SPACE AND TIME SCALES IN PACIFIC HAKE RECRUITMENT PROCESSES: LATITUDINAL VARIATION OVER ANNUAL CYCLES

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ABSTRACT

Habitat of North Pacific hake (*Merluccius productus*) can be partitioned into three life-history zones: an adult feeding area along the coastal shelf and slope from California to British Columbia, a spawning area off central California south to Baja California, and a brood area extending along the coastal shelf and slopes of California and, at times, into Oregon. Recruitment is potentially influenced by a complex mixture of physical and biological processes that operate over a wide range of spatial and temporal scales. We quantify the relative importance of demographic (natality, mortality), growth (physical influences, food supply), and kinematic (passive motion with flow structures, active locomotion) processes that can influence recruitment of Pacific hake in scale diagrams of dimensionless ratios. We found that changes in larval hake biomass are dominated by mortality and drift with prevailing currents. Location of adult spawning is therefore important to survival. Changes in juvenile biomass are influenced more by changes caused by somatic growth and active locomotion. Annual survey data show multiyear trends in the latitudinal placement of spawn toward the equator (1951–55, 1959–64, 1980–83) or toward the pole (1955–59, 1964–69), but strong recruitment only in single years (1961, 1970, 1977, 1980, 1984, 1987, 1990, 1993). We surmise that sharp adjacent year changes in recruitment may not be induced by slow trends in spawning location. The center of adult spawning shifts toward the pole during warm years (>10°C at 100-m depth off Point Conception) and toward the equator during cold years. There has been an overall shift in the mid-spawning location of 444 km toward the pole during the 34-year period from 1951 to 1984. On average, three times as many recruits survive from warm years than from cold years. Unfortunately, a warm-water year does not guarantee higher than usual recruitment.

INTRODUCTION

As the most abundant fish species along the west coast of North America, North Pacific hake (*Merluccius productus*; referred to hereafter as hake) is commercially valuable and important to the biological oceanography of the region. Interest in hake as an exploitable resource began during the 1800s in localized fisheries and continues to the present day. Even though the commercial hake fishery represents a multimillion-dollar enterprise, efforts to quantify and explain recruitment to the adult stock have resulted from fortuitous sampling during other research programs. For example, the range of the hake stock was not understood until spawning grounds were delineated during California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises in 1951 (Ahlstrom and Counts 1955). Total spawning biomass was later estimated from ichthyoplankton samples as 2–3.5 million metric tons (Ahlstrom 1968).

Before the commercial hake fishery was fully established, Alverson and Larkins (1969) estimated that annual catch rates of 136,000–245,000 metric tons (t) would ensure a sustainable resource. These estimates have proven robust. Mean annual estimates of hake biomass have remained at approximately 2 million t for the past two decades, and the mean annual fishery yield over the past three decades has been 192,000 t (Dorn 1996). Despite extensive efforts to sample population abundance and to model population dynamics, processes influencing the success of hake recruitment are not fully understood.

Empirical evidence suggests that successful recruitment of a hake cohort depends on the interaction of biological and physical processes. Using Marsden square 120-2 January-to-March mean water temperatures, Bailey and Francis (1985) found that in eleven of the warmer than average years (>14.8°C at surface) recruitment was higher than average. In contrast, none of the seven colder than average years (<14.8° at surface) resulted in above average recruitment. Early data (Smith 1975; Bailey 1980) showed that colder water temperatures coincided with southern and offshore shifts in adult hake spawning, but it is uncertain whether the absence of large cohorts born during "cold years" is a direct or an indirect result of water temperature (cf. deYoung and Rose 1993).

Another mechanism influencing recruitment is demographic population structure. Shifts in population structure due to fishing mortality reduce the proportion of older and larger adults. A potential consequence of changing population structure is a shift in the location and extent of adult hake spawning (cf. McCall 1990; Hutchings and Myers 1994). Bailey and Francis (1985) recognized the importance of physical-biological coupling

to hake recruitment and recommended an examination of "temporal and spatial variability in [hake] spawning related to environmental conditions." Quantifying variability in hake recruitment success may improve precision of population abundance estimates.

