VERTICAL DISTRIBUTION OF PACIFIC HAKE EGGS IN RELATION TO STAGE OF DEVELOPMENT AND TEMPERATURE

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ABSTRACT

The vertical distribution of eggs of Pacific hake (*Merluccius productus*) was determined from 27 MOCNESS samples taken on cruises off southern and central California in March 1995 and February 1996. In 1995, nine depth strata (0–25, 25–50, 50–75, 75–100, 100–125, 125–150, 150–200, 200–250, and 250–300 m) were sampled. In 1996, nine 25-m depth strata were sampled down to 225 m. In 1995 Pacific hake eggs were taken in all strata down to 250–300 m; most of the eggs were found between 50 and 150 m, with the highest densities in the 50–75- and 75–100-m strata. Average temperatures for developing Pacific hake eggs were estimated to be 10.2°–11.3°C. Early-stage eggs were generally deeper in the water column than later-stage eggs. Most early-stage eggs were found between 75 and 150 m, with highest densities in the 125–150-m stratum. In contrast, mid- and late-stage eggs were most dense in the 50–75- and 75–100-m strata. Early-stage eggs were taken primarily in tows between 2200 and 0600 hrs, suggesting diel periodicity in spawning. On the 1996 cruise hake eggs had a slightly shallower distribution compared with 1995, and there was more overlap in vertical distribution between stages. Methods are given for separating Pacific hake eggs from similar eggs of other species, and criteria are described for staging Pacific hake eggs.

INTRODUCTION

The daily egg production method (DEPM) is an effective fishery-independent means of estimating the biomass of commercially important fish stocks (Hunter and Lo 1993). It has been applied principally to coastal pelagic fishes; however, a modification of this method, the daily fecundity reduction method (DFRM), has been used for demersal fishes such as Dover sole (Lo et al. 1993), orange roughy (Zeldis 1993), and sablefish (Moser et al. 1994). Application of the DFRM to Pacific hake may be confounded by the difficulty of sampling egg patches produced by the reputed large spawning aggregations about 100–400 m deep off central and southern California (observations of M. V. Stepanenko reported by Stauffer 1985).

During March 9–27, 1995, the Coastal Fisheries Resources Division, Southwest Fisheries Science Center, conducted Cruise 9503-JD (figure 1), partly to determine the vertical distribution of Pacific hake eggs in relation to stage of development, age, and temperature; this information is needed to construct the mortality curves required for DFRM biomass estimation. Additional vertically stratified samples of Pacific hake eggs were obtained from a cruise (9602-RGS) conducted by Shannon Cass-Calay during February 8–13, 1996, in the Southern California Bight (Cass-Calay 1997).

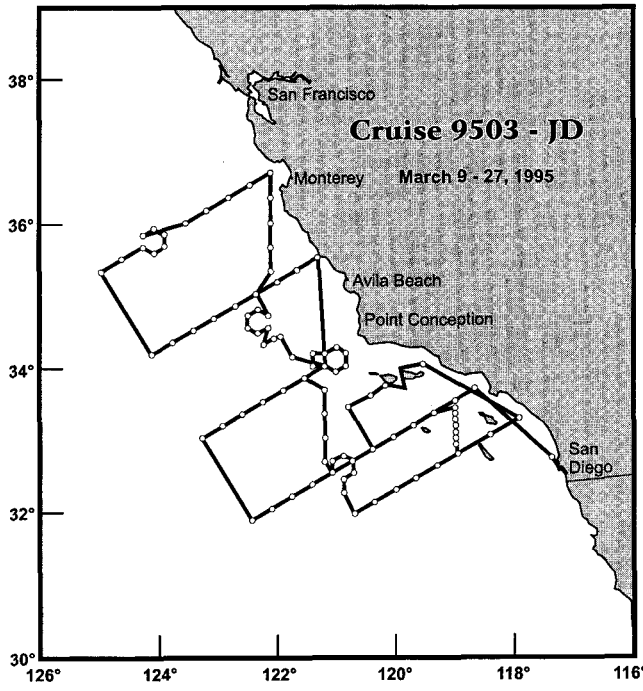

Figure 1. Sampling pattern for Cruise 9503-JD. Pacific hake eggs from MOCNESS stations indicated by the three hexagonal sampling areas extending northwest from Point Conception were used in this analysis.

