

SPATIAL AND TEMPORAL DISTRIBUTIONS OF PACIFIC HAKE, *MERLUCCIUS PRODUCTUS*, LARVAE AND ESTIMATES OF SURVIVAL DURING EARLY LIFE STAGES

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ABSTRACT

Information on the distribution and abundance of Pacific hake larvae was examined for evidence of strong or weak year classes and larval drift. Estimates of larval mortality rates were derived and applied to a life-table simulation to examine hypotheses about factors that produce strong or weak year classes. Indices of late-stage larval abundance indicated that strong year classes were established during the egg or larval stage of development. Estimates of larval mortality applied to a life-table simulation also indicated that strong year classes were established during the early or late larval period. Analysis of the spatial distribution of larvae indicated that inshore regions and regions west of Point Conception are favorable to survival of hake larvae.

RESUMEN

Se examinaron datos de distribución y abundancia de larvas de merluza del Pacífico para examinar la deriva larvaria y descubrir la presencia de clases anuales fuertes o débiles. A fin de investigar hipótesis sobre los factores que producen clases anuales fuertes o débiles se utilizaron tablas de vida con datos simulados, a las que se les aplicó datos estimados de mortalidad larvaria. Indices de abundancia de estadios larvarios tardíos indicaron que las clases anuales fuertes se determinaron durante las fases de huevo o larvarios. Asimismo, las estimaciones de mortalidad larvaria aplicadas a las tablas de vida con datos simulados indicaron que las clases anuales fuertes se determinaron durante las fases larvarias tempranas o tardías. Análisis de la distribución de larvas revelaron que tanto la zona costeras como la región al oeste de Point Conception son favorables para la sobrevivencia de las larvas de merluza.

INTRODUCTION

Numerous studies of environmental influences on recruitment of commercially exploited fish stocks in the northeast Pacific Ocean have been conducted. These investigations suggest that environmental

factors affect survival through four primary mechanisms: larval transport, concentration of prey, changes in the location of spawning, and physiological influences on embryonic or larval development (table 1). Secondary mechanisms such as predation can be inferred from these initial factors. Many of these conclusions were based on correlative models. Walters and Collie (1988) described some of the problems associated with using correlative models to study recruitment processes of marine fish. Drinkwater and Myers (1987) showed that correlative models seldom have continuing predictive power.

The potential for spurious correlation in recruitment studies can be minimized by identifying plausible mechanisms through examination of egg, larval, and juvenile distribution and abundance. Subsequent investigations of processes underlying recruitment can proceed in three stages. First, key events in the life history that influence survival should be identified. Such identification would limit the number of environmental variables and the time of year to be considered in an investigation. Identification of key events can also be useful in developing hypotheses about recruitment processes. Second, the distribution of individuals within the selected time frame should be analyzed for spatial features that may influence recruitment and define the area for environmental-recruitment comparisons. Finally, the time series of key indicators of temporal and spatial processes that potentially influence survival should be compared with the time series of recruitment. This three-stage research approach was applied in an evaluation of factors underlying recruitment of Pacific hake (Hollowed 1990). This paper presents the results of the temporal and spatial analyses found in the first two stages of this approach.

The coastal stock of Pacific hake (*Merluccius productus*), also known as Pacific whiting, varies widely in year-class strength. Early in their lives, Pacific hake are found in waters off the coast of California, an upwelling region with a dynamic oceanic environment. In this region, the interannual oceanic variability causes a strong biological response (Chelton et al. 1982). The strong signals in recruitment of

TABLE 1

Summary of Oceanic Influences on Recruitment of Commercially Exploited Fish and Shellfish in the Northeast Pacific

Species	Reference	Proposed mechanism	Variable
Bluefin tuna	Mysak 1986	Alteration of migration routes	El Niño–Southern Oscillation (ENSO)
Coho salmon	Nickelson 1986	Reduced predation offshore, increased prey availability and thus faster growth	Upwelling during spring and summer
Dover sole	Hayman and Tyler 1980	Prey concentrations, location of settling	Upwelling
Dungeness crab	Johnson et al. 1986	Transport of zoea	Wind stress
	Jamieson et al. 1989	Transport	Current patterns
English sole	Kruse and Tyler 1983	Alteration of spawning period, rates of gonadal development	Temperature
	Hayman and Tyler 1980	Prey concentrations	High storm frequency, low mean wind speed
	Botsford et al. 1989	Prey concentrations	Productivity
	Forrester 1977	Egg viability	Temperature
	Ketchen 1956	Pelagic stage duration and transport	Temperature
Jack mackerel	Zwiefel and Lasker 1976	Incubation period, larval growth	Temperature
	Theilacker 1986	Starvation, predation	Productivity
	Hewitt et al. 1985	Starvation, predation	Productivity
Northern anchovy	Lasker 1975, 1981	Prey concentration	Wind-driven turbulence
	Peterman and Bradford 1987	Prey concentration	Wind-driven turbulence
	Husby and Nelson 1982	Transport and prey concentrations	Turbulence, upwelling, strength of thermocline
	Power 1986	Larval transport	Upwelling
	Fiedler 1984	Extension of spawning range	ENSO
	Zwiefel and Lasker 1976	Incubation period, larval growth	Temperature
	Methot 1986	Maturity schedule	Temperature
Pacific cod	Tyler and Westrheim 1986	Larval transport, survival of eggs and larvae	Transport and temperature
Pacific hake	Bailey 1981	Larval transport	Upwelling, temperature
	Zwiefel and Lasker 1976	Incubation period, larval growth	Temperature
	Bailey and Francis 1985	Larval transport, growth, spawning location	Upwelling, temperature
	Hollowed and Bailey 1989	Larval transport, growth, prey concentration	Upwelling, spring transition
Pacific halibut	Parker 1989	Larval transport	Wind
Pacific herring	Pearcy 1983, Mysak 1986	Wide range of factors	ENSO
	Alderdice and Hourston 1985	Embryonic and larval survival	Temperature, salinity
	Stocker et al. 1985	Physiological effect, prey production	Temperature, river discharge
	Schweigert and Noakes 1991	Transport	Ekman transport, upwelling
	Tanasichuk and Ware 1987	Ovary weight and fecundity	Temperature
Pacific mackerel	Sinclair et al. 1985	Reduced southward transport	ENSO, temperature
	Parrish and MacCall 1978	Prey concentrations, vulnerability to predation, change in distribution	Temperature, upwelling, wind stress
Pacific sardine	Zwiefel and Lasker 1976	Incubation period	Temperature
	Bakun and Parrish 1980	Prey concentrations and circulation	Annual upwelling 39°N Feb.–June upwelling and wind-stress curl
Petrale sole	Alderdice and Forrester 1971	Incubation, hatching success	Temperature and salinity
	Forrester 1977	Pelagic stage duration, settling time, prey concentrations	Temperature
Rock sole	Fargo and McKinnell 1989	No proposed mechanism	Temperature
	Forrester 1977	Egg development, larval retention	Temperature (Feb.–Apr.), transport
Sablefish	McFarlane and Beamish 1986	Prey concentrations	Transport and temperature
Sockeye salmon	Mysak 1986	Alteration of migration routes	ENSO
	Thomson et al. 1992	Alteration of migration routes	Wind-driven current
Walleye pollock	Ingraham et al. 1991	Egg transport, spawning location	Large-scale atmospheric forcing
	Kim 1989	Depth distribution of eggs and larvae	Density
	Hinckley et al. 1991	Larval transport	Advection
	Schumacher and Kendall 1991	Larval transport, larval retention	Advection, storm frequency
Widow rockfish	Norton 1987	Larval transport	Advection, atmospheric circulation

Pacific hake and in the region's oceanic conditions provide an opportunity to study the relationship between recruitment success and interannual variations in ocean conditions.

Bailey et al. (1986) showed that strong year classes of Pacific hake could be clearly identified from in-

dices of juvenile abundance (2 months–1 year old). From this observation, the authors concluded that the magnitude of a hake year class was determined by processes occurring during the first year of life.

For this analysis, I examined interannual variability in both the larval and juvenile phases to identify

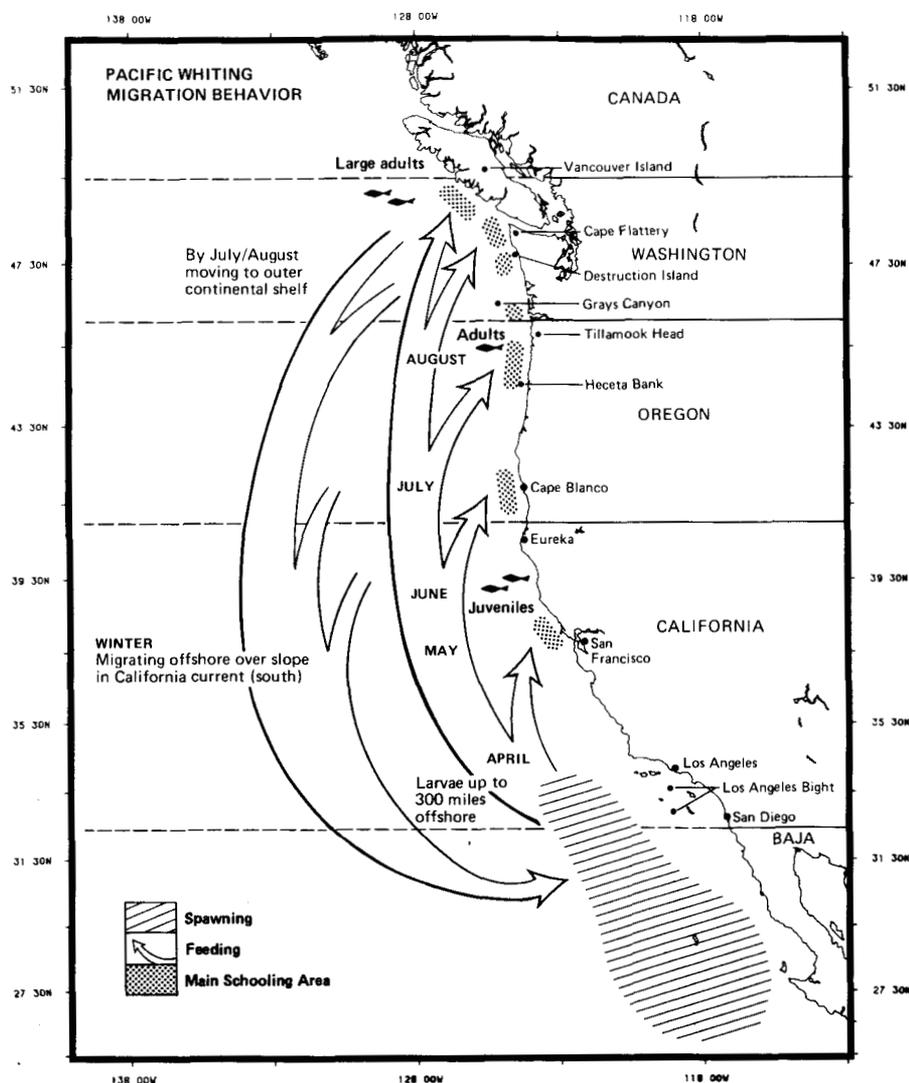


Figure 1. Migratory pattern of Pacific hake.

the point in the life history when a strong relationship between early abundance (larval or juvenile) and observed recruitment to the fishery was established. Next I analyzed the spatial distribution of larval hake, using an extended time series of larval and juvenile abundance from California Cooperative Oceanic and Fisheries Investigation (CalCOFI) surveys and California Department of Fish and Game (CDFG) anchovy (*Engraulis mordax*) surveys.

Pacific hake are most abundant over the continental shelf and slope within the California Current system from roughly 25°N to 50°N (figure 1). In summer, adult hake migrate to the northern end of their distribution to feed. In autumn the adults migrate southward to spawn off the coasts of central and southern California and the Baja California peninsula.

Indices of larval abundance show that most of the spawning occurs between January and March. The fish spawn in midwater depths (130–500 m) over the continental slope; after hatching, larvae are distributed within or just below the mixed layer (Bailey et al. 1982). Early-stage hake (eggs, larvae, and juveniles less than 2 years old) are found in waters off the coast of California. Hake larvae eat a broad size-range of prey, predominantly copepod eggs, nauplii, copepodites, and adults (Sumida and Moser 1980).

DATA SOURCES

Larval Data

CalCOFI survey data formed the basis for my examination of the distribution and abundance of

larval hake. From 1950 to 1960, monthly surveys were conducted along a fixed sampling grid. From 1961 to 1969, annual surveys were conducted every third month (January, April, July, and October), and from 1969 to 1984, the grid was completely sampled every third year (i.e., 1972, 1975, 1978, 1981, and 1984; Hewitt 1988). From 1969 to 1984, stations were not consistently sampled in any particular month, but always in the first and second quarters of the year (Hewitt 1988). Since 1985, quarterly surveys have been conducted over a reduced portion of the sampling grid.

Larval hake were sampled by oblique tows with a 1-m ring net from 1951 to 1976 and with bongo nets after 1976. The depth of the tows was 150 m from 1951 to 1965, and 210 m thereafter. The number of fish larvae captured was standardized to the number per 10 m² of sea-surface area on the basis of the depth and duration of each tow as described in Smith and Richardson (1977). Estimates of the number of larval hake observed were available for most years from 1951 to 1986, except for 1970, 1971, 1973, 1974, and 1976. Information on the size distribution of larval hake was available for 1961, 1963–69, 1972, 1975, and 1977–85.

