning-dates generally agreed with the known spawning season of San Francisco Bay herring, and several peaks in back-calculated spawning dates match known spawning events quite closely (Fig. 4, A and B).

Second, juvenile growth rates appear to be high enough for daily growth (McGurk, 1984b). Clear length-frequency modes were visible for three sampling events

in 2000. Assuming linear growth between these time periods, the advancement of these length-frequency modes resulted in growth rates of 0.75 mm/d (Fig. 6, arrow in A), 0.83 mm/d (arrow in B), and 0.64 mm/d (arrow in C). McGurk (1984b) demonstrated daily increment deposition in herring if the larval growth rate exceeded 0.36 mm/d. Our data did not allow us to estimate growth rates of larvae; however, the estimated juvenile growth rates presented above are much greater than necessary for daily increment deposition.

Discussion

Catches of juvenile herring were much greater in 2000 than in 1999. Between the months of March and June 2000, cumulative CPUE was more that seven times greater than during the same period in 1999, yet an estimated 12% more eggs were deposited during the 1988–99 spawning season. Because observed differences in recruitment between 1999 and 2000 far exceeded differences in the total eggs spawned, differential survivorship during the egg or larval stages (or both) must be responsible for disparate year-class strengths.

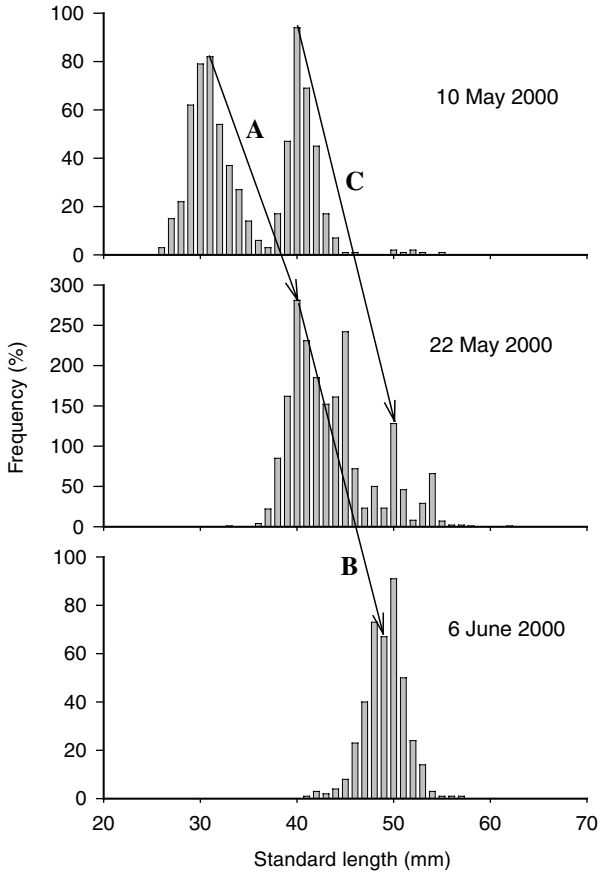

Figure 6

Length frequencies for juvenile herring (*Clupea pallasi*) captured on 10 May 2000, 22 May 2000, and 6 June 2000. Arrows represent the estimated propagation of length modes through time. Linear growth rates, calculated from each trajectory, are as follows: A=0.75 mm/d; trajectory B=0.83 mm/d); and C=0.64 mm/d.

The spawning-date distributions presented for 1999 and 2000 did not contain all herring caught by the mid-water trawl survey between the months of March and June. Because they could not be accurately assigned ages with an age-length key (Table 1), 178 herring were omitted from the distribution in 1999. Most specimens omitted from this distribution were caught in the early April 1999 and late June 1999 survey legs. As a result, the spawning-date distribution likely underestimated the recruitment from very early and very late season spawnings. In 2000, 208 specimens, from a variety of survey legs, were omitted from the spawning-date distribution (Table 1). Because a large number of herring were caught in 2000, it is unlikely that these omissions would significantly change the shape of the spawning-date distribution. The loss of data in this case does not change the overall result of large year-class-strength variation.