Precision of population estimates depends on spatial and temporal scales of measurement. Scale-dependence in the variability of biological quantities such as population density is best summarized in a plot of variance as a function of spatial and temporal scale (e.g., Haury et al. 1978). This approach explicitly diagrams variability in a quantity of interest across a range of scales rather than concentrating on time and space scales of anthropocentric convenience (Smith 1978). The relative importance of biological and physical processes influencing the magnitude of biological variance can then be plotted as a set of dimensionless ratios over the same range of scales by means of a Lagrangian (Horne and Schneider 1994) or Eulerian frame of reference. This technique diagrammatically summarizes ranges of scales over which concomitant processes dominate. This approach has not been used to examine processes influencing the recruitment of a commercially important fish species.

We use this technique to quantify the relative importance of biological and physical processes that potentially influence the survival of hake as a function of spatial and temporal scale. Results of this analysis prompted further examination of CalCOFI data to determine latitudinal variation in adult spawning activity. Pacific hake was chosen as an illustrative example because recruitment rates can vary over two orders of magnitude in adjacent years (Hollowed 1992; Dorn et al. 1993); it has the largest biomass of any fish species in its latitudinal range (25° to 55° north); it has a 37-year series of recruitment rates; and it has been monitored at spawning time since 1951.

METHODS

Analyses in this study can be divided in two parts. First, we qualitatively summarize the influence of physical and biological processes on changes in larval and juvenile hake biomass as a function of spatial and temporal scale. Values of dimensionless ratios are plotted and contoured in rate diagrams. A second set of analyses uses CalCOFI hake data from 1951 through 1984 to estimate the median position of larval hake distribution from cumulative abundance data as an index of adult mid-spawning latitude. Bootstrap techniques are then used to examine the utility of these estimates under variable sampling effort. Larval surveys were not conducted in 1967–68, 1970–71, 1973–74, 1976–77, 1979–80, and 1982–83. Quarterly larval surveys did not cover the usual latitudinal extent in 1985–94.

Rate Diagrams

Quantities of interest in this study are concentrations of larval B_l and juvenile B_j hake biomass in the eastern Pacific. We use a Eularian perspective and fix the frame of reference to encompass the total spawning and nursery area of hake in the eastern Pacific. Following the notation of Schneider et al. (1997), biomass concentration B is defined as the number N of organisms times the average mass of an individual M per unit volume V. Local change in biomass concentration is defined as

$$\frac{\partial B}{\partial t} = \frac{\partial M \cdot N}{\partial t} \qquad (1)$$

Applying the conservation equation to an infinitesimally small water volume results in a local rate of change in the concentration of biomass defined by convergent or divergent movement of biomass, the density of the net reproductive rate R, and somatic growth rate M_0:

$$\frac{\partial B}{\partial t} = -\nabla \cdot (\mathbf{u}B) + M \cdot R + M_0 \cdot N \qquad (2)$$

where $\mathbf{u}B$ is the flux of biomass through a volume per unit time, expressed as the product of biomass concentration B and a velocity vector $\mathbf{u}$ with components u,v,w in two horizontal (x,y) and one vertical (z) direction. If mass flux differs between two locations, a gradient is formed and biomass will converge or diverge between points. The term ∇ is a gradient operator (see Dutton 1975; ch. 5) with components $\frac{\partial}{\partial x}$, $\frac{\partial}{\partial y}$, and $\frac{\partial}{\partial z}$ in the x, y, and z directions. When combined, the term $\nabla \cdot (\mathbf{u}B)$ is the mass flux gradient that describes the accumulation or loss of biomass due to organism movement. Changes in the concentration of biomass are also due to changes in the net reproductive mass rate $M \cdot R$ and somatic growth rate $M_0 \cdot N$, where M_0 is change in mass per unit time and N is the population abundance.

Since organisms are discrete entities, calculations are simplified by partitioning the volume into small parcels and averaging variables within the volume. Integrating over volume V:

$$\int_V \frac{\partial B}{\partial t} dV = -\int_V \nabla \cdot (\mathbf{u}B) + \int_V M \cdot R dV + \int_V M_0 \cdot N dV \qquad (3)$$

or

$$\frac{\partial B}{\partial t} = -B_s \frac{\partial V}{\partial t} + \oint \mathbf{n}(\mathbf{u}B) dA + M \cdot R + M_0 \cdot N \qquad (4)$$

Equation 4 states that the local change in biomass within the volume is equal to the expansion or contraction of the volume occupied, the flux of organisms through boundaries of the volume, the net reproductive rate, and the somatic growth rate. In equation 4, B_s is biomass at

the surface of the volume; $\oint$ represents the surface integral; **n** is a unit vector perpendicular to the surface; **u**B is the biomass density flux across the surface; and dA is the area of the flux.