Juvenile Survey Data

Data on juvenile abundance were obtained from CDFG pelagic fish surveys (Bailey et al. 1986). Data for juvenile hake were available from 1965 to the present. Indices of juvenile abundance were updated to include more recent years, 1984–85. In general, hydroacoustic surveys were conducted during the day, and midwater trawl samples were collected at night along the same track lines. A midwater trawl with a 50- or 60-ft² opening and 1.27-cm mesh at the cod end was deployed for 20 minutes in the upper 15 fathoms of the water column. Data from hauls taken between 30° and 35°N were used in this study. Two indices of juvenile abundance based on the percent occurrence and catch per unit effort (CPUE) of juvenile hake observed between April and March of the next year are presented. Percent occurrence was calculated as the percent of all autumn or winter hauls that recorded catches of 0-age hake (Bailey et al. 1986). Catch per unit effort was calculated as

$$\text{CPUE} = \ln[(\text{number hake/hours trawled}) + 1]/n, \quad (1)$$

where n is the number of tows (Bailey et al. 1986).

The number of months available for the Bailey et al. study varied between years. For example, in 1984 the year-class index was based on a single cruise

made in November. I used only data collected during autumn-winter cruises (September–March) for this study.

Recruitment Estimates

Estimates of the number of fish recruited to the fishery at age 2 were derived from the recruitment estimates of Dorn and Methot (1989). These recruitment estimates were produced using the stock synthesis model (Methot 1986, 1989) and are dependent on age-composition data from the fishery and adult surveys.

METHODS

Larval Abundance and Distribution

Early-stage hake larvae have been observed off central and southern California and Baja California. The sampling area used for CalCOFI surveys was divided into 23 regions covering 1.7556×10^{11} m² (Lo 1986). The southern regions (12–20) were not sampled from 1980 to 1988; regions 1–3 were sampled only in 1969 and 1972. Therefore, for time-series comparisons, I used a consistently sampled subset including regions 4, 5, 7, 8, 9, and 11 (figure 2).

The regional subset was further broken down into four areas representing nearshore locations, areas west of Point Conception, and offshore areas north or south of Point Conception. The boundaries of these subareas are illustrated in figure 3.

Indices of larval abundance were based on the mean number of larvae per 10 m² over the sampling area. I divided the indices of abundance and the size distribution of larvae (standard length) into three categories corresponding to early (1.75–4.25 mm)¹, middle (4.25–11.25 mm), and late (11.25–15.5 mm) stages of development.

For early and late-stage larvae, I used observations from the subset of consistently sampled regions to estimate abundance. For early-stage larvae, I calculated a weighted mean number of larvae per unit area (γ) for the regional subset using samples collected between January and March.

$$\gamma = \sum_{r=4,5,7,8,9,11} (W_r \gamma_r) \quad (2)$$

where W_r was the regional weight based on the surface area within each of the six regions in the subset (table 2, following Lo 1985), and γ_r was the sample mean count per station for the region. I used a similar weighted mean for late-stage larvae collected between March and May.

¹Observations showed yolk-sac larvae of hake were never smaller than 2 mm.

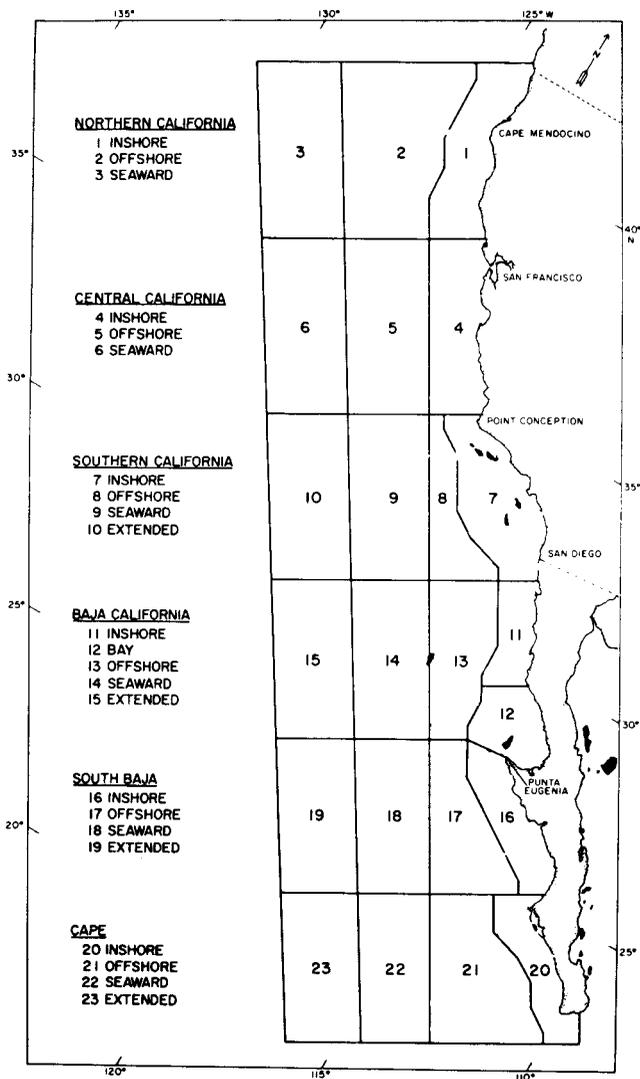


Figure 2. Sampling regions for CalCOFI larval fish surveys.

TABLE 2
Surface Areas and Weights for CalCOFI Regions 4-11

CalCOFI region	Area (million m ²)	Regional weight
4	61.05	0.152
5	98.78	0.247
7	68.96	0.172
8	41.16	0.103
9	98.78	0.247
11	31.71	0.079
Total	400.44	1.000

To identify relationships between the larval abundance indices and adult hake populations, I compared the time series of larval data to recruitment indices and egg production estimates. I divided the time series of larval abundance indices into two intervals corresponding to periods when the meter net

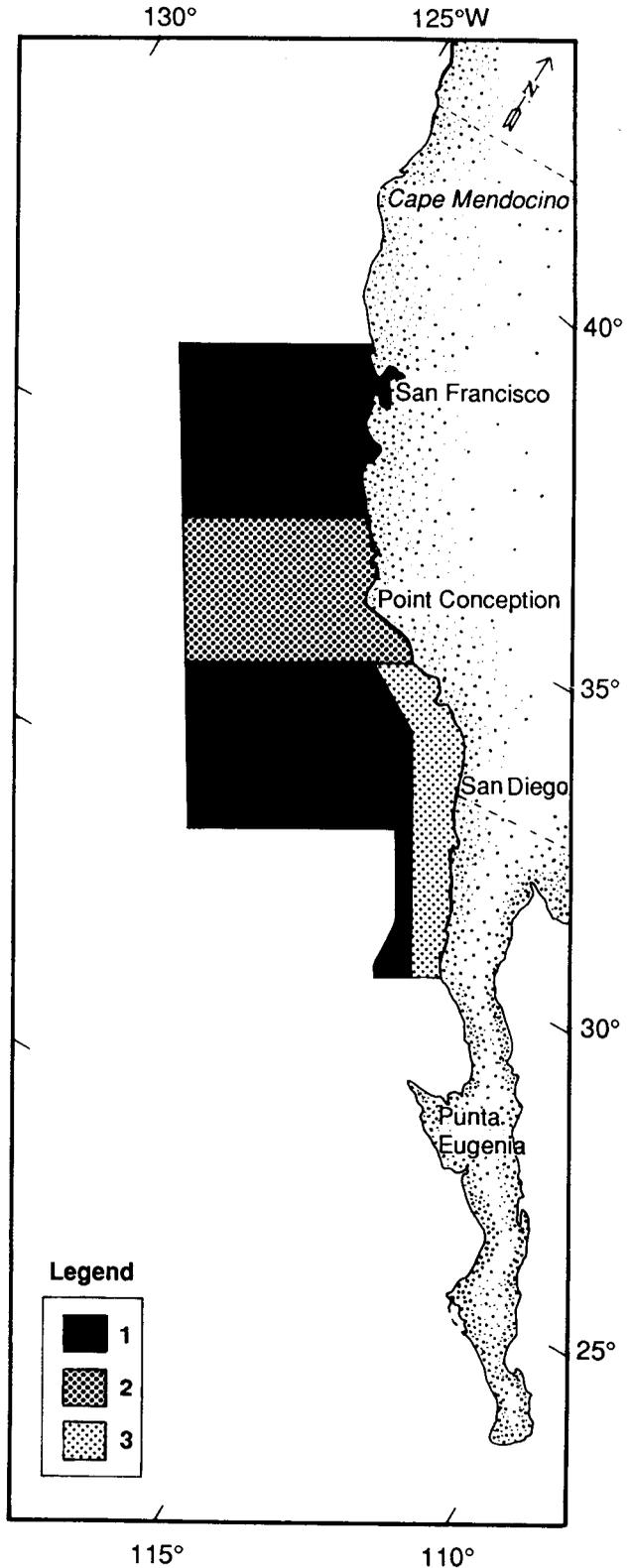


Figure 3. Subareas within the regional subset representing areas north or south of Point Conception (1), west of Point Conception (2), and near shore (3).

(1961–75) and bongo nets (1977⁺–84) were used. This division is necessary because the catchability of the two configurations cannot be considered equivalent (Lo 1985, 1986). Data after 1985 were not included in this analysis because the sampling area was reduced to include only regions 7, 8, and 9.

To summarize the spatial distributions of early and late-stage larvae, I used the distributional centroid and the variance of the spatial distribution (Koslow et al. 1985; Heath and MacLachlan 1987; Kim 1987; Kendall and Picquelle 1990). I also plotted the observed distribution of larvae to examine the relative fit of the centroid to the observed data. The centroids were estimated in terms of the mean latitude and longitude weighted by the number of larvae at each station. The centroid equals the weighted mean position. An ellipse representing the standard deviation of the first two principal axes of the bivariate normal distribution was plotted to illustrate the central location of the larvae (Kendall and Picquelle 1990).

I compared distributions of early and late-stage larvae using years with a well-defined temporal peak in abundance in both larval stages. This criterion was imposed to limit the comparisons to years when a cohort of larvae could be identified in both the early and late-stage data sets. I also compared the distributions of late-stage larvae in years of strong recruitment into the fishery.

Construction of Life Table

Using the format of Smith (1985), I constructed a life table for hake. Independent estimates of natural mortality rates were obtained for embryonic and early-stage larvae based on estimates of egg production and larval abundance. For juveniles less than 135 mm, I assumed mortality to be a function of size. I also assumed that the estimated mortality rates within a size range for juvenile northern anchovy (*Engraulis mordax*) were generally applicable to Pacific hake. For juveniles greater than 135 mm (1 year +) daily mortality rates were based on an estimate of adult annual instantaneous mortality (0.2) for hake (Hollowed et al. 1988).

Estimate of Daily Mortality for Embryonic Stage

I estimated the abundance of hake larvae for the embryonic stage as follows. I calculated the total number of eggs spawned in a given year from the most recent estimates of numbers-at-age, percent mature-at-age provided by Dorn and Methot (1989), and an estimate of the fecundity-at-age. I calculated fecundity-at-age from the relationship between fork length (FL) and fecundity (E) for the Georgia Strait

Pacific hake stock (equation 3; Mason 1986) and the population mean length-at-age:

$$E = 0.5501 * FL^{3.3896} \quad (3)$$

Where E is number of yolked oocytes $>200 \mu\text{m}$, and FL is the fork length in centimeters.

An estimate of the total abundance of early-stage larvae (1.75–4.25 mm) was derived from CalCOFI data. I estimated the total number of early-stage larvae by multiplying the mean number of early-stage larvae per m^2 in a given region by the area of that region and summing over all regions. The total number of early-stage larvae was calculated from areas 4–13 (figure 2).

Daily instantaneous natural mortality (M) was estimated from the following equation:

$$N_t = N_o * \exp(-M * d) \quad (4)$$

where N_t was the total abundance of early-stage larvae in a given year; N_o was the egg production for that year; M was the estimate of daily natural mortality; and d was the duration in days between the egg and early larval stages.

In an analysis of growth rates derived from daily increments on otoliths, Bailey (1982) found that hake grew linearly during the first 20 days after hatching. He concluded that larval growth could be described with the following equation:

$$SL = 2.75 + 0.16 * d \quad (5)$$

where SL is the standard length of the preserved larvae in millimeters. I used equation 5 to estimate that early-stage larvae were 0–10 days old.

Bailey (1982) noted that growth increments begin 1 to 2 days before complete yolk-sac absorption. He found that the time from hatching to complete absorption of the yolk sac was temperature-dependent. Fifty percent of laboratory-reared larvae had completely absorbed their yolks after 6.4 days at 12°C and 4.2 days at 15°C . Hake larvae tend to aggregate at the bottom of the thermocline. Barilotti et al. (1984) found that the thermocline depth generally corresponded with the depth of the 14°C isotherm. Assuming temperatures of 14°C , I estimated the time to complete absorption of the yolk sac as 5 days, and assumed that daily rings began to be added after 3 days.

I estimated the incubation time for hake eggs as a function of average water temperature at 100 m. The mean temperature at 100 m for the first quarter (1954–87) was 9.97°C within a 3° square including

the California Bight (30°–33°N; J. Norton, Pacific Fisheries Environmental Group, Monterey, pers. comm.). Bailey (1982) found the time for 50% hatching of eggs reared at 12°C was 4.5 days, and at 8°C, 6.5 days. Using a Gompertz-type growth relationship, Zwiefel and Lasker (1976) estimated that the incubation time of hake eggs reared at 9°C was 5 days; at 10°C the time was 6 days. Using these estimated incubation times and the mean temperature at 100 m, I assumed that eggs hatch after approximately 5 days. Growth ring deposition began after 3 days, so I assumed that early larvae were 8 to 18 days old, and I estimated mortality assuming that early larvae were 13 days old.

Estimate of Daily Mortality for Early to Late Larvae

Daily mortality rate for the period between early and late stages of development was estimated as follows. I used growth rates derived from daily increments on hake otoliths (Bailey 1982) to calculate the age of late larvae:

$$SL = 1.72 * \exp(3.15 * (1 - \exp(-0.02624 * d))) \quad (6)$$

For larvae from 11.25 to 15.25 mm, approximately 40 days would have elapsed since deposition of the first daily growth ring.