The noncontinuous sampling schedule for juveniles may have resulted in either an underestimation or overestimation of CPUE and thus year-class strength. In several months, the mid-water trawl survey was conducted over two legs separated by several days (Table 1, Fig. 3). This noncontinuous sampling could have produced error in our estimates because aggregations of juveniles, through movement between areas, could conceivably have escaped detection by trawls (resulting in CPUE underestimation) or have been sampled twice in the same month (resulting in CPUE overestimation). However, O'Farrell (2001) showed that dispersal of herring from a successful spawning event could occur through much of San Francisco Bay. Therefore, we do not believe that aggregations of juveniles were completely missed by the mid-water trawl survey. The degree to which aggregations of juveniles were sampled more than once in a sampling month is not known.

Variation in age estimates undoubtedly produced back-calculated spawning-dates that did not match exactly with true spawning dates. Yet, for some spawning events, very good matches between back-calculated and reported spawning events indicate that the age estimations were accurate for many of the cohorts examined (O'Farrell, 2001). Other cohorts that did not match as well with reported spawnings may be the result of 1) a spawning event undetected by the spawn-deposition study, 2) a small, "spot" spawning that did not qualify as a true spawning event for the spawn-deposition study, or 3) very slow or fast growth through a portion of the larval life history that interrupted daily increment deposition (McGurk, 1984b, 1987).

Increased survival did not occur throughout the entire 2000 spawning season. Instead, periods of good survival and poor survival were present, yet the

periods of good survival in 2000 led to a much stronger year class than that of 1999. Detecting a "match" of favorable conditions that led to recruitment success was not possible in our study because of the myriad factors that can determine recruitment success. Rather than attempting to explain the observed survival differences with specific mechanisms, we suggest what may possibly contribute to the observed patterns.

Larval survival

The degree to which larval survival depends upon biotic or abiotic factors is difficult to estimate. Fox (2001) presented data showing that year-class strength in the Blackwater stock of Atlantic herring (*Clupea harengus* L.) was determined by survival after the egg stage. However, it is not clear whether variation in survival was due to density-dependent or environmental factors. A recent study has shown that salinity can affect larval survival after hatching in San Francisco Bay herring (Griffin et al., 2004). Here, the salinity during embryonic development was a factor in yolksac larval survival in different salinity treatments. Regardless of the form of mortality operating on larvae, small changes in larval growth rate can lead to large changes in levels of recruitment (Houde, 1987). Faster larval growth results in shorter larval stage duration and thus decreased exposure to the characteristically high mortality of the larval stage. Age at size for herring in this study decreased significantly as the spawning season progressed both in 1999 and 2000. From this finding, we infer that positive changes in growth rate occurred during the spring and summer. Seasonal positive shifts in growth have also been observed in Pacific herring populations in Prince William Sound, Alaska, between the months of June and October (Stokesbury et al., 1999).

In 1999, the greatest number of recruits came from mid to late-season spawning events. The late February to early March spike in recruitment (Fig. 4A) may be partially explained by within-year growth variation. This group of survivors appeared to be derived from a relatively small number of eggs. Recruits from that spawning period grew significantly faster than recruits from earlier spawning events. The largest spawning events of the 1998–99 spawning season produced recruits that grew slower than the recruits spawned in early March and thus may have experienced lower relative survival.