When the equation is divided by B, the local change in biomass concentration is described by the expansion or contraction of the occupied volume, immigration or emigration across the outer boundary, somatic growth, and demographics.

$$\frac{1}{B}\frac{\partial B}{\partial t} = -\frac{B_s}{B}\frac{\partial V}{\partial t} + \frac{1}{B}\oint(\mathbf{u}B)\,dA + \frac{1}{B}M\cdot R + \frac{1}{B}M_0\cdot N \tag{5}$$

Since $B = M\cdot N$ then

$$\frac{1}{B}\frac{\partial B}{\partial t} = -\frac{B_s}{B}\frac{\partial V}{\partial t} + \frac{1}{B}\oint(\mathbf{u}B)\,dA + \frac{R}{N} + \frac{M_0}{M} \tag{6}$$

where $\frac{R}{N}$ and $\frac{M_0}{M}$ are the per capita reproductive and growth rates. To simplify, each term is represented by a single symbol:

$$\underset{\text{biomass distribution}}{\dot{B}_0} = \underset{\text{volume occupied}}{-\dot{V}} + \underset{\text{flux}}{F} + \underset{\text{demographics}}{r} + \underset{\text{growth}}{m} \tag{7}$$

Some of the terms in this equation can be further partitioned. Changes in biomass concentration in the two kinematic terms, $\dot{V}$ and F, can be categorized by changes due to passive drift with the surrounding fluid and by changes due to organism locomotion.

$$-\dot{V} + F = -\dot{V}_{fl} - \dot{V}_{loc} + F_{fl} + F_{loc} \tag{8}$$

The demographic term r can be categorized into the per capita birth rate r_b and the per capita death rate r_d. If data exist, the per capita death rate can be further partitioned into natural r_n, predatory r_p, and harvesting r_h mortality.

$$r = r_b - r_n - r_p - r_h \tag{9}$$

To determine the relative importance of these biological and physical sources of variation, dimensionless ratios (cf. Taylor 1974; Langhaar 1980) were formed with terms in equations 7 through 9. If all terms have the same units, ratios can be formed in any combination relative to a process of interest (e.g., Schneider 1992), in functional groups (Fischer et al. 1979), or through biological reasoning.

The first ratio of interest is the comparison of somatic growth to changes in population dynamics. In this study the range of observation is set to encompass total spawning and brood areas used by hake in the eastern Pacific over the last three decades, and does not change. This eliminates any change in biomass concentration due to changes in total volume occupied $\dot{V}$, and the term goes to zero. The resulting population dynamics term is a combination of recruitment and flux of individuals in or out of the population.

$$\frac{m}{r-F} \tag{10}$$

The second ratio evaluates the relative importance of population dynamic processes by comparing demographic r to kinematic F terms.

$$\frac{r}{F} \tag{11}$$

A demographic ratio compares changes in biomass due to recruitment with those due to mortality.

$$\frac{r_b}{r_d} \tag{12}$$

Sources of mortality will not be partitioned in this study. The fourth ratio examines the relative importance of kinematic terms. Flux in biomass due to organism locomotion F_{loc} is compared to that due to passive drift with the fluid F_{fl}.

$$\frac{F_{loc}}{F_{fl}} \tag{13}$$

Where possible, values for each ratio were calculated at discrete spatiotemporal scales for larval and juvenile hake from available hake data and published velocities of the California Current system. Additional values of dimensionless ratios were estimated from physiological limits. Order of magnitude calculations showed whether the absolute value of any dimensionless ratio was less than, equal to, or greater than 1 at a specified spatiotemporal scale. Nominal values (<1, =1, >1) for each ratio were plotted in rate diagrams as a function of spatial and temporal scale for larval and juvenile hake. Ratio values <1 indicate the predominance of processes in the denominator; values =1 indicate a potential interaction between processes in the numerator and denominator; and values >1 indicate that processes in the numerator prevail over those in the denominator. Contour lines drawn on rate diagrams indicate spatial and temporal scales where dimensionless ratios change value. Dotted lines extend contours across the range of scales lacking data to mark boundaries where ratios are believed to change value. The construction of a rate diagram is an iterative process. Ratio values and contour locations should be adjusted as additional data become available.