In this paper we describe the methods of identifying Pacific hake eggs, the criteria for assigning developmental stages to them, and their vertical distribution on Cruises 9503-JD and 9602-RGS. The age of the eggs will be determined when a stage-to-age key becomes available.

METHODS AND MATERIALS

In 1995 a total of 102 oblique bongo net tows (505-μ mesh) was made on five onshore-offshore transects from Dana Point to Monterey, California. When live-sorting of these catches revealed high concentrations of Pacific hake larvae, a close-interval hexagonal set of six vertically stratified plankton tows was taken, sampling

nine depth strata (0–25, 25–50, 50–75, 75–100, 100–125, 125–150, 150–200, 200–250, and 250–300 m). Pacific hake eggs were identified and staged from these samples; eggs from the three sets taken off central California were used in this analysis. One of the 18 tows (station 19) produced >27,000 Pacific hake eggs; this tow was not included in our analyses of frequency distribution, because the extremely high number of eggs overshadowed the egg frequencies of the other tows.

Another source of material was a series of 10 vertically stratified tows (25-m strata to 225-m depth) taken in the Southern California Bight by Shannon Cass-Calay in 1996 (Cass-Calay 1997). Pacific hake eggs from these tows were identified and staged, and provided additional data for this study.

The sampler employed on both cruises was a MOCNESS-1 (Wiebe et al. 1976) with a 1-m^2 mouth opening and 505-μ mesh.

Identification of Pacific Hake Eggs

Pacific hake eggs were identified with criteria of Ahlstrom and Counts (1955), Matarese et al. (1989), Ambrose (1996), and several other criteria established in this study. Preserved eggs have a smooth shell (1.04–1.20-mm diameter); a relatively large oil globule (0.27–0.34-mm diameter) that is deep yellow to slightly orange; a deep yellow, homogeneous yolk; and a narrow perivitelline space.

Eggs of a bathylagid (*Leuroglossus stilbius*) commonly co-occur with Pacific hake eggs and overlap with them in size, but have a pale, segmented yolk and multiple oil globules that migrate and coalesce during development. In preserved early-stage eggs of both species, the yolk membrane is often broken, and in *L. stilbius* the membranes of the yolk segments may be broken, so that the yolk appears homogeneous. When no remnants of yolk segmentation are present the eggs of the two species may be difficult to separate. The oil globule is usually intact in Pacific hake eggs, whereas in *L. stilbius* it is fragmented and paler in color than in Pacific hake. In *L. stilbius* eggs the inner surface of the chorion is faintly ornamented with minute pustules (see Moser and Ahlstrom 1996), which are lacking in Pacific hake. Usually this ornamentation is visible in preserved eggs and can aid in separating eggs of the two species.

Early-stage eggs of Pacific mackerel (*Scomber japonicus*) are similar to those of Pacific hake and are difficult to distinguish from them. The oil globule is paler in Pacific mackerel than in Pacific hake. When pigment develops in mid-stage eggs, the two species are easily distinguished. In Pacific hake, melanophores are present on the yolk anterior to the head; head pigment extends forward to the snout; and pigment is absent on the tip of the tail. Pacific mackerel eggs lack yolk pigment forward of the head and on the snout; melanophores on the head and body are larger and less dense than in Pacific hake; and pigment extends farther posteriad on the tail. In late-stage eggs, the pigment pattern is distinctive for these species.

Staging of Pacific Hake Eggs

Each egg was assigned to one of 11 developmental stages. Stage criteria were similar to those used for pelagic eggs of other species (Moser and Ahlstrom 1985; Lo et al. 1992; Lo et al. 1996), but some modification was required. In a large proportion of early stage 2 eggs the yolk membrane was broken and the blastodisc was disassociated, with the blastomeres scattered throughout the yolk and often partially or totally disintegrated. Because eggs in this condition could not be distinguished from stage 1 eggs, for practical purposes the two stages were combined as stage 2.

Stage 1: Begins with extrusion and fertilization and ends with the beginning of cell division. In the few intact stage 1 eggs in our samples, the cytoplasm is paler than the yolk and may contain minute granules that are easily distinguishable from the minute cells (blastomeres) that form the blastodisc of late stage 3 eggs.

Stage 2 (figure 2a): Begins with the initial division of the cytoplasm into two cells; ends when the individual blastomeres have undergone numerous divisions and the blastodisc has the appearance of tissue when viewed at 12 power with the dissecting microscope.