I further adjusted the average age of late-stage larvae estimated from equation 6 to include 5 days for the egg stage and 3 days until the beginning of daily growth ring deposition. Thus I assumed the late-stage larvae to be roughly 48 days old.

I calculated natural mortality by comparing the early and late-stage larval abundance indices discussed above for years when abundance peaked in the early and late-stage indices. I calculated mortality from equation 4, where N_0 was the abundance of early-stage larvae, N_t was the abundance of late-stage larvae, and the duration was 35 days — i.e., 48 days (the mean age of late-stage larvae) minus 13 days (the mean age of early-stage larvae).

Estimate of Stage Duration for Juveniles

Juvenile-stage durations were based on observed length at age from CDFG surveys. Figure 4 shows the length range of 0-age juvenile hake from the CDFG surveys. I estimated juvenile-stage durations by assuming a growth rate of 0.39 mm per day, derived from the linear relationship between the midpoint of the length range and Julian date for juveniles from spring, summer, and autumn cruises (figure 4).

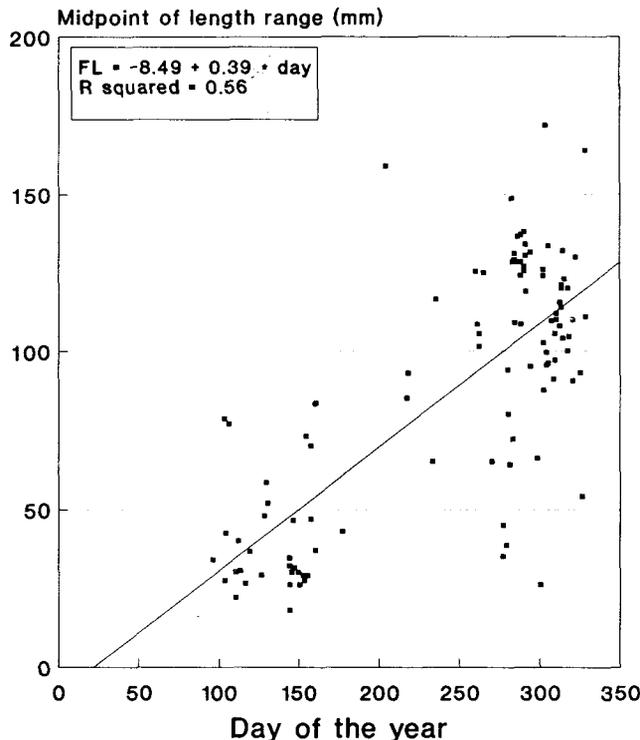


Figure 4. Midpoint of length ranges of 0-age Pacific hake in individual hauls by day. The regression of length versus day was used to estimate daily growth rates of juvenile hake.

$$FL = -8.4897 + 0.3911 * DAY \quad R^2 = 0.56. \quad (7)$$

If early-stage larval growth followed this regression, the hatch date would be in late January. Such a date would be consistent with temporal distributions of early-stage larvae.

Life-Table Simulation Model

Mortality through each life stage was followed, beginning with an estimate of egg production. The number of eggs used to initiate the model was the average of estimated numbers based on population from Dorn and Methot (1989). I used the initial estimate of eggs as the starting point for the hypothetical cohort. Then I varied each duration and mortality rate for each life stage to produce a twenty-fold increase or decrease in recruitment.

RESULTS

Larval Spatial and Temporal Distribution

When stations were sampled over a wide geographic area (1963–75), an average of 84% of the early-stage larvae and 96% of the late-stage larvae were taken in regions 4, 5, 7, 8, 9, and 11 (table 3;

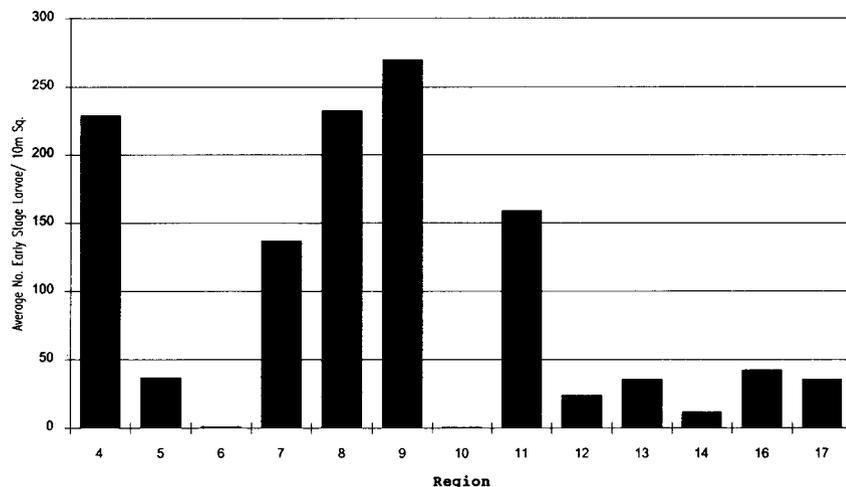


Figure 5. Summary of the average abundance of early-stage hake larvae (1.75–4.25 mm) by region, collected between January and March in CalCOFI surveys from 1963–1975. No early stage hake larvae were collected in regions that are not represented.

TABLE 3
Percentage of Total Early and Late Larvae Observed within the Subset (CalCOFI Regions 4, 5, 7, 8, 9, and 11)

Year	Percentage early larvae (1.75–4.25 mm)	Percentage late larvae (11.25–15.25 mm)
1961	—	98.30
1962	—	—
1963	88.20	97.84
1964	65.32	94.48
1965	47.77	79.07
1966	88.94	94.57
1967	—	—
1968	99.87	—
1969	91.30	100.00
1970	—	—
1971	—	—
1972	96.88	100.00
1973	—	—
1974	—	—
1975	90.94	100.00
1977	100.00	100.00
1978	96.22	100.00
1979	99.89	100.00
Average	87.76	96.75

figure 5). These regions were well sampled in most years. Based on these observations, I defined the regional subset as the area encompassing regions 4, 5, 7, 8, 9, and 11 (figure 2).

The temporal distribution of larvae over the entire time period (1961–85) revealed peak periods of early and late-stage abundance. Within the regional subset, most early-stage larvae were taken in the first three months of the year, with a peak in February (figures 6a, b). Most late-stage larvae were taken between March and May (figure 6c, d). In years when sampling was distributed across all three

months, late-stage abundance was generally highest in April (figures 6c, d).

Mortality Estimates

Comparisons of egg production to early-stage larval abundance were made for eight years when sampling occurred in January, February, and March (1966, 1972, 1975, 1978, 1979, 1981, 1982, and 1984; figure 6). Estimates of instantaneous natural mortality during the embryonic stage for these eight years ranged from 0.23 to 0.41 d⁻¹ (table 4). The differences in mortality estimates may be due in part to incomplete sampling of the spawning range of coastal hake. The average daily mortality ($M = 0.31$) for embryonic hake fell between the mortality estimates for anchovy calculated by Smith (1985; $M = 0.25$) and Peterman et al. (1988; $M = 0.41$). Peterman et al. gave annual estimates of daily natural mortality for northern anchovy between the time of spawning and the mean of the yolk-sac larvae. The annual estimates of hake and anchovy embryonic mortality were not correlated (table 4).

Larval abundance clearly peaked for the early and late-stage indices in nine years (1963, 1964, 1966, 1969, 1972, 1978, 1979, 1981, and 1985; figure 6). Estimates of daily mortality rates between early and late stages of larval development for these nine years ranged from 0.11 to 0.20 (table 5). The average daily mortality rate for early-stage hake larvae (0.15) was similar to estimates for larval anchovy between approximately 4 and 10 mm long (Smith 1985; 0.160), and for yolk-sac-to-19-day-old anchovy larvae (Peterman et al. 1988; 0.186). The estimates indicate that roughly 14% of the hake larvae are lost per day in the early-to-late larval period.

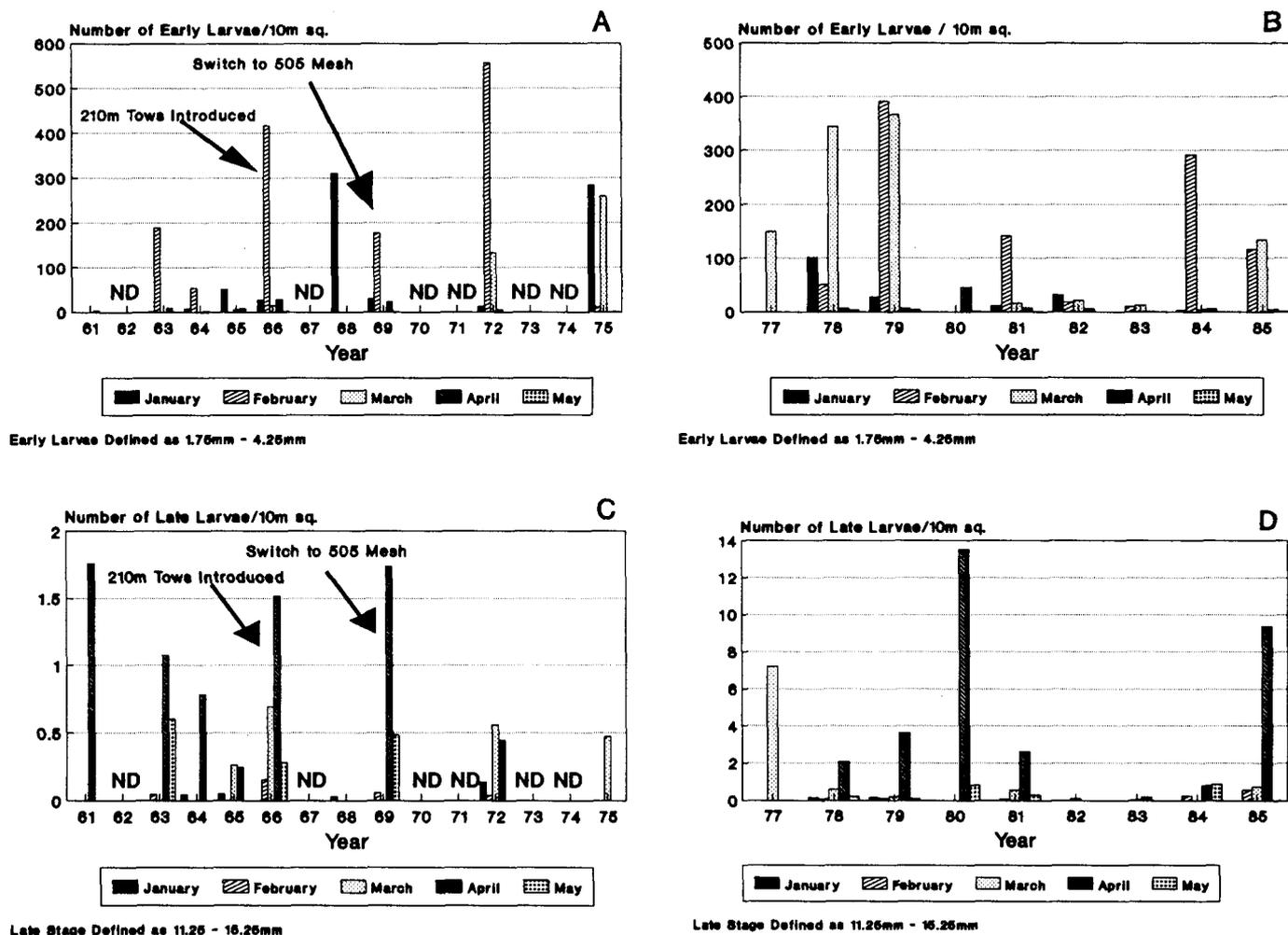


Figure 6. Summary of the monthly average number of early or late larvae per 10 m².

TABLE 4
 Estimated Abundance and Corresponding Daily Natural Mortality Rates for Embryonic Hake (1.75–4.25 mm) Compared with Daily Mortality for Embryonic Northern Anchovy

Year	Eggs (trillion)	Larvae (trillion)	Estimate of hake mortality (d^{-1})	Estimate* of anchovy mortality (d^{-1})
1966	731.2	8.46	0.34	0.42
1972	437.8	11.01	0.28	0.25
1975	476.3	18.55	0.25	0.44
1978	378.1	12.42	0.26	0.59
1979	326.1	17.20	0.23	0.48
1981	298.6	2.35	0.37	0.38
1982	275.8	1.41	0.41	0.36
1984	344.6	3.32	0.36	0.36
Average			0.31	0.41

*Peterman et al. 1988

TABLE 5
 Estimated Daily Mortality Rates for Intermediate Hake Larvae Compared with Daily Mortality for Northern Anchovy Larvae

Year	Early larval ^a abundance no./10 m ²	Late larval ^b abundance no./10 m ²	Estimate of hake mortality ^c	Estimate of anchovy mortality ^d
1963	69.921	0.992	0.12	—
1964	32.261	0.827	0.10	—
1966	203.551	1.105	0.15	0.17
1969	132.426	0.761	0.15	0.21
1972	270.932	0.797	0.17	0.18
1975	407.620	0.358	0.20	0.18
1978	310.222	0.642	0.18	0.17
1979	428.142	0.884	0.18	0.22
1981	58.240	1.362	0.11	0.18
1985	273.755	1.984	0.14	0.19
Average			0.15	0.19

^a1.75–4.25 mm

^b11.25–15.25 mm

^cBased on differences in the abundance indices of early and late larvae assuming a 35-day period of growth

^dPeterman et al. 1988

Life-Table Simulations

The estimate of recruitment (0.060 billion) produced from the life-table simulation was similar to the observed estimates of poor recruitment at age 2 (0.063 billion; table 6). Strong recruitment at age 2 was estimated to be 3.180 billion. Estimates of strong and poor recruitment were calculated as the mean of the upper and lower quartiles of the recruitment time series presented in Dorn and Methot (1989). Approximately 99% of the cohort is lost by the time the young reach 10 mm. Estimates of early-stage abundance showed no significant relationship with egg abundance (figure 7). This may indicate that significant embryonic mortality already occurred, and that the rate of embryonic mortality must vary interannually.