Hake Movement and Spawning

In this study we arbitrarily define the spawning and brood boxes as the area encompassed by a southern

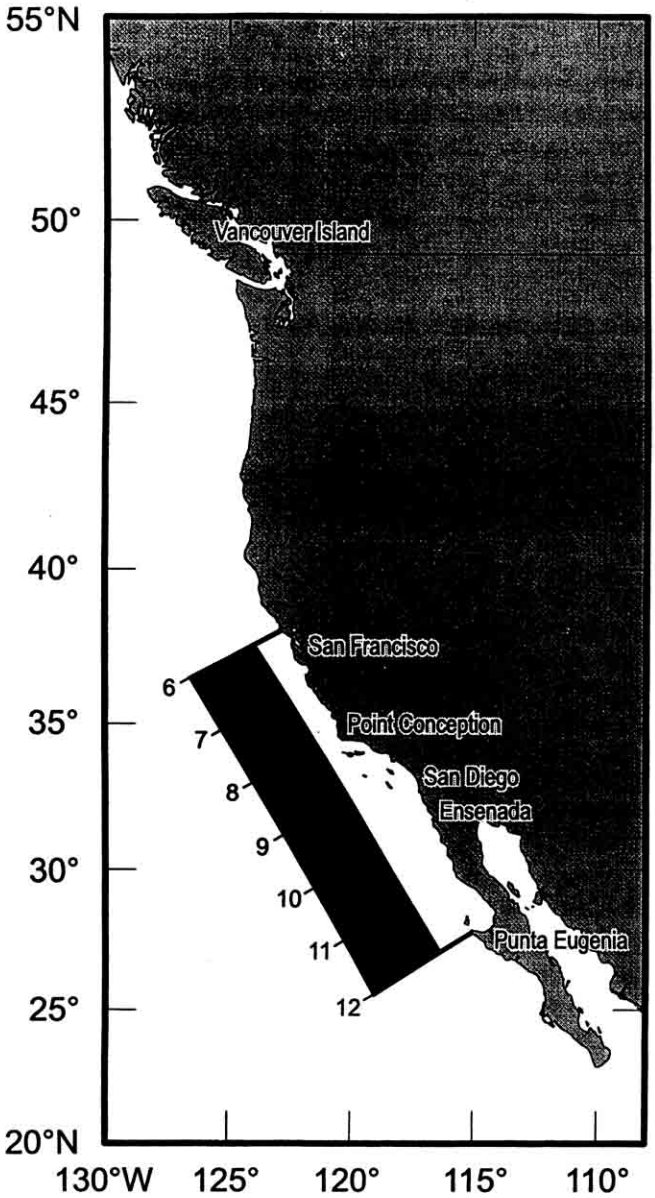

Figure 1. Pacific hake larval and juvenile habitat within the CalCOFI basic station plan. The arbitrary spawning area is shaded and extends from San Francisco (line 60) in the north to Punta Eugenia (line 120) in the south. The seaward boundary is set at station 120. The clear zone represents the brood area of older larvae and juveniles at the time of recruiting to the coastal slope and shelf habitat. The brood area boundary is set at station 60. The numbers at the left margin of the shaded habitat represent the latitudinal zones into which larval abundance is assembled for illustrating interannual changes in cumulative abundance from north to south.

boundary set at Punta Eugenia (line 120), a northern boundary at San Francisco (line 60), a seaward boundary at station 120, and the larval-juvenile boundary at station 60 (figure 1). We summarize the annual adult migration as 50% (183 days) in the feeding area, 39% (142 days) in transit and resident in the spawning area, and 11% (40 days) in transit to the adult feeding area. All spawning is assumed to occur within zones 6 to 12 (figure 1). We also assume that spawning rates per adult female and survival rates of eggs and larvae are constant. Larvae are defined as fish smaller than 20 mm (Smith 1995; Ambrose 1996).