Stage 3: Begins when cell division has progressed to the point where the individual blastomeres are no longer apparent (viewed at 12 power); ends when the embryonic shield covers half of the blastodisc. The embryonic shield is a bell-shaped mass of cells that proliferates inward from the margin of the blastodisc, eventually forming the axis of the embryo.

Stage 4: The yolk mass begins to be covered by cell proliferation and movement of the blastoderm around the yolk (epiboly). Stage 4 begins when the germ ring (thickened margin of blastodisc) has progressed one-third of the way around the yolk mass. The embryonic shield becomes denser and begins to form the axis of the embryo.

Stage 5 (figure 2b): Begins when the germ ring has progressed two-thirds of the way around the yolk mass, and the embryonic axis extends to the edge of the germ ring. At the end of stage 5 the brain, optic vesicles, and trunk somites of the embryo are becoming apparent. Late in stage 5, melanophores form on the embryo and on the yolk anterior to the head (not shown in figure 2b).

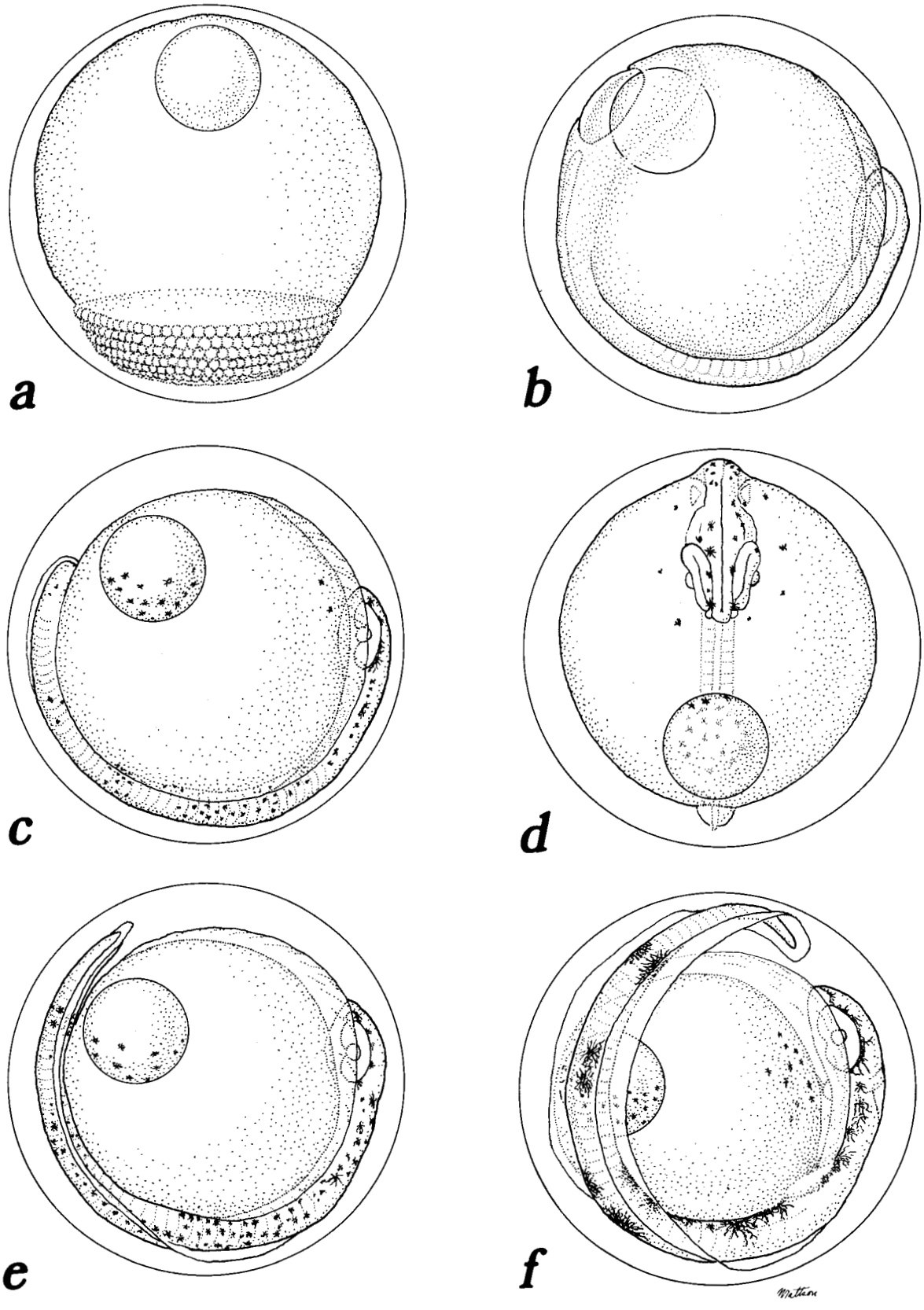

Figure 2. Examples of developmental stages of Pacific hake eggs: *a*, stage 2; *b*, late stage 5; *c* and *d*, lateral and front view of early stage 7; *e*, stage 9; *f*, stage 11. Illustrations from Ahlstrom and Counts (1955).

Stage 6: Begins with closure of the "blastopore" at the posterior tip of the embryonic axis. By the end of stage 6, the somites are present along most of the embryo; the brain has begun to differentiate; the lens primordia are forming in the eyes; and the tip of the tail has thickened slightly.

Stage 7 (figure 2c and d): Begins when the tip of the tail has become rounded and has begun to separate from the yolk mass. The tail becomes pointed as it lengthens.

Stage 8: Begins when the length of the free section of the tail (the portion that has separated from the yolk mass) is half the length of the head (head length defined for this purpose as the distance from the tip of the snout to the back of the midbrain).