Recruitment levels at age 2 on the order of 1.2 billion hake (a twenty-fold increase, a level similar to the lowest of the strong year classes) could only be produced by shortening the larval stage or the natural mortality rate during the egg or larval stages (table 7). In contrast, recruitment levels at age 2 of .012 billion hake (a twenty-fold decrease, a level similar to the lowest of the weak year classes) could result from variations in the mortality rate or duration of any life stage (table 7).

Juvenile and Larval Indices of Abundance

Figure 8 illustrates the updated time series of indices of age-0 juvenile hake abundance (based on autumn and winter cruises) and recruitment to the fishery at age 2 (Dorn and Methot 1989). Although the pattern of year-class strength was not exactly

TABLE 6

Estimated and Postulated Life Table for the Coastal Stock of Pacific Hake

Category	Length (mm)	Mortality (daily)	Duration (days)	Initial number
Embryo ^a	Egg-4	0.313	16	4.48×10^{14}
Early larva ^b	4-10	0.150	23	2.99×10^{12}
Late larva ^c	10-35	0.050	89	9.51×10^{10}
Juvenile II	35-60	0.020	64	1.11×10^9
Juvenile III	60-110	0.010	128	3.09×10^8
Juvenile IV	110-135	0.0027	64	8.58×10^7
Juvenile V	135+	0.00056	346	7.22×10^7
Recruits @ age 2	—	—	—	5.95×10^7

^aDuration of the embryonic stage was estimated by assuming a 5-day incubation period, 3 days before daily ring deposition, and 8 days of growth to reach 4 mm (derived from equation 5).

^bDuration of stage estimated from equation 6 (31 days) and assuming a 5-day incubation period and 3 days before daily ring deposition. The duration represents the estimated age (39 days) minus the embryonic stage (16 days).

^cDuration of stage estimated from equation 6 (120 days) and assuming a 5-day incubation period and 3 days before daily ring deposition. The duration represents the estimated age (128 days) minus the embryonic and early larval stages.

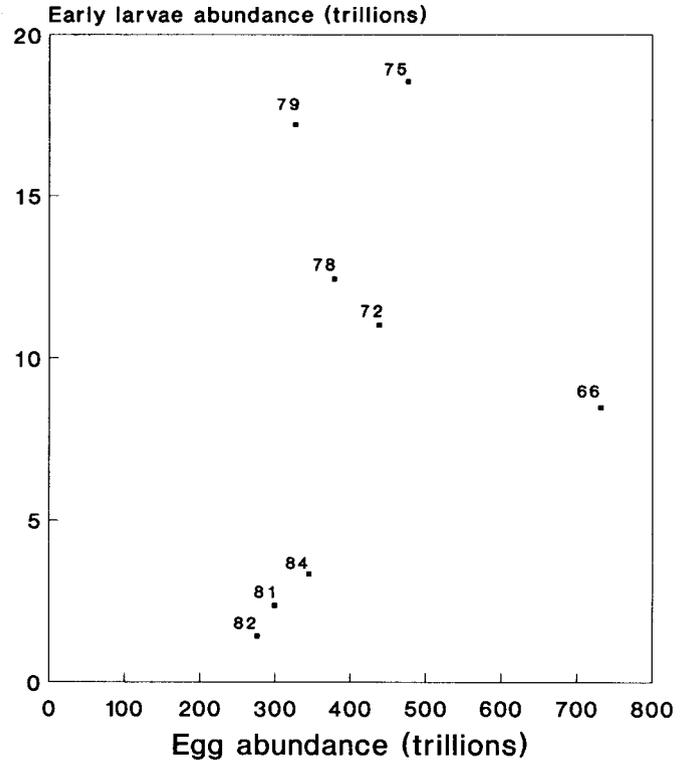


Figure 7. Relationship between estimated levels of egg production and observed abundance of early larvae.

mirrored in the juvenile indices, juvenile percent occurrence or CPUE was usually elevated when there were strong year classes (figure 8). The notable ex-

TABLE 7

Parameter Changes Leading to a Twenty-Fold Increase or Decrease in Recruitment for Coastal Pacific Hake

Stage	Instantaneous daily mortality	Duration of stage (days)
Embryo (egg to 4 mm)		
Starting	0.313	16.00
1/20 ×	0.414	21.14
20 ×	0.126	6.43
Early larva (4-10 mm)		
Starting	0.150	23.00
1/20 ×	0.220	33.74
20 ×	0.020	3.03
Late larva (10-35 mm)		
Starting	0.050	89.00
1/20 ×	0.068	121.20
20 ×	0.016	29.08
Early juvenile (35-60 mm)		
Starting	0.020	64.00
1/20 ×	0.045	144.50
20 ×	unr	unr
Juvenile II (60-110 mm)		
Starting	0.010	128.00
1/20 ×	0.022	289.00
20 ×	unr	unr

unr = unreasonable value

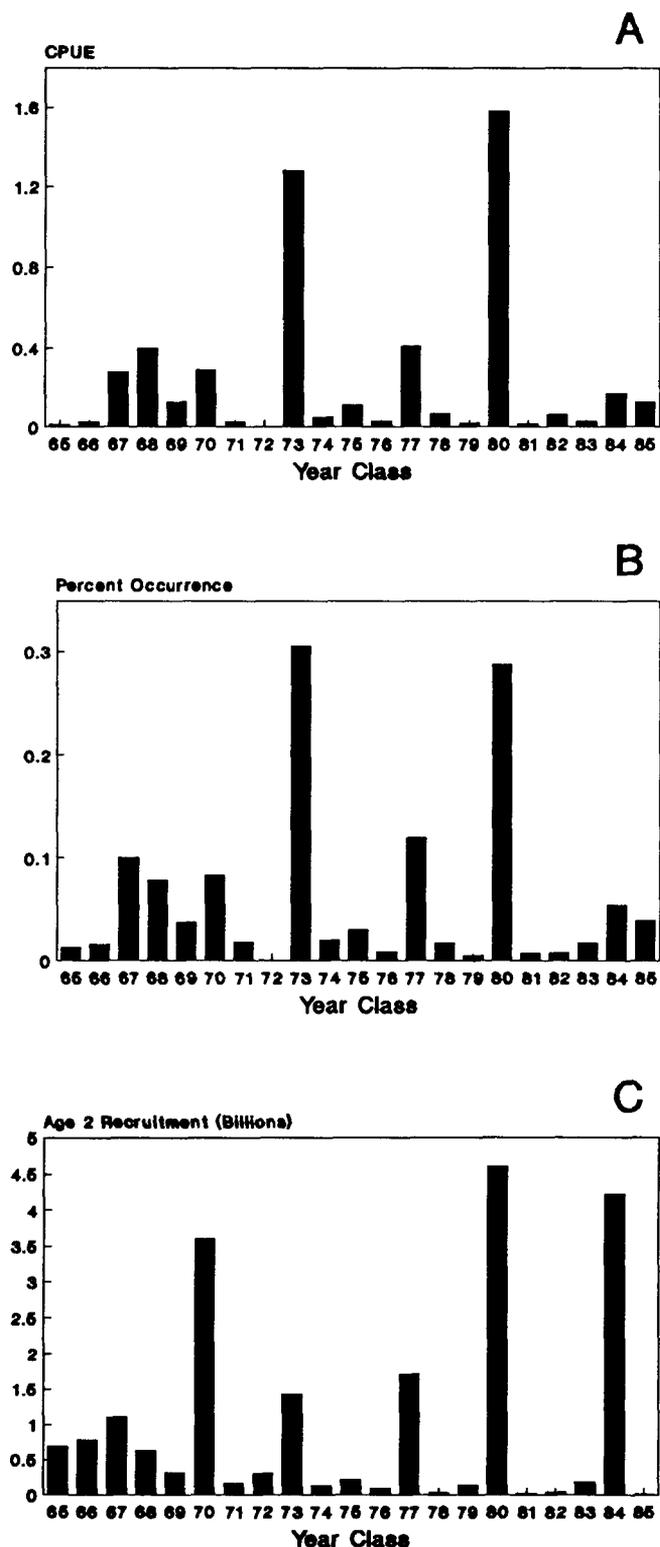


Figure 8. Catch per unit of effort (CPUE, top) and percent occurrence (middle) of 0-age hake in midwater trawl surveys compared with year-class strength determined by catch-at-age analysis (bottom).

ception was a low juvenile index in 1984, a year that produced a strong year class.

The time series of late-stage larval abundance also seems to be related to year-class strength. Again, with the notable exception of the 1984 year class, the index of late-stage larval abundance was high when there were strong year classes (1961, 1977, and 1980; figure 9). This relationship is most apparent from samples taken with a bongo net (figure 9), possibly because that net more efficiently samples large larvae. A strong relationship is not readily apparent in the pre-bongo data because there were no data for three of the four strong year classes (1967, 1970, and 1973).

The indices of mean larval abundance could have been influenced by rare encounters with larval patches of high abundance. Large concentrations of larvae were observed in a few stations. The influence of these patchy concentrations can be minimized by using trimmed means in which the upper and lower 5% of the distribution is ignored. Comparison of the trimmed mean catch-per-tow values with the mean catch-per-tow values shows that the large concentrations of larvae increased the mean substantially. But the trend showing high late-stage larval abundance in years that produced strong year classes was still apparent in the trimmed means (table 8).

Larval Distribution

Clearly defined peaks of abundance for both early and late-stage larvae were identified in nine years (1964, 1966, 1969, 1972, 1975, 1978, 1979, 1981, and 1985; figure 6). The early-stage larvae were widely distributed throughout the region, whereas the late-stage larvae were more concentrated (appendix). On average, early-stage larvae were observed in 47% of the stations; late-stage larvae in only 11% of the stations (table 8). Comparison of the mean catch-per-tow values with the trimmed mean-per-tow values shows that there were also localized patches where early-stage larvae were abundant (table 8).

The distributions of late-stage larvae that produced strong year classes are shown in figure 10. Most late-stage larvae were found south of Point Conception in 1961 and 1977; most were found north of Point Conception in 1980 and 1984, perhaps because spawning locations differed. Average temperatures at stations in region 7 (south of Point Conception) during January and February were 14.6°C in 1961, 16.0°C in 1980, and 15.3°C in 1984. Hollowed (1990) estimated the 1977 temperature in region 7 as 14.4°C. So the fish may have spawned farther south in 1961 and 1977 because temperatures were lower. The early-stage larval distributions

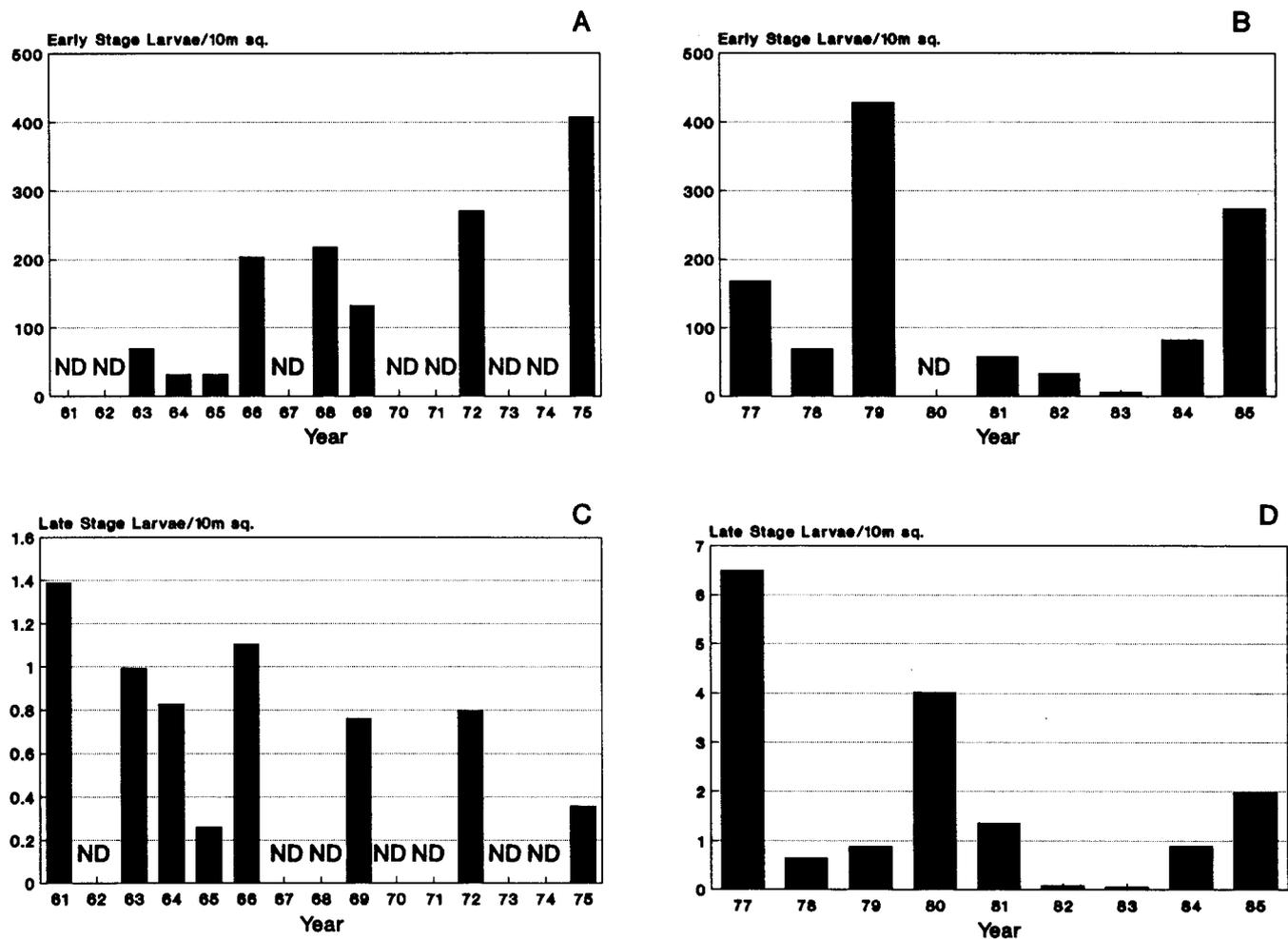


Figure 9. Time series of larval abundance indices for early and late Pacific hake larvae. The early-stage index is based on the average number of larvae (1.75–4.25 mm) per 10 m² in surveys conducted from January to March. The late-stage index represents the average number of larvae (11.25–15.25 mm) in surveys from March to May.

observed in 1984 (appendix) indicated northward spawning. Early-stage larval distributions were not available for 1961, 1977, or 1980.