Within-year growth rate variation also partially explains the 2000 year class. The 2000 year class was dominated by late season recruitment, primarily from spawning in February 2000. Herring from spawning events occurring between late October 1999 and mid-January 2000 had a significantly higher median age at length than herring produced from subsequent spawning times. This slow growth may in part explain the near lack of recruitment from the two highest magnitude spawns occurring from 1 to 3 Jan 2000 and from 19 to 24 Jan 2000. However, age at length decreased (and thus growth rate increased) for spawning events occurring from late January 2000 to early March 2000. The timing of the growth rate switch (from slow to fast) coincided closely with the spawning period producing the greatest amount of recruitment. The general trend of high levels of recruitment from late season spawning events indicates that increased growth rate played a role in the good survival during this period. However, recruitment from very early spawning events and the small number of recruits resulting from late March 2000 spawning was not explained solely by this within-year growth variation.

Egg mortality

Variation in mortality during the egg stage may also affect recruitment in San Francisco Bay herring. Fertilization, embryonic development, and hatching success of Pacific herring are strongly tied to environmental conditions (Alderdice and Velsen, 1971, Griffin et al., 1998). The optimal range for fertilization and development of the San Francisco Bay population is between 12 ppt and 24 ppt, and both percent fertilization and percent hatching is maximized at 16 ppt (Griffin et al., 1998). The herring spawning season in San Francisco Bay is a time of rapidly changing salinities. High salinities generally persist through the fall months. In winter, rapid decreases in salinity due to freshwater from the San Joaquin–Sacramento Delta, storm drain runoff and local creek purges (Oda[3]) are common, yet the magnitude varies between years (Conomos et al., 1985). In the two years examined, salinity during the winter spawning season varied both above and below the optimum range determined by Griffin et al. (1998). These salinity fluctuations could have a large effect on the supply of larvae into the San Francisco Bay system.

Mortality during the egg stage can be exceedingly high in Pacific herring due to predation and other biotic interactions (Alderdice and Velsen, 1971; McGurk, 1986; Rooper et al., 1999, Bishop and Green, 2001). As a result, egg incubation time may have a significant effect upon eventual recruitment. The length of times of egg incubation and the yolksac larval stage were combined in our study and the combined period was given a constant value of 14 days. In actuality, egg incubation time (Taylor, 1971; McGurk, 1987) and embryonic development (Alderdice and Velsen, 1971; Griffin et al., 1998) are strongly linked to environmental factors and likely have a significant effect upon recruitment before growth rates can determine survival. Analysis of egg incubation and yolksac larval duration for separate cohorts was not performed in our study. It may, however, play a large role in larval abundance.

Conclusion

The 1999 and 2000 spawning-date distributions indicate that year classes can be shaped by periods of good and

[3] Oda, K. 2000. Personal commun. Calif. Dep. Fish and Game, 411 Burgess Dr., Menlo Park, CA 94025.

poor survival lasting shorter than the duration of the spawning season, yet longer than the duration of an individual spawning event. The distributions indicated that variation in survivorship was not only a function of individual spawn success. Rather, periods of good and poor survivorship in 1999 and 2000 were of longer duration than one spawning event. The period of exceptionally good survival that led to the majority of the strong 2000 year class was approximately one month in duration and incorporated several spawning events. Yet this window of good survival was much shorter than the entire 2000 spawning season. Variation in survivorship between individual spawnings may be less important in shaping the year class than survivorship variation on a longer time scale.

Visual examination of the spawning-date distribution superimposed upon juvenile age at length indicate that faster growth had a positive effect on recruitment in 2000, and a negligible effect in 1999. For larval growth to affect recruitment, larvae must be available from hatching eggs. Year-class strength variation in Pacific herring could depend upon both egg and larval survival.

The timing of peak herring spawning in San Francisco Bay may be a tradeoff between maximizing larval growth rates and spawning when hydrographic conditions are optimal for embryonic development. In the two years examined, growth rate increased with the progression of the spawning season. It follows that the herring population could maximize recruitment by spawning later so that larvae grow faster. However, because delta outflow is generally high in February and March on account of winter storms, late season spawning may expose eggs to low salinities and thus decreased hatching rates. Peak spawning may occur in January as a trade off between growth-rate and egg-hatching success.

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