Stage 9 (figure 2e): Begins when tail length is ≥head length.

Stage 10: Begins when the tail has reached halfway around the yolk mass. Pigment is becoming organized into a characteristic pattern.

Stage 11 (figure 2f): Begins when the tail has reached three-quarters of the way around the yolk mass. Pectoral fin primordia are obvious. The posterior pigment bar on the tail is distinct. Stage 11 ends at hatching.

RESULTS

On Cruise 9503-JD, Pacific hake eggs were taken in all strata down to 250–300 m. Most came from strata between 50 and 150 m, with the 50–75- and 75–100-m strata showing the highest densities (figures 3, 4). This is generally consistent with results of previous studies of the vertical distribution of Pacific hake eggs (Ahlstrom 1959; Bailey 1982). Early-stage eggs were generally deeper in the water column than later-stage eggs (figure 5). Most stage 2–3 eggs were found between 75 and 150 m, with highest densities in the 125–150-m stratum. In contrast, highest densities of mid- and late-stage eggs were found in the 50–75- and 75–100-m strata.

The Weibull distribution function (shown below) was used to model the distribution of eggs of four groups of stages (2–3, 4–6, 7–9, and 10–11) from Cruise 9503-JD in relation to depth and temperature (table 1).

$$y = 1-\exp[-(x/p1)^{p2}]$$

Stages were grouped because data were sparse for some stages. In our model, y ($0<y<1$) is the cumulative proportion of eggs down to depth (m) or up to temperature (°C) where depth or temperature are denoted by x. The parameter $p1$ is the scale parameter, and $p2$ is the shape parameter. When $p2 = 1$, the Weibull distribution is reduced to an exponential distribution. The scale parameter $p1$ is the average of x for either $p2 = 1$ or for

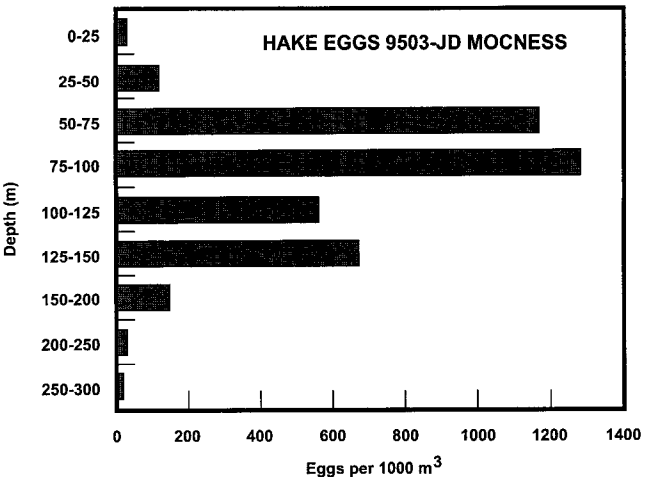

Figure 3. Vertical distribution of Pacific hake eggs based on 17 MOCNESS tows taken during Cruise 9503-JD off central California, March 3–20, 1995; values are average densities (eggs/1,000 m^3) for each of 9 depth strata.