We have further assumed that active swimming by adults and passive transport of eggs and larvae with water currents are uniform. Although not all swimming by adults results in progress toward the spawning area, we estimate that the distance traveled is 1,100 km and the rate of progress is 20 cm per second, or nominally 0.4 body lengths (bl) per second. Neither the stimuli to which the hake respond while migrating nor the stimuli that cause them to stop and spawn are known. What is known is that commercial fishing stops in mid-October and doesn't resume until mid-April (Dorn 1996). Larvae begin to appear in mid-December, and smaller larvae are not readily found after the first week of March (Smith 1995). Northerly movement by adults continues through the feeding season (Dorn 1996).

Owing to the extreme patchiness of hake larvae, we used two nonparametric methods to index adult mid-spawning locations: the median larva position, and bootstrap estimates of mean and variation of estimated annual larval distribution. The median larval index of adult spawning is defined as the 0.5 position of the cumulative proportion of hake larvae in each of six bands between line 60 off San Francisco and line 120 at Bahía Sebastián Vizcaíno. This covers a distance of 1,333 km (720 nautical miles) in a plane parallel to the North American west coast. The midpoint of larval distribution was determined with a precision of 222 km from this cumulative curve and was used as an index of adult mid-spawning location.

To classify annual surveys as warm- or cold-water years, we linearly regressed the annual mid-spawning location against the 100-m water temperature off Point Conception, California. Pacific hake live at depth during spawning. There is a tendency for cold anomalies from the California Current to flow at the surface, and for warmer countercurrent to flow at depth. Given the potential indirect relation between water temperature and hake spawning, we fit a linear function to the data from 19 survey years as an indicative rather than an analytical solution:

$$y = 4111 + 375x \qquad (14)$$

where y is the distance (km) of mid-hake spawning from Point Conception, and x is the water temperature (°C) at 100-m depth off Point Conception. Data from 19 years were used in the regression. The r^2 value of 0.64 has little value given the violated assumption of independent adjacent points and the comparison of values with measurement error in both horizontal and vertical sampling planes. Water temperature as an index of spawn-

ing location was used only to discriminate warm from cold years in figure 4.

Bootstrap estimates of mean spawning location are based on 12,535 stations regularly sampled during January–April from 1951 to 1984 in an area bounded by lines 60 off San Francisco and 116.7 in Bahía Sebastián Vizcaíno off central Baja California, and stations 24.8 and 130. The area extends from the coast to 780 km (421 nautical miles) offshore. Thirty bootstrap sets of 10,000 stations were chosen with replacement. Means and standard errors of spawning location were calculated in the usual way. One advantage of interannual bootstrap estimates of mean spawning location is that the standard error of the estimate is calculable when sampling effort differs among years. Intraseasonal variation in spawning location has been ignored.

Recruitment estimates do not exist for the highest-quality spawning data between 1951 and 1960. Conversely, high-quality data on spawning position have not been collected during the period of the greatest contrasting recruitment rates in the 1980s. For example, spawning data were insufficient to determine mid-spawning location in 1980, when recruitment was highest. Only the second highest recruitment of hake (1984) coincided with a larval survey that permitted calculation of spawning locations. Beginning in 1985, the CalCOFI survey design was changed from one that monitors abundance to one that monitors habitat. Off southern California, this represents approximately one-third of potential hake spawning habitat in an average year.

Estimates of the mid-hake spawning location were compared to subsequent recruitment of age-2 hake from 1958 to 1994, and to the number of recruits per ton of female spawning biomass from 1960 to 1994. Because the temporal and spatial sampling scales of the biological and environmental series differ, it is not appropriate to correlate recruitment with mid-spawning location or a water-temperature index.

RESULTS

Rate Diagrams

The rate diagram of the growth-to-population dynamics ratio (figure 2a) for hake indicates that changes in larval biomass concentration due to somatic growth exceed those due to demographic and flux processes at the scale of a spawning season. From the time that eggs are first laid until larvae are transported out of the spawning area, individual fish biomass increases from approximately 5×10^{-7} kg to 7×10^{-5} kg, or 140% of the birthweight (Smith 1995). Annual recruitment is 100% of the cohort, and virtually all of the biomass fluxes out of the spawning area. The resulting value of the ratio is much greater than one. At daily scales, changes in biomass due to somatic growth are less than those due to demographics and the flux of larvae out of the spawning area. The resulting ratio is less than one.