Larvae that survived to the late stage were concentrated near shore or directly west of Point Conception (appendix). Mean catch per station for near-shore areas and areas west of Point Conception combined was generally higher than for other areas (table 9). Mean catch per station was higher in offshore regions in 1961 and 1985 (table 9). In 1961, the late-stage larvae were concentrated in offshore areas south of Point Conception (figure 10). In 1985, late-stage larvae were concentrated in offshore areas north of Point Conception (appendix).

DISCUSSION

This study produced three major findings. Processes controlling the production of strong year classes of Pacific hake seem to occur during the early

or late larval period. Estimates of larval mortality rates were similar in magnitude to estimates for northern anchovy but did not show similar interannual variations. Finally, transport to nearshore nursery grounds in the California Bight or areas within the offshore plume near Point Conception seems to play an important role in producing strong year classes.

The estimates of larval distribution, abundance, and mortality must be considered rough because of several sampling problems associated with the data sets used in this analysis. Crecco et al. (1983) noted that accurate estimates of larval abundance and daily mortality rates depend on the assumption that larvae of all size groups are equally vulnerable to capture. This assumption may not have been met because the data were not corrected for gear selectivity, extrusion, or avoidance by hake larvae. Differences in gear selectivity were indirectly addressed, however,

TABLE 8
 Comparison of Abundance Indices for Early and Late-Stage Hake Larvae

Year	Percent occurrence	Weighted mean	Mean	SD	Trimmed mean	Maximum no./10m ²
Early-stage larvae						
1963	—	69.9	—	—	—	—
1964	58	32.3	26.5	112.6	10.5	1,463.1
1965	—	32.4	—	—	—	—
1966	65	203.6	221.0	836.3	65.8	7,238.4
1968	—	218.0	—	—	—	—
1969	51	132.4	112.5	556.4	41.8	8,485.1
1972	66	270.9	251.8	1340.6	70.0	19,444.7
1975	50	407.6	255.0	1222.2	62.4	14,269.1
1977	—	168.6	—	—	—	—
1978	38	310.2	211.6	1701.5	25.9	28,272.0
1979	54	428.1	305.0	1493.0	67.0	14,994.0
1981	28	58.2	52.9	518.5	8.0	7,352.0
1982	—	34.2	—	—	—	—
1983	31	6.3	11.3	518.5	4.3	459.0
1984	21	83.0	103.7	964.2	3.9	14,143.3
1985	58	273.8	129.4	738.7	18.6	7,721.1
Average	47	170.6	152.8	—	34.4	11,258.3
Late-stage larvae						
1961	25	1.390	1.667	4.071	0.961	25.9
1963	—	0.992	—	—	—	—
1964	16	0.827	0.784	2.322	0.361	16.7
1965	—	0.262	—	—	—	—
1966	17	1.105	0.848	2.595	0.389	19.6
1969	14	0.761	1.055	3.835	0.333	28.6
1972	8	0.797	0.629	2.761	0.104	21.1
1975	2	0.358	0.289	2.252	0.000	27.5
1977	15	6.495	7.200	21.620	3.600	154.3
1978	6	0.642	0.924	5.681	0.064	91.0
1979	8	0.884	1.119	4.492	0.349	46.2
1980	11	4.071	7.120	48.400	0.640	503.2
1981	10	1.362	1.663	9.078	0.474	124.7
1982	—	0.094	—	—	—	—
1983	—	0.061	—	—	—	—
1984	6	0.893	0.653	2.853	0.049	20.2
1985	7	1.984	1.376	6.022	0.183	46.0
Average	11	1.352	1.948	—	0.577	86.5

by dividing the larval time series into periods when the 1-meter ring nets and the bongo nets were used.

Extrusion of small larvae may have been significant for early-stage hake. Lo (1983) found that within the size range for early-stage larvae (1.75–4.25 mm), high percentages of anchovy larvae (93% of 1.75-mm larvae and 47% of 4.25-mm larvae) would have been extruded through the 505- μ m–555- μ m-mesh netting frequently used in CalCOFI surveys. Lo showed only minor differences between larval extrusion rates with the 550- μ m ring net and 505- μ m bongo nets. Because hake larvae have larger heads than anchovy larvae, fewer of them may be extruded (Smith and Richardson 1977); however, the heads are soft because they are not fully ossified, so extrusion could bias the estimates of early-stage mortality.

If extrusion rates for hake larvae were similar to those estimated for anchovy larvae by Lo (1983), the

estimates of early-stage larval abundance would exceed the estimates of annual egg production. In such a case, the estimates of egg production would be erroneous. My estimates of the maturity schedules and fecundity of hake were approximations based on early examinations of hake maturity (Best 1963) and fecundity schedules for Georgia Strait Pacific hake (Mason 1986).

The mortality estimates for early-stage larvae also could have been biased by larger larvae's avoidance of the net. Hewitt and Methot (1982) noted that more large anchovy larvae were captured at night than during the day. Therefore, I estimated the ratio of mean catch during the day (0830–1630 h) to mean catch during the night (2030–0230 h) for the early and late-stage size classes. In 11 out of 15 years the mean catch of early-stage larvae was higher during the day than during the night (table 10). In all years sampled, the mean catch of late-stage larvae was

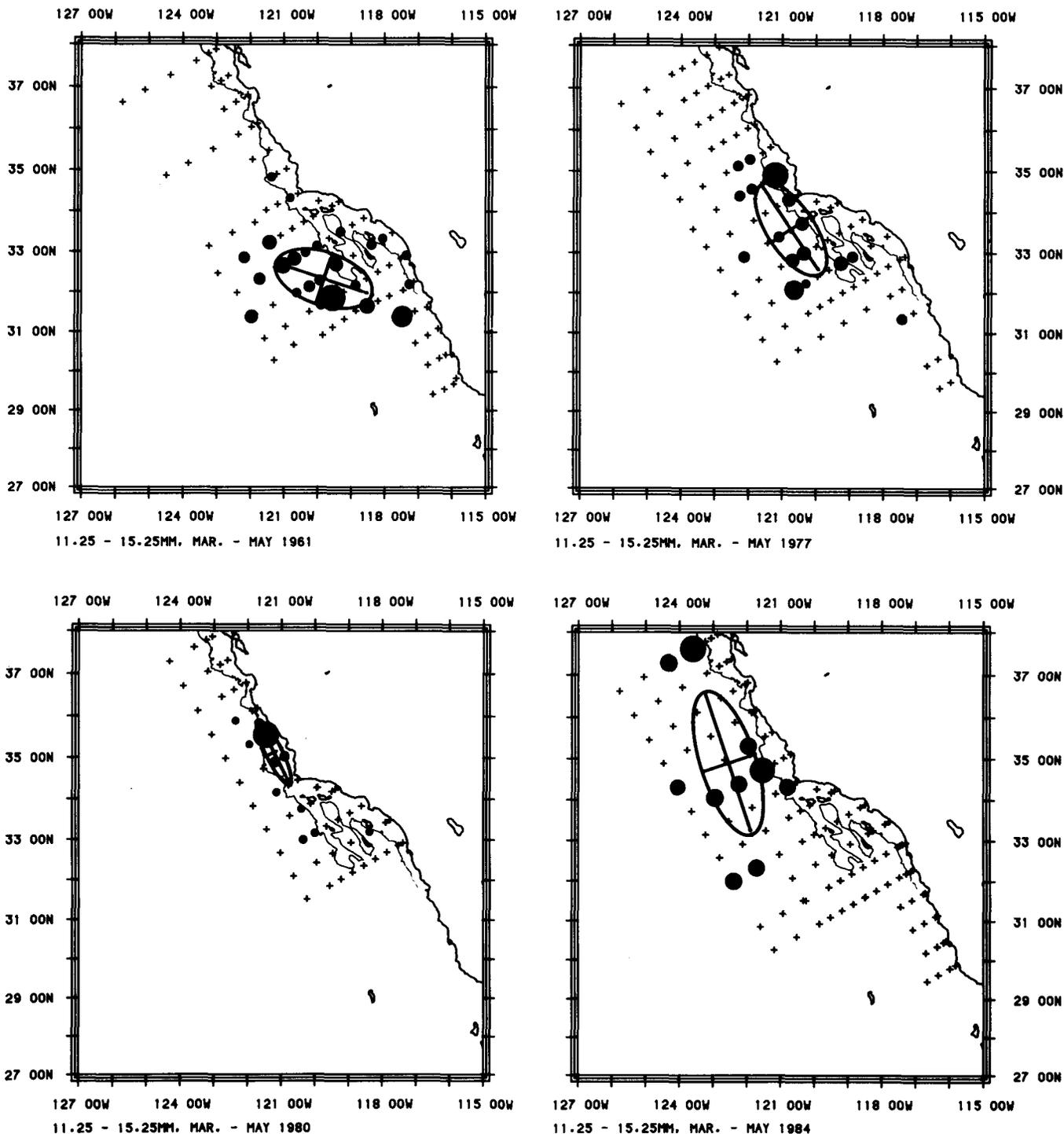


Figure 10. Comparison of late-stage larval distributions observed in years that produced strong year classes: 1961, 1977, 1980, and 1984. Dot size indicates the abundance of larvae relative to the maximum value observed in that year (1961 = 26, 1977 = 154, 1980 = 503, and 1984 = 20). The relationship between the abundance at each station and the size of the dot is linear. Crosses indicate stations where hake larvae were not observed.

lower during the day than during the night (table 10). This may indicate that late-stage hake larvae migrate vertically in a diurnal pattern.

Alternatively, the lower mean catch of late-stage

larvae observed during the day may be attributed to net avoidance. The higher mean catch of early-stage larvae during the day may result from larval behavior. If early-stage larvae are more active during the

TABLE 9
Mean Density of Late-Stage Hake Larvae That Were Near Shore or West of Point Conception* in Regions 4, 5, 7, 8, 9, and 11

Year	Density (no./10 m ²)			
	Inshore*	Point Conception	Other areas	Combined areas ^b
1961	1.308	0.909	2.245	1.125
1964	0.447	1.152	0.797	0.775
1966	0.221	2.060	0.660	1.000
1969	0.771	2.000	0.646	1.396
1972	0.381	1.568	0.000	0.988
1975	0.206	0.611	0.125	0.321
1977	1.000	13.806	5.333	9.630
1978	1.099	1.757	0.252	1.473
1979	0.396	1.696	1.103	1.131
1980	0.379	24.929	0.875	12.439
1981	2.702	1.902	0.606	2.400
1984	0.000	2.167	0.565	0.729
1985	0.000	1.189	2.479	0.494

*See figure 3 for definition of subareas.

^bCombined areas refers to the mean number of hake larvae per station found in nearshore areas and areas west of Point Conception.

day, they may be concentrated higher in the water column. If extrusion rate is a significant factor for early-stage larvae, then larvae captured at deeper depths would spend more time in the net and would probably have greater extrusion rates than those captured at shallower depths. Because the day:night mean catch ratios varied considerably between years (table 10), a more rigorous method of examining net avoidance must be undertaken before a correction factor is applied to the larval data set.

Finally, the CalCOFI larval surveys were not designed to sample Pacific hake larvae. The depth of the tows (standard at 210 m to surface) may not have adequately sampled the entire vertical distribution of hake larvae, which may extend deeper. In addition,

the distribution of hake larvae can be patchy in both space and time, and sampling at a few selected locations each month cannot precisely reflect the true dynamics of larval birth and death rates.

Problems also exist in interpreting the results from the midwater trawl juvenile surveys. The mesh size of the net, depth of tow, and geographic distribution of the midwater surveys were not optimal for sampling hake juveniles, which are only captured incidentally. The midwater sampling data, however, generally reflect relative year-class strength, further indicating that the signal of variations in abundance of young-of-the-year hake is strong.

This study shows that relative year-class strength can be determined in the larval and early juvenile stages of Pacific hake. Strong year classes are characterized by high abundances of large larvae and young-of-the-year juveniles; weak year classes occurred when the indices of large larvae or young-of-the-year juvenile abundance were low. Given the sampling problems described above, the observation that relative abundance of larvae usually reflects year-class strength indicates that the larval signal of hake must be very great, particularly in years of high abundance.

An exception to this relationship was observed in 1984, when relatively few late-stage larvae and juveniles were observed but recruitment was high. One explanation is that the traditional spawning locations of hake shifted north in 1984. Several pieces of evidence support this explanation.