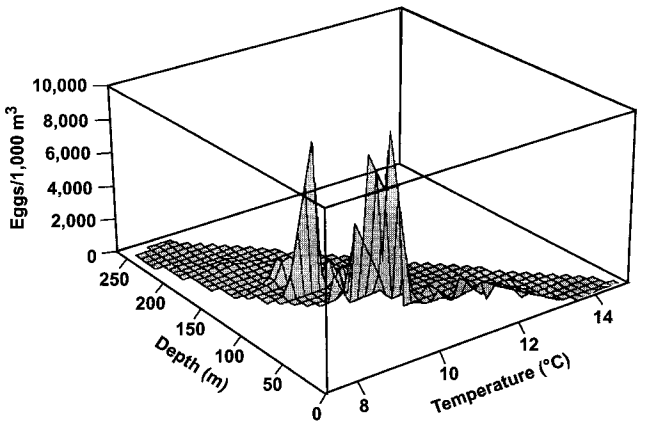

Figure 4. Relation of hake egg density to depth (m) and temperature (°C) based on hake eggs collected in 17 MOCNESS tows taken during Cruise 9503-JD off central California, March 3–20, 1995.

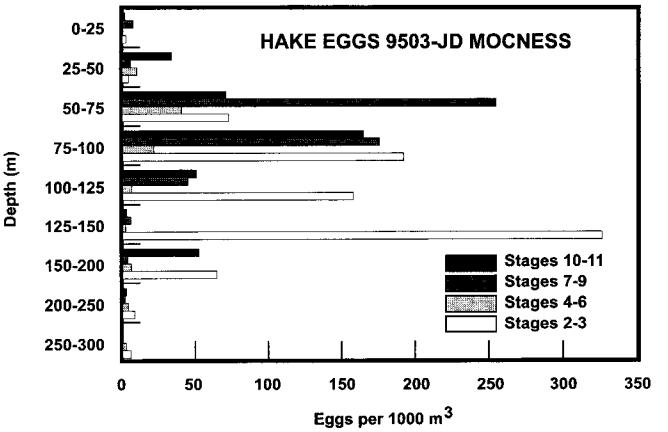

Figure 5. Vertical distribution of four stage-groups of Pacific hake eggs, based on 17 MOCNESS tows taken during Cruise 9503-JD off central California, March 3–20, 1995; values are average densities (eggs/1,000 m^3) for each of 9 depth strata.

TABLE 1
Parameter Estimates for Weibull Distribution Function[a] Used to Calculate Cumulative Proportions of Depth and Temperature for Eggs of Pacific Hake Collected on Cruise 9503-JD

Stage	*p*1 Estimate	*p*1 Std. error	*p*1 *t* value	*p*2 Estimate	*p*2 Std. error	*p*2 *t* value	Mean
Depth (m)							
2–3	134.17	1.08	124.22	4.08	0.18	23.35	125.21 m
4–6	109.17	1.44	75.85	4.47	0.35	12.86	103.14 m
7–9	83.80	0.50	167.30	6.58	0.39	16.86	81.73 m
10–11	82.08	0.55	149.96	5.76	0.30	19.45	79.41 m
All	106.97	0.83	129.70	3.46	0.13	27.65	96.91 m
Temperature (°C)							
2–3	10.29	0.03	408.06	19.38	0.96	20.25	10.23°C
4–6[b]	11.03	—	—	14.93	—	—	11.02°C
7–9	11.77	0.05	255.65	10.49	0.04	23.61	11.29°C
10–11	11.17	0.06	198.69	11.44	0.67	17.22	11.02°C
All	10.88	0.04	249.92	13.43	0.75	17.94	10.96°C

[a]See text for description of Weibull distribution function.
[b]The estimates of parameters were interpolated from values of stage-groups 2–3 and 7–9, because the estimates of parameters did not converge.

large values. In either case, *p*1 is similar to the average depth or temperature for Pacific hake eggs in each of the four stage-groups. The fitted curves for the depth distributions (figure 6) indicated that the shape parameters were greater than 1 (ca. 4), which means that the vertical distribution of each of the four groups was not exponential, and that *p*1's were close to the mean depth. Based on *p*1 values, early-stage eggs were deeper in the water column than later stages, ascending from a mean depth of about 125 m to about 80 m (table 1).