Changes in larval hake biomass due to demographics at temporal scales larger than an annual cycle are balanced by those due to kinematics in the spawning area (figure 2b). Over an annual cycle, changes in biomass due to active and passive flux ($\simeq$100%) greatly exceed those due to net recruitment ($\simeq$2.21%, see below). On a daily basis during an average spawning season of 76 days, the ratio of recruitment to kinematics is approximately equal. The spawning rate of hake averages 1.3% of eggs per day, and larval mortality averages 13% per day (Smith 1995), resulting in a net recruitment rate of 1.13% per day. Passive flux of larvae from the midline to the eastern boundary of the spawning box (222 km), based on a net eastern transport by the coastal jet (1 cm s^{-1} south) and the California Current (4 cm s^{-1} southeast), is 1.48% per day. If all surviving larvae leave the spawning area, total flux out of the spawning area is 2.21% per day averaged over the spawning season. At the scale of a spawning event, biomass changes due to egg deposition exceed those due to flux of eggs with water currents.

Persistence of a population requires that biomass changes due to somatic growth must equal or exceed those due to mortality at the largest temporal and spatial scales. Since there is a net flux out of the spawning area, the demographic ratio will exceed unity (figure 2c). At the scale of a spawning season (76 days) natality does not exceed 14% $week^{-1}$, and larval mortality is estimated at 13% day^{-1} (Smith 1995). The resulting value of the demographic ratio is less than one. During a spawning event by an aggregation ($\simeq 10^6$ m^2 over a 24-hour cycle) or a spawning pair ($\simeq 10^{-1}$ m^2, minutes), natality exceeds mortality, and the value of the ratio exceeds one. Ratio values are less than one at spatiotemporal scales of an individual organism's dying (seconds, mm^2).

The rate diagram of the kinematics ratio (figure 2d) indicates the dominance of passive flux over active locomotion across most spatiotemporal scales. Fluxes of larvae due to drift with tides, currents, and upwellings exceed fluxes due to active locomotion except over very short time scales. If eggs are released at the midpoint in the northern half of the spawning area, the net drift is 3.8 cm s^{-1} eastward. A total of 67.6 days would elapse for these larvae to drift 222 km to the boundary of the juvenile brood area. Residence time in the spawning area is 102 days (Smith 1995), so an additional 34.4 days can be attributed to active locomotion. There is a net 1% per day movement from the midline of the spawning area to the boundary of the juvenile brood area. The kinematic ratio will exceed unity only at the scale of a larval swimming burst.