Evidence of spawning in the north in 1983 and 1984 is substantiated by hake eggs in National Marine Fisheries Service ichthyoplankton surveys off the coasts of Oregon and Washington (Art Kendall, Alaska Fisheries Science Center, Seattle, WA, pers. comm.). Ichthyoplankton surveys were conducted

TABLE 10
Ratio of Mean Catch during Day (0830–1630 h) to Mean Catch during Night (2030–0230 h) for Early and Late-Stage Larvae

MP* Size (mm)	1-Meter ring net										Bongo net							
	1961	1963	1964	1965	1966	1968	1969	1972	1975	1978	1979	1980	1981	1982	1983	1984	1985	
2.0	—	7.15	2.69	0.59	0.94	2.00	0.68	11.88	18.63	0.33	0.25	—	1.25	—	—	—	0.00	
2.5	—	5.57	0.38	1.43	1.21	1.93	1.28	17.57	5.48	1.58	0.52	—	3.17	47.25	2.15	417.20	0.92	
3.0	—	4.53	0.16	1.14	3.10	11.91	0.42	1.50	3.23	0.35	0.24	—	1.35	22.05	0.85	16.54	0.82	
3.5	—	3.28	0.41	1.38	1.49	8.63	0.49	0.28	3.67	0.19	0.44	—	0.49	14.06	1.45	2.86	5.33	
4.0	—	1.10	0.36	3.96	1.20	3.25	0.33	0.48	1.95	0.29	1.43	—	0.40	—	0.77	1.92	4.69	
Average	—	4.33	0.80	1.70	1.59	5.54	0.64	6.34	6.59	0.55	0.58	—	1.33	27.79	1.31	109.63	2.35	
11.75	0.31	0.30	0.16	0.38	0.17	—	0.00	0.00	0.00	0.00	0.00	0.66	0.13	—	0.00	0.00	2.21	
12.75	0.08	0.00	1.58	0.00	0.12	—	0.38	0.00	0.62	0.27	0.18	0.00	0.00	—	—	0.00	0.37	
13.75	0.00	1.33	0.20	0.00	0.42	—	0.09	0.00	—	0.80	0.92	0.33	0.50	—	—	0.00	0	
14.75	0.31	0.44	0.79	0.00	0.00	—	0.31	0.00	—	0.00	0.00	1.33	0.00	—	—	1.31	—	
Average	0.18	0.52	0.68	0.10	0.18	—	0.20	0.00	—	0.27	0.28	0.58	0.16	—	—	0.33	—	

*Midpoint of size range

in the springs of 1980–84 and 1987, and covered an area from 40°N to 48°N. Except for 1983 and 1984, no hake eggs or larvae were observed in these surveys. The percent occurrence of hake eggs in spring (March–April) surveys was 10.48 in 1983 and 14.52 in 1984. In those years most eggs were found between 40° and 44°N.

The 1982–83 El Niño may have influenced the 1983–84 spawning distribution of Pacific hake in several additional ways. Pearcy and Schoener (1987) speculated that the northern extension of hake egg and larval distribution correlated with oceanic conditions associated with the strong 1983–84 El Niño, including reduced southerly flow of the California Current, weak upwelling, onshore transport of oceanic and Columbia River plume waters, and anomalous poleward currents.

Fiedler (1984) noted that anchovy spawning distributions also extended north of Point Conception in 1983. He suggested that under normal ocean conditions, anchovy spawning is excluded from regions north of Point Conception by the plume of cold California Current water. There was no evidence of the cold-water plume south of Point Conception during CalCOFI survey 8302 (Feb. 9–Mar. 29). The absence of the cold-water plume in the spring of 1983 may also explain the northward spawning of Pacific hake in that year.

Chelton et al. (1988) describe a strong poleward flow along the central California shelf between Point Conception and Point Sur throughout February–July 1984. This observation was based on current measurements taken from eleven locations off the central California coast as part of the Central California Coastal Circulation Study. The enhanced poleward surface flow may partly explain the spawning off Oregon and the northerly distribution of hake larvae in 1984.

The observation that events during larval life may be important in determining year-class strength differs from Peterman et al. (1988), who made a similar study of northern anchovy and concluded that year-class strength was established in the juvenile stage. The conclusions of Peterman et al. (1988) may not reflect the importance of mortality during the early developmental stages of northern anchovy. The poor relationship between anchovy pre-recruits and recruitment indices may have resulted from data gaps in the CalCOFI sampling program. There appears to be a correspondence between anchovy pre-recruits and recruitment indices in 1965–75, when the sampling was best, whereas the relationship erodes from 1978 to 1985, when the sampling area and frequency were reduced (Peterman et al. 1988).

An alternative explanation for the different conclusions drawn from the analysis of northern anchovy and Pacific hake lies in the different growth and behavior of the two species. Northern anchovy tend to spawn closer to shore than Pacific hake. The growth characteristics of northern anchovy also differ from those of Pacific hake. And because anchovy is an important prey to many other animals throughout its life, predation may have a greater effect on recruitment than it does for postlarval Pacific hake.

The life-table simulation showed that decreases in recruitment could originate at any stage, but substantial increases could only originate from lower mortality rates or shorter egg or larval stages. This result corroborates the analysis of late-stage abundance data, which indicated that strong year classes could be detected early in the life history.

The results of this study are consistent with those of Smith (1985), who constructed a life table for northern anchovy and conducted simulations to identify critical life stages. He also concluded that strong year classes of northern anchovy could only be produced by accelerating the growth through early and late larval stages, or diminishing mortality during the early or late larval period.

Evidence that strong year classes are established early in development has been noted in other fish stocks. The magnitude of American shad (*Alosa sapidissima*) year classes appears to coincide with years of high juvenile abundance, and can be attributed to mortality in the larval period (Crecco et al. 1983; Crecco and Savoy 1987; Savoy and Crecco 1988). Sundby et al. (1988) concluded that year-class strength of Arcto-Norwegian cod (*Gadus morhua* L.) is established during the larval stage. Houde (1987) analyzed the impact of variations in life-stage duration or mortality during the egg, yolk-sac, larval, and juvenile stages in five different fish species. He concluded that for most species the larval stage holds the greatest potential for regulating year-class size.

The observation that weak year classes could be manifested by changes in growth or natural mortality in the egg, larval, or juvenile stages was addressed by Houde (1987). He noted that although codlike species exhibited moderate potential for regulating recruitment in the juvenile stage, the major processes controlling year-class strength probably occurred in the larval phase. He based this conclusion on the assumption that the initial number of juveniles upon which variable mortality or growth can operate depends on survival during the larval stage. A similar conclusion could be applied in the case of Pacific hake.

Analysis of the distribution of hake larvae showed that animals surviving to late stages were usually concentrated in nearshore areas or regions west or southwest of Point Conception. The latter regions correspond closely with the large offshore plume which is a prominent feature off the California coast in most years (Fiedler 1984; Davis 1985; Poulain and Niiler 1989). One explanation for the survival of larvae located nearshore in the California Bight or west of Point Conception is that these regions are highly productive.

Survival of larval hake may also depend on the relative availability of prey. A principal prey of Pacific hake, *Calanus pacificus*, produces eggs after exposure to increased phytoplankton production. These eggs and nauplii serve as prey for larval hake. Thus factors influencing the phytoplankton bloom may also influence hake survival.

Runge (1981) found that zooplankton production was generally higher in regions rich with phytoplankton. Therefore, high phytoplankton concentration may be associated with higher concentrations of larval prey. Hakanson (1987) found that *C. pacificus* volumes off Point Conception generally corresponded with areas of high chlorophyll. In 1984 high volumes of *C. pacificus* were located between Monterey Bay and Point Conception.

Sumida and Moser (1980) found that hake larvae ingested a broad size range (70–200 μm) of copepods. Willason et al. (1986) found that two euphausiids (*Euphausia pacifica* and *Nematoscelis difficilis*) and a copepod (*C. pacificus*) collected in April 1981 were most abundant in waters off Point Conception. They also found that *E. pacifica* and *C. pacificus* found near Point Conception and south of San Francisco had higher lipid content and more active digestive enzymes than animals collected from other areas of the California Current. These findings led the authors to conclude that zooplankton in regions off Point Conception and south of San Francisco undergo prolonged periods of better nutritional conditions.

Reduced offshore advection may favor survival of hake larvae. In the nearshore regions, offshore transport is minimized. Power (1986) simulated drift patterns for northern anchovy larvae in the California Bight. The model included long-term mean geostrophic, wind-driven current velocities to 50 m, and turbulent diffusion. Power's simulations indicated that offshore-directed Ekman transport did not strongly affect anchovy larvae in the nearshore region. There was significant seaward transport of larvae out of the California Bight when spawning extended into offshore regions or when Ekman transport increased considerably.

More complicated processes may reduce offshore advection of larvae in the plume west of Point Conception. Entrainment in eddies, or vertical migrations of late-stage larvae may retard offshore transport and may be important in keeping hake larvae west of Point Conception, where prey is most abundant. Fiedler (1986) used satellite imagery to show a general correspondence between the distribution of larval anchovy and a displaced eddy in 1985.

Bakun (in press) noted that areas influenced by Ekman transport exhibit a layered structure, with surface waters directed offshore and subsurface waters directed onshore. He speculated that pelagic organisms migrating vertically in an area influenced by Ekman transport could maintain their relative position. Myers and Drinkwater (1988/1989) showed that diurnal vertical migration of fish larvae in the northwest Atlantic could reduce horizontal advection by Ekman transport. Evidence presented earlier in this paper suggests that late-stage hake larvae migrate diurnally (table 10). This mechanism may explain how hake larvae remain in the region west of Point Conception.

In conclusion, the results of this study indicated that production of strong year classes of Pacific hake was regulated by factors influencing survival during the early and late larval periods. Estimates showed that mortality was very high at young ages. The life table simulation also indicated that strong year classes were established during the early or late larval periods. Analysis of the spatial distribution of hake larvae revealed that inshore areas and regions west of Point Conception seem favorable for survival of hake larvae. Zooplankton abundance is high in these areas, and transport offshore is minimized near shore. These findings establish the temporal and spatial setting for future analyses of factors underlying the recruitment of Pacific hake.

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APPENDIX

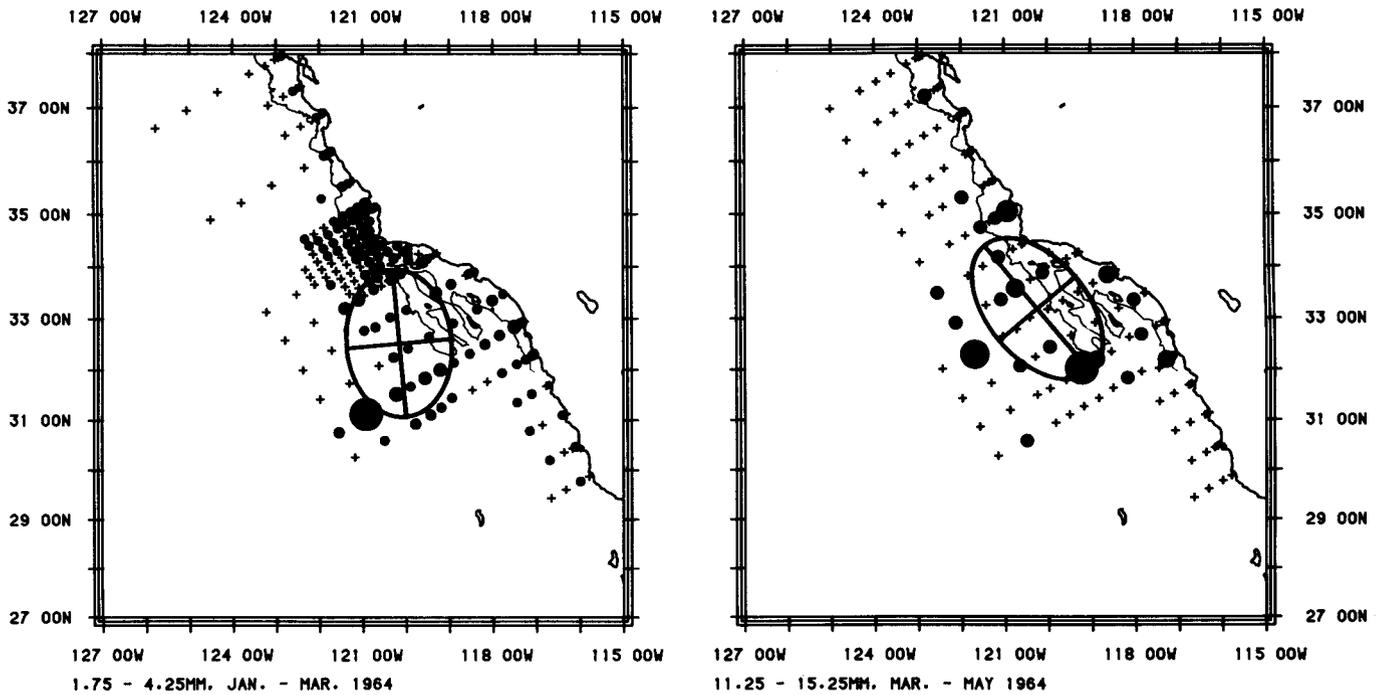


Figure A-1. Early and late-stage larval distributions observed in 1964. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 7,352, late stage = 17). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.