Estimates of Weibull parameters for the temperatures associated with each stage-group were also obtained, and the estimates of the shape parameters, *p*2, were even greater than those of the depth distribution (figure 7). Therefore, *p*1 was close to its mean temperature. Younger stages encountered slightly colder temperatures (ca. 10.3°C) than older stages (ca. 11.0°–11.3°C; table 1). Slopes of the curves in figures 6 and 7 indicate that early-stage eggs were rather broadly distributed below the thermocline (figure 6), where they encountered a narrow range of temperatures (figure 7), but older eggs ascended and became mostly concentrated in a narrower depth zone in the lower part of the thermocline (figure 6), which had a broader range of temperatures (figure 7).

Pacific hake eggs from Cruise 9602-RGS had a slightly shallower distribution than those from Cruise 9503-JD (figures 3, 8). Eggs were taken in all strata down to 200–225 m, most from strata between 25 and 125 m. The 50–75- and 75–100-m strata showed the highest densities. Early-stage eggs were generally deeper in the water column than later-stage eggs, but there was more overlap in vertical distribution between stages than in Cruise 9503-JD (figure 9).

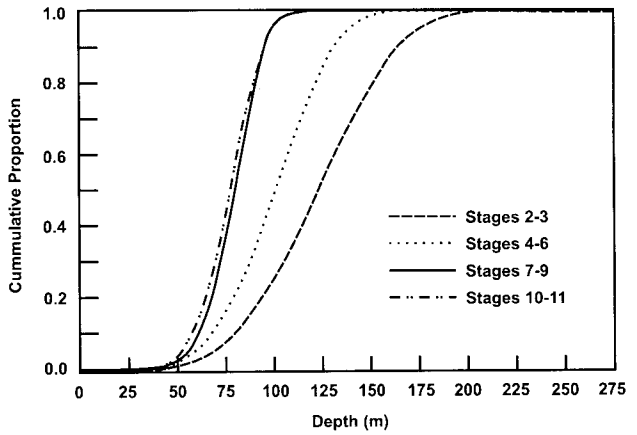

Figure 6. Cumulative proportion of Pacific hake egg density versus depth of collection for four stage-groups, based on 17 MOCNESS tows taken during Cruise 9503-JD off central California, March 3–20, 1995. Values are derived from Weibull distribution function (table 1).

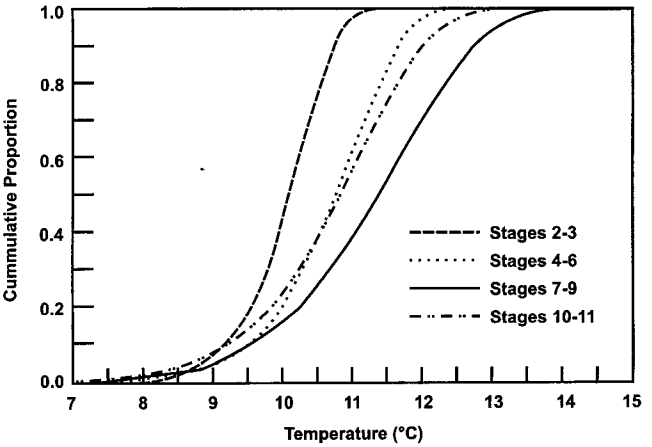

Figure 7. Cumulative proportion of Pacific hake egg density versus habitat temperature for four stage-groups, based on 17 MOCNESS tows taken during Cruise 9503-JD off central California, March 3–20, 1995. Values are derived from Weibull distribution function (table 1).

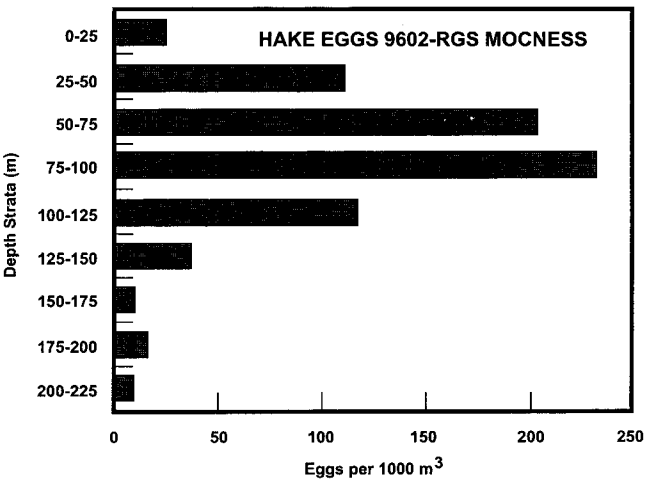

Figure 8. Vertical distribution of Pacific hake eggs based on 10 MOCNESS tows taken during Cruise 9602-RGS off southern California, February 8–13, 1996. Values are average densities (eggs/1,000 m^3) for each of 9 depth strata.