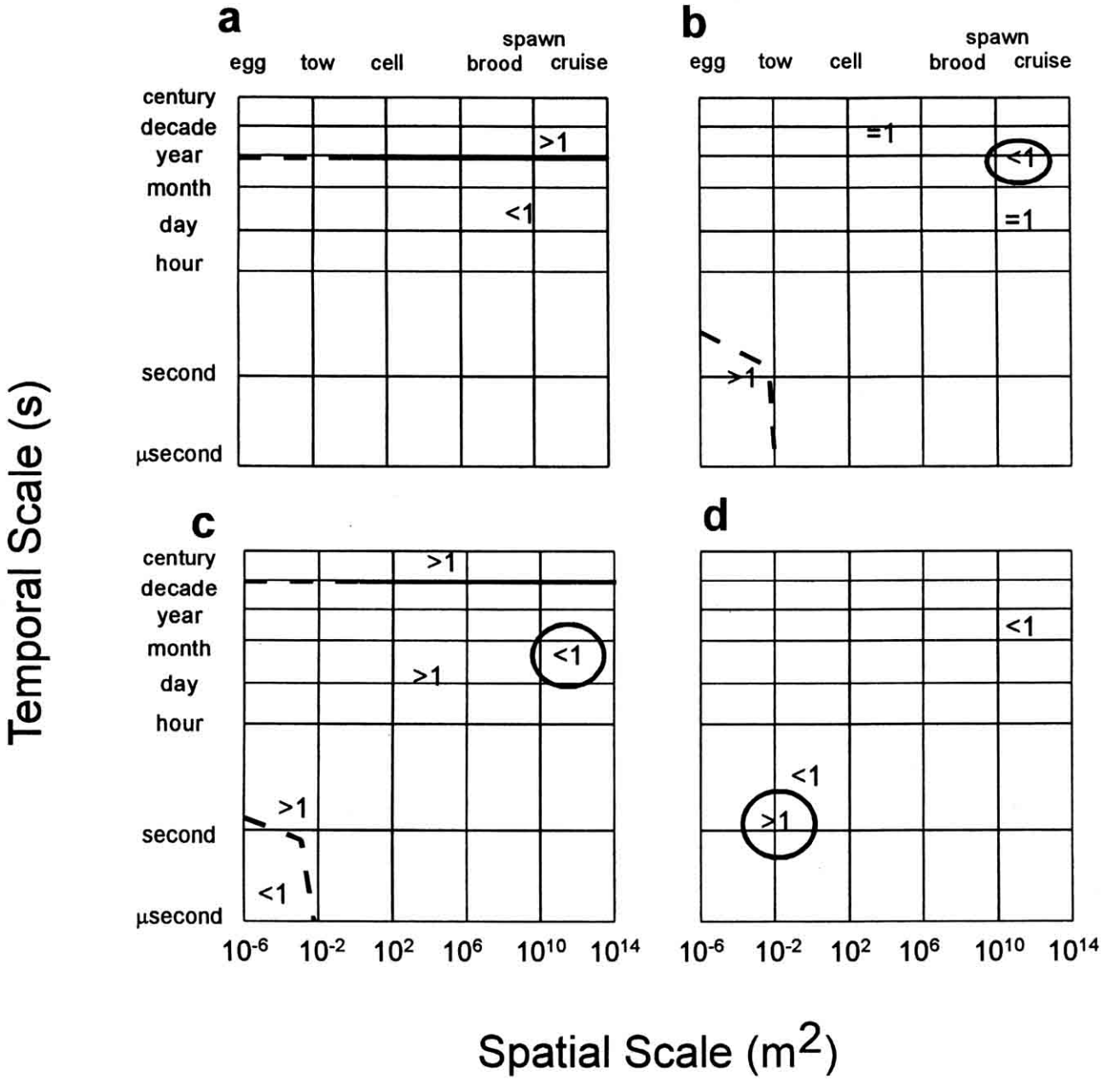

Figure 2. Contoured rate diagrams of dimensionless ratio values for larval Pacific hake (*Merluccius productus*) biomass distribution in the eastern Pacific. Ratio values are contoured less than 1 (<1), equal to 1 (=1), and greater than 1 (>1). *Broken lines* extend contours across scales where data are lacking. Ratio of (*a*) somatic growth to population dynamics (demographics − kinematic fluxes), $m/r - F$; (*b*) demographic (natality, mortality) to kinematic fluxes (passive drift, active locomotion), r/F; (*c*) demographics, r_b/r_d; and (*d*) kinematic fluxes, F_{loc}/F_{fl}.

In the juvenile hake rate diagrams, the growth-to-population-dynamics ratio (figure 3a) is greater than one at the scale of the brood area. Changes in biomass due to somatic growth rate (500% over a two-year residence period; Smith 1995) exceed those due to changes in recruitment (58% mortality) and changes due to active flux (100%) of two-year-old fish to the adult population.

At spatiotemporal scales greater than a brood cycle, the rate diagram of the recruitment-to-flux ratio (figure 3b) indicates that changes in biomass due to the flux of juveniles into and out of the brood area (100% in two years) exceed those due to recruitment (58% mortality by age two; Smith 1995). Even if the flux of larvae into the brood area is considered juvenile "natality," changes in biomass due to natility and mortality do not exceed the net flux of biomass out of the brood area. A newly recruited juvenile hake weighs 7×10^{-5} kg when leaving the spawning area and 0.155 kg at the end of the second year of life (Smith 1995). At temporal scales less than a year, biomass changes due to mortality (41% year 1, 30%