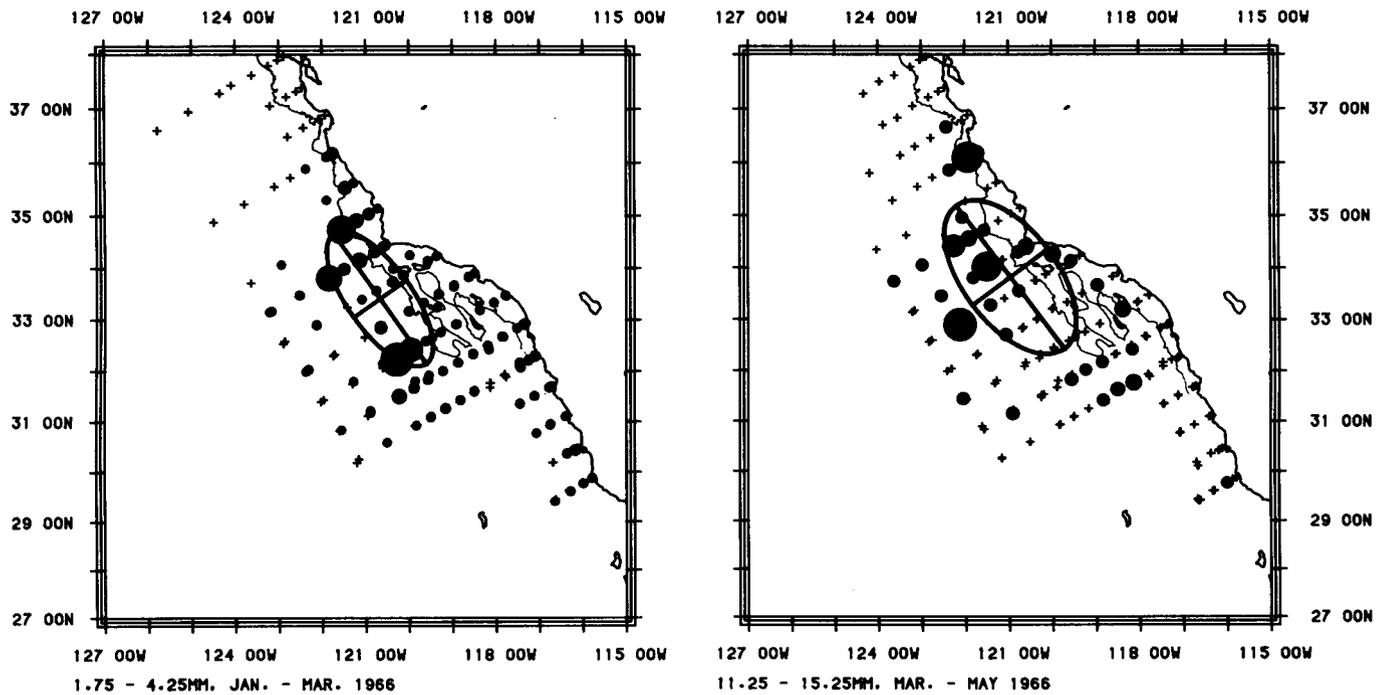


Figure A-2. Early and late-stage larval distributions observed in 1966. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 7,238, late stage = 20). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.

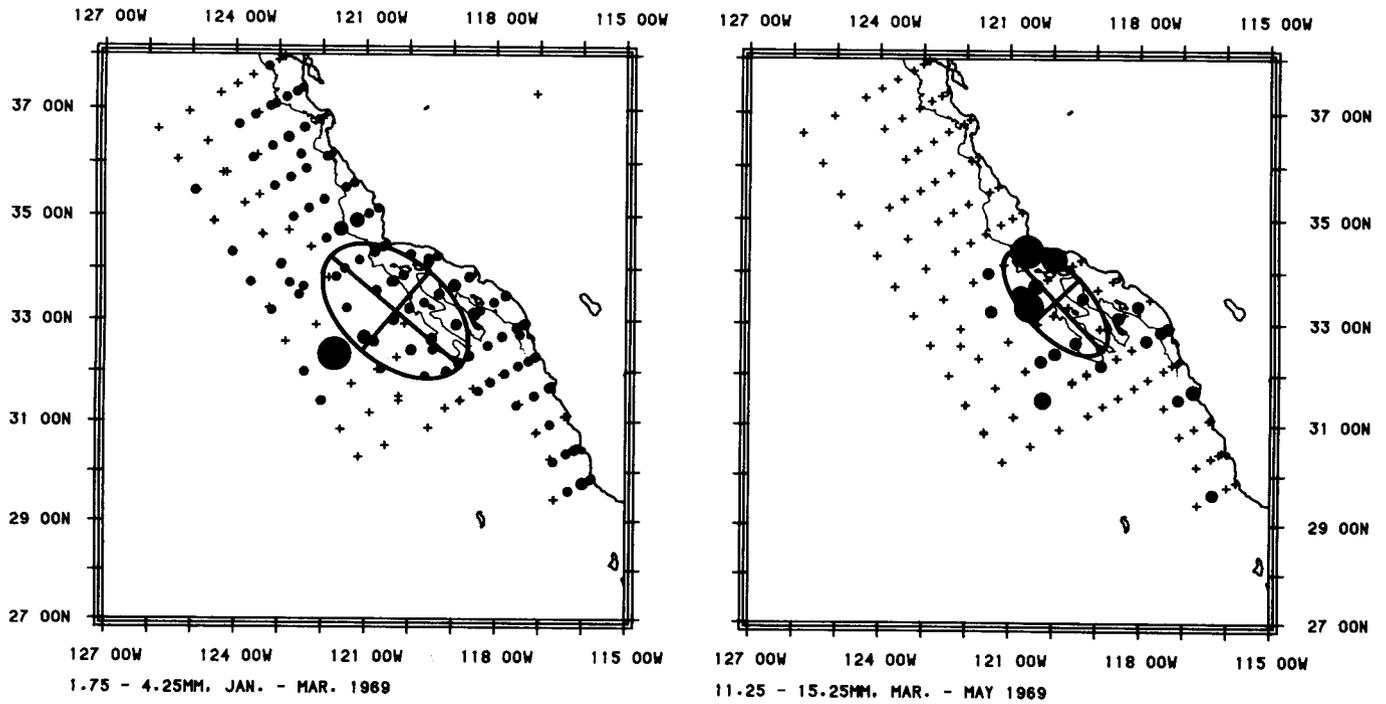


Figure A-3. Early and late-stage larval distributions observed in 1969. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 8,485, late stage = 29). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.

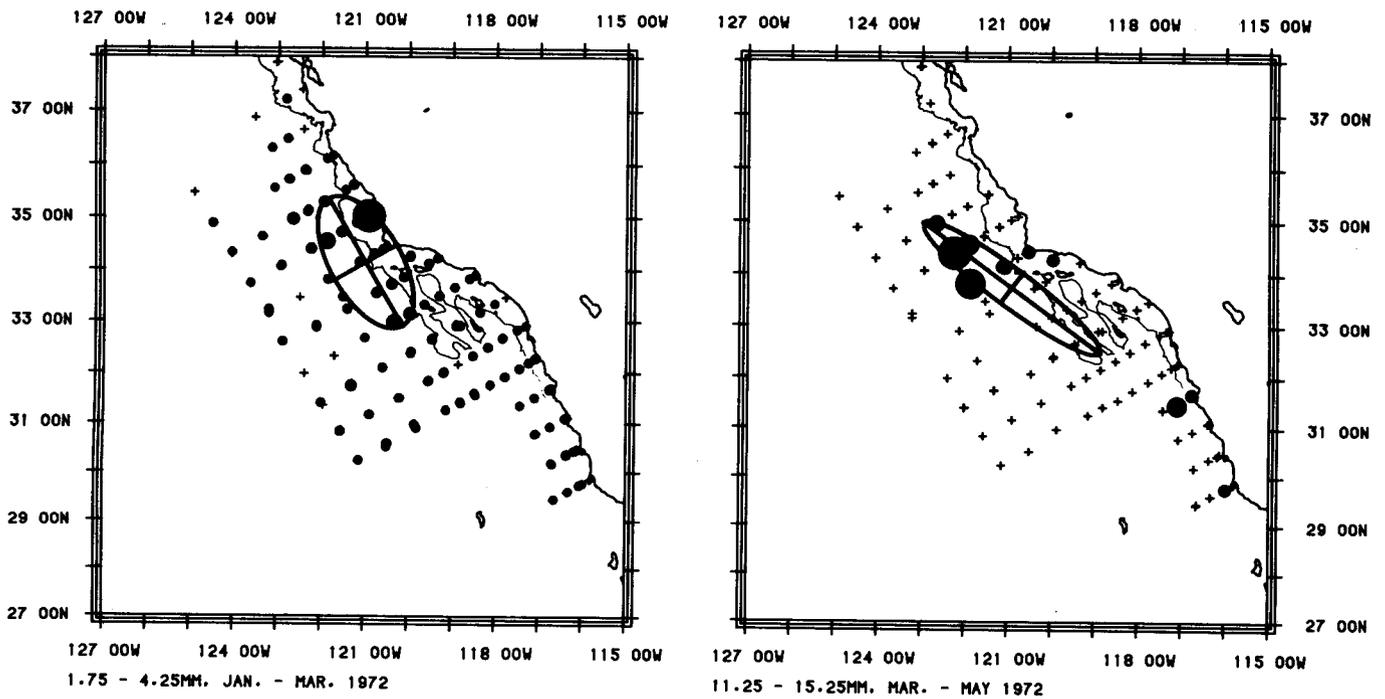


Figure A-4. Early and late-stage larval distributions observed in 1972. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 19,445, late stage = 21). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.

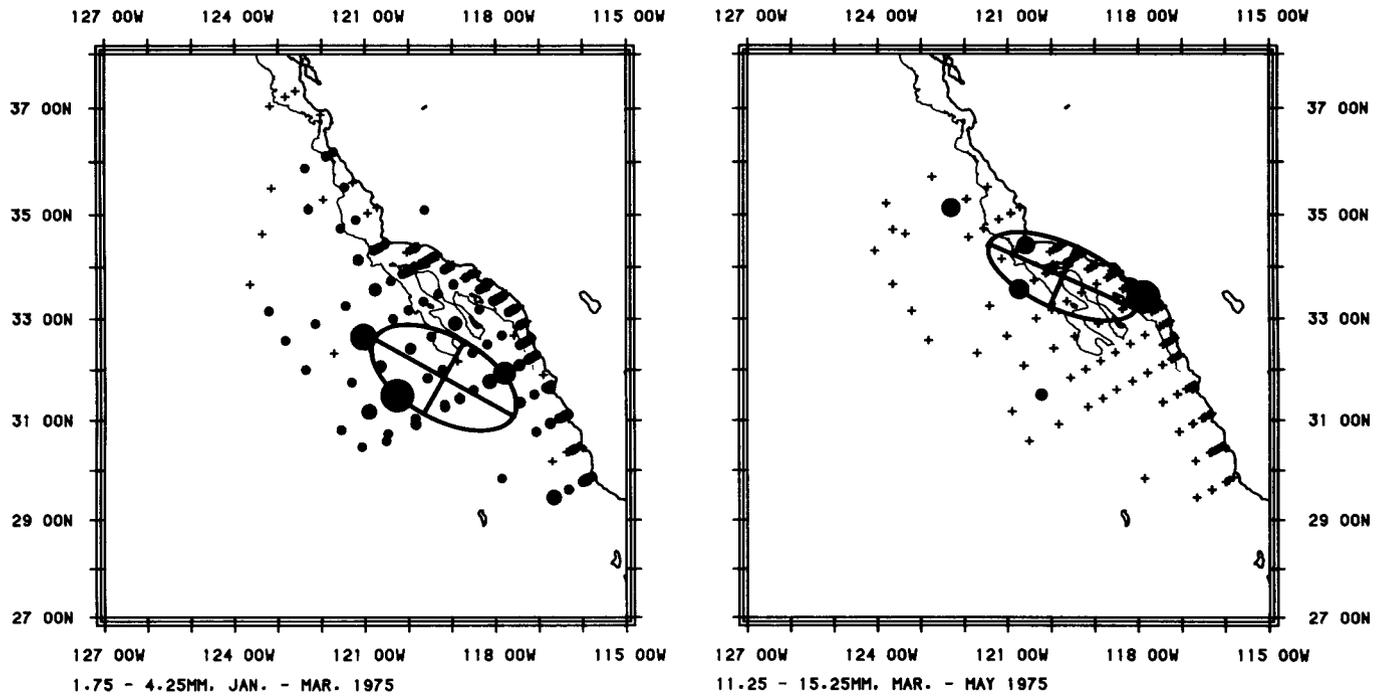


Figure A-5. Early and late-stage larval distributions observed in 1975. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 14,269, late stage = 27). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.

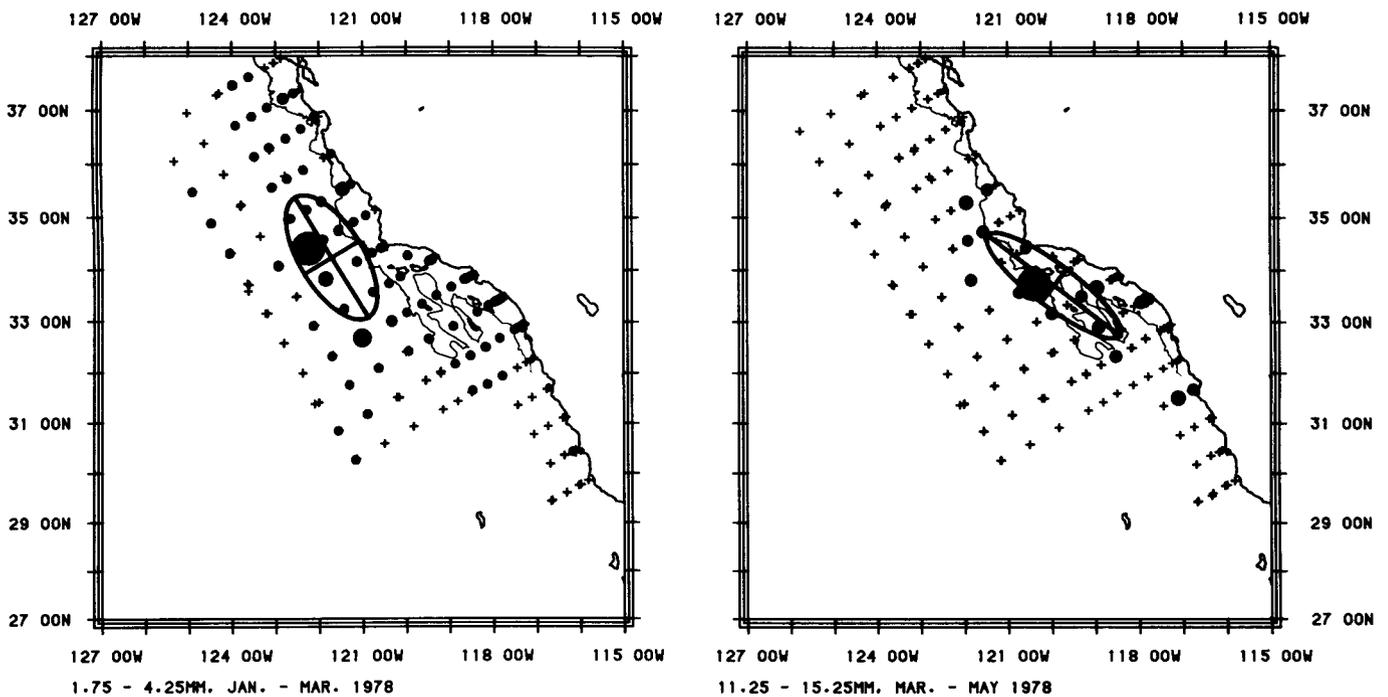


Figure A-6. Early and late-stage larval distributions observed in 1978. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 5,871, late stage = 91). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.