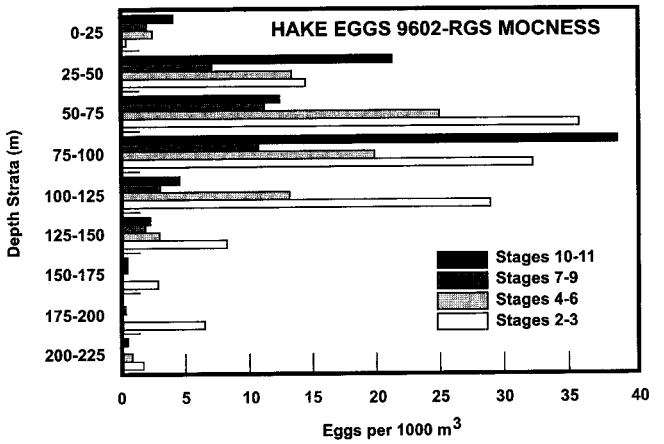

Figure 9. Vertical distribution of four stage-groups of Pacific hake eggs, based on 10 MOCNESS tows taken during Cruise 9602-RGS off southern California, February 8–13, 1996. Values are average densities (eggs/1,000 m^3) for each of 9 depth strata.

DISCUSSION

March 1995 MOCNESS tows from central California show that Pacific hake eggs range from the surface to as deep as 250–300 m. Relatively few, however, occur below 200 m, the maximum depth of the standard CalCOFI oblique plankton tow. The eggs are most abundant between 50 and 100 m (lower limit of the mixed layer and thermocline). These findings correspond to those of Ahlstrom (1959), who found the highest abundance of Pacific hake eggs at about 75 m in two series of vertically stratified tows in the Southern California Bight. Eggs of the reproductively isolated Puget Sound population of *M. productus* occur at approximately the same depth as those off California, but in the bottom 25 m of the water column at a bottom depth of about 110 m (Bailey 1982). Coombs and Mitchell (1982) found the eggs of *M. merluccius* at about 50 and 150 m off the west coast of the British Isles.

Vertically stratified tows in 1995 showed highest densities for stage 2–3 eggs at 75–150 m, with some as deep as 250–300 m; in 1996 the highest densities for these stages were at 50–125 m. This suggests that newly spawned eggs may ascend from aggregations spawning in the 100–400-m depth range, as reported in Stauffer (1985). Thus, tows made for egg production biomass assessment should be taken to at least 300 m to assure that the vertical distribution is encompassed. Another consideration in developing sampling procedures in DEPM surveys is time of spawning. On Cruise 9503-JD, stage 2 eggs occurred primarily in tows taken between 2200 and 0600 hrs, suggesting diel periodicity, but more information is needed to determine the time of spawning.

Average temperatures encountered by developing Pacific hake eggs were estimated to be 10.2°–11.3°C. The incubation period for Pacific hake eggs developing at this temperature is 4–5 days (Zweifel and Lasker 1976; Bailey 1982). Estimating the age of Pacific hake eggs with morphological criteria will require experimentally rearing eggs to allow development of a temperature-specific stage-to-age key.

Pacific hake eggs can be separated from eggs of other fishes present off California during the compressed spawning season in January–March, but early-stage eggs of Pacific mackerel may be indistinguishable from those of Pacific hake. This is most problematic when sampling is done after February off southern and central California. Although Pacific mackerel generally spawn later in the year than Pacific hake, we encountered late-stage eggs of both species in the same tows during March 1995 in the Southern California Bight; consequently, we did not use eggs from the MOCNESS tows in the Southern California Bight in our analysis. Other methods of species identification, such as genetic markers, would be required to separate eggs of these species where their eggs may co-occur.

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