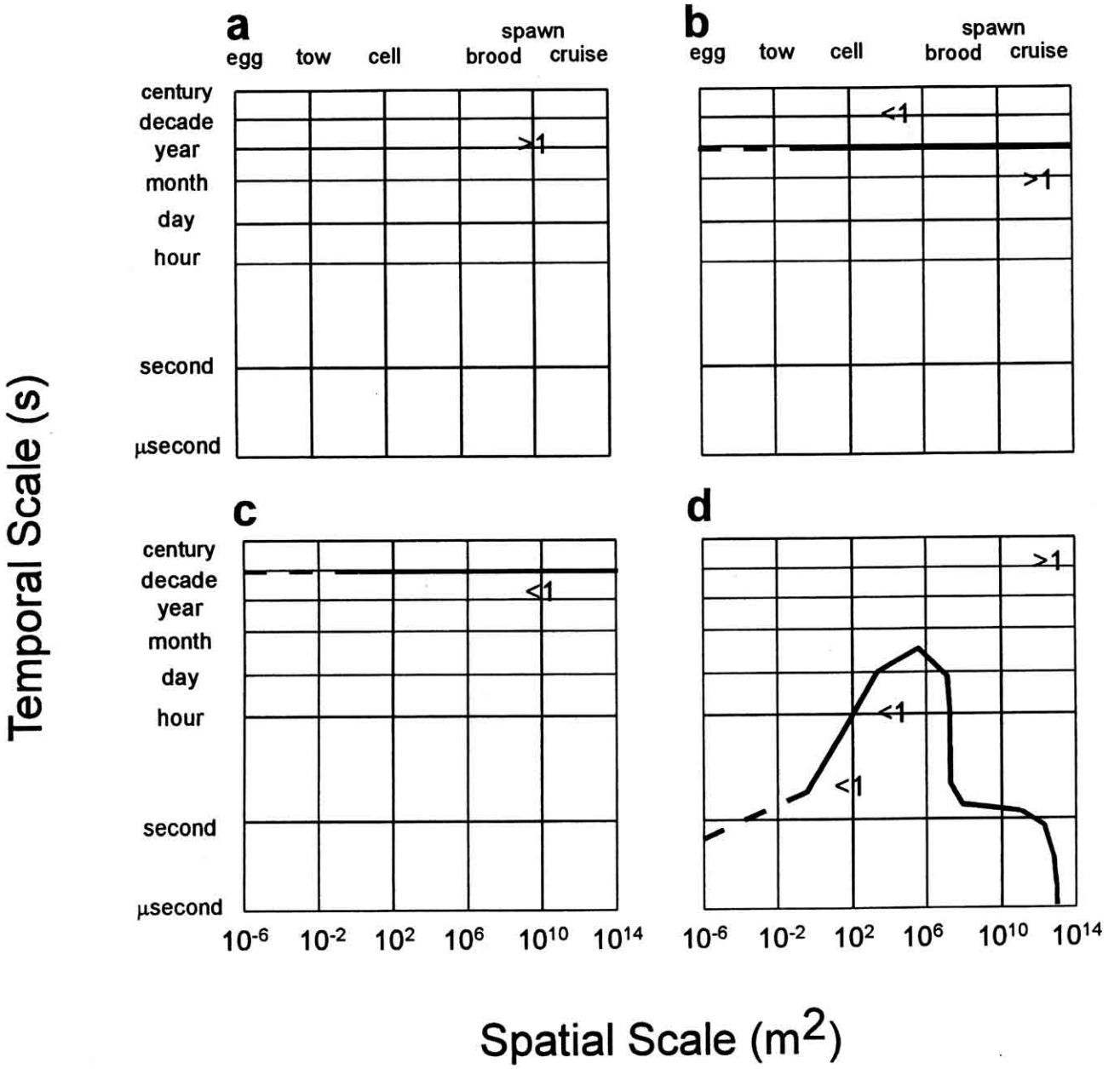

Figure 3. Contoured rate diagrams of dimensionless ratio values for juvenile Pacific hake (*Merluccius productus*) biomass distribution in the eastern Pacific. Ratio values are contoured less than 1 (<1), equal to 1 (=1), and greater than 1 (>1). *Broken lines* extend contours across scales where data are lacking. Ratio of (*a*) somatic growth to population dynamics