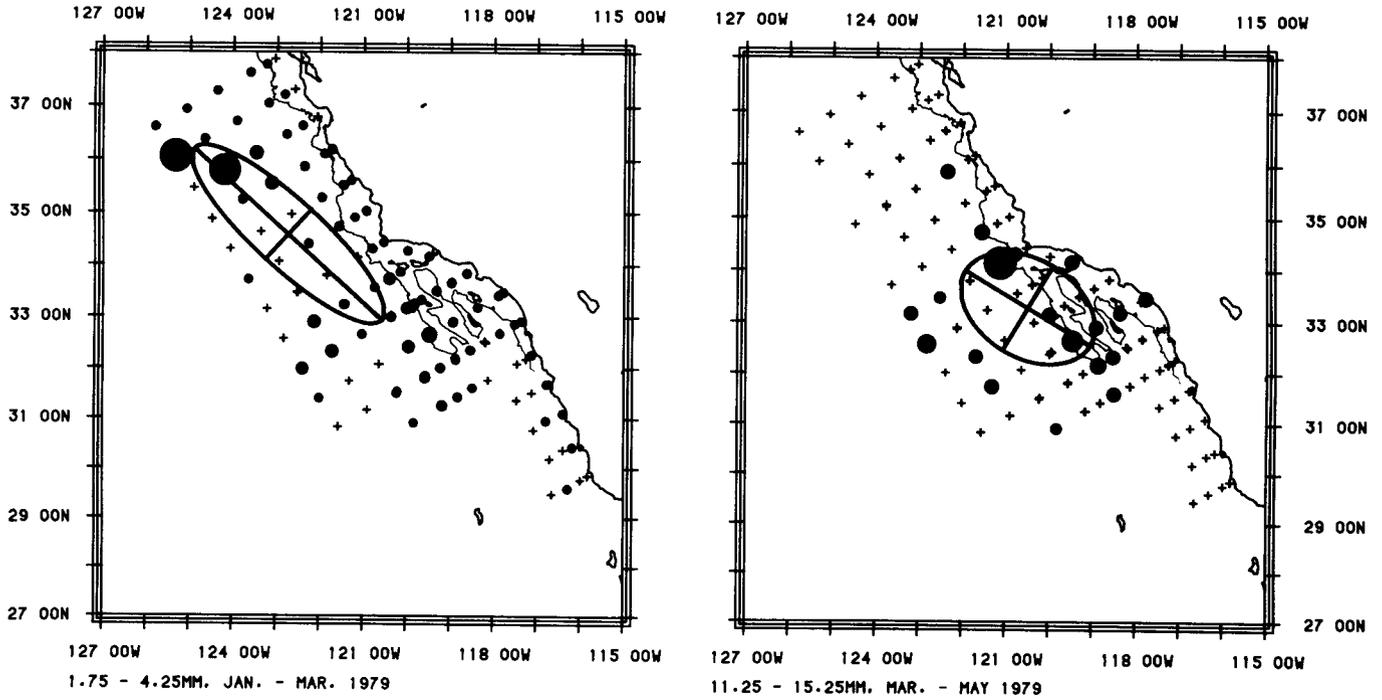


Figure A-7. Early and late-stage larval distributions observed in 1979. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 14,994, late stage = 46). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.

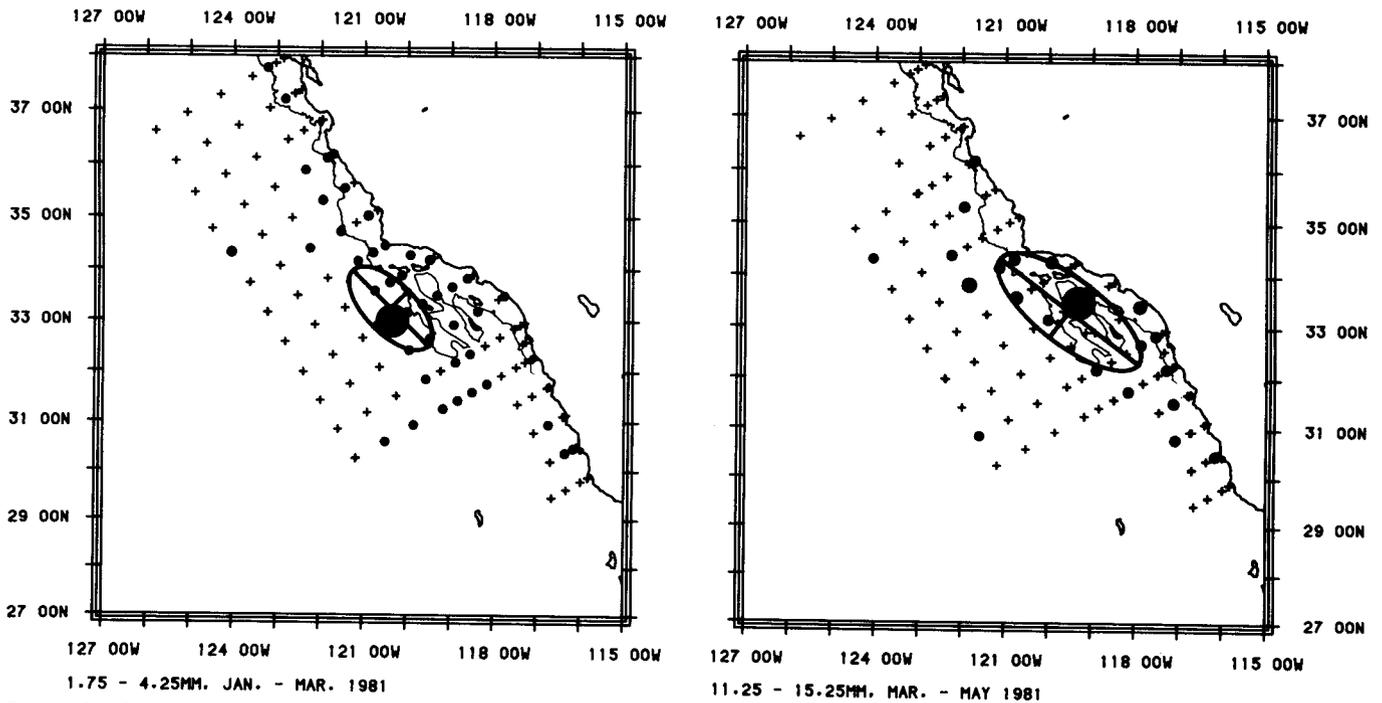


Figure A-8. Early and late-stage larval distributions observed in 1981. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 7,352, late stage = 125). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.

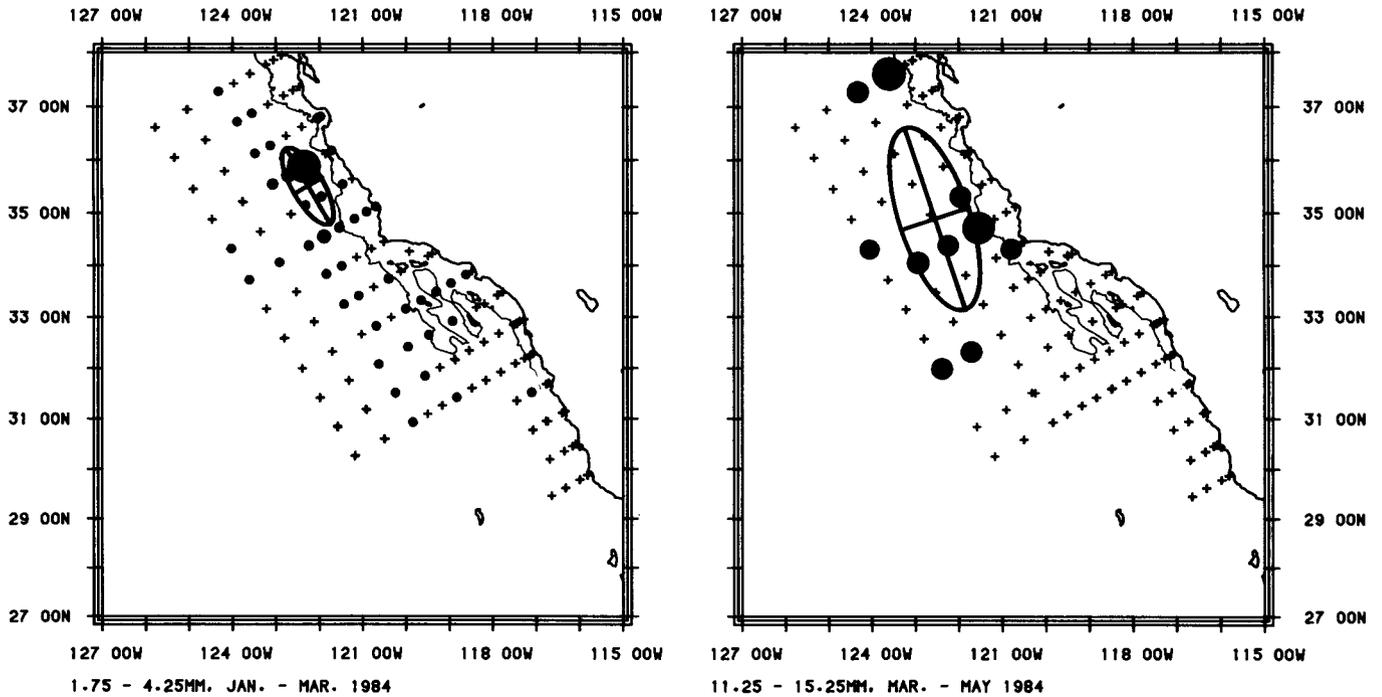


Figure A-9. Early and late-stage larval distributions observed in 1984. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 14,143, late stage = 20). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.

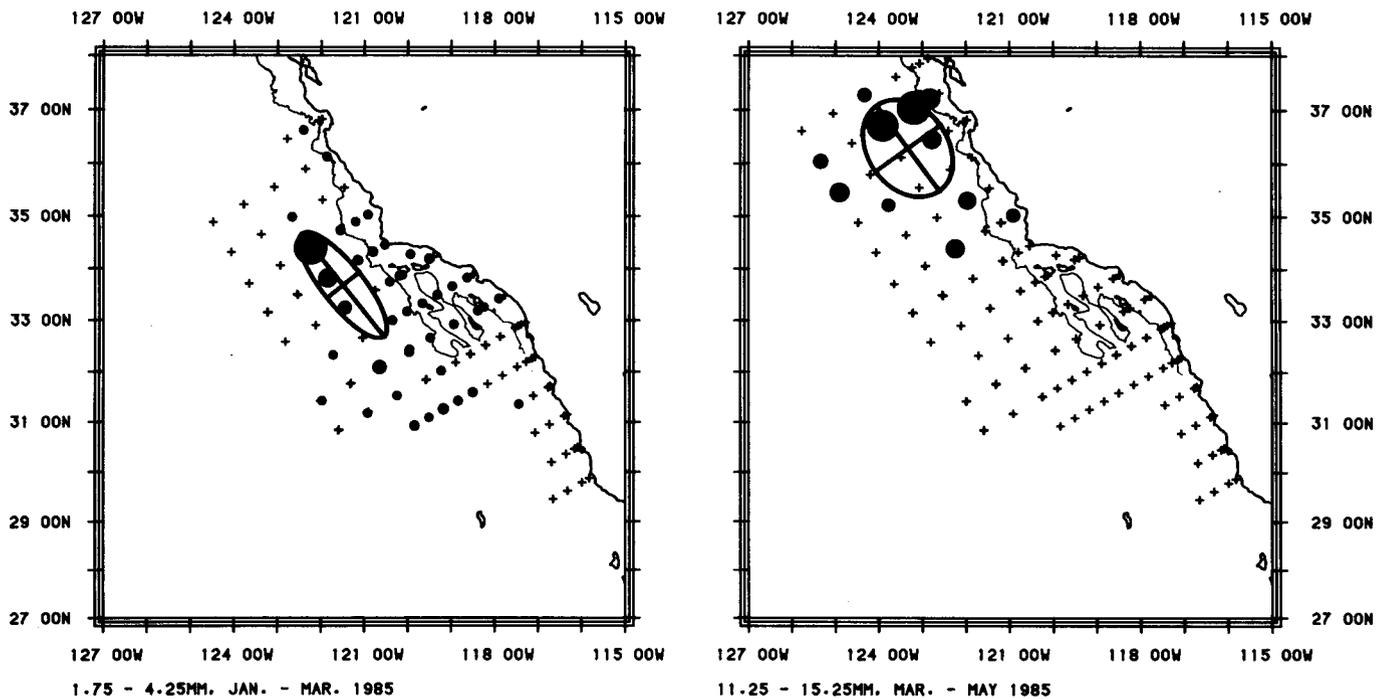


Figure A-10. Early and late-stage larval distributions observed in 1985. Dot size indicates the abundance of larvae relative to the maximum value observed (early stage = 7,721, late stage = 46). The relationship between the abundance at each station and the size of the dot is linear. Stations where larval hake were not observed are marked by a plus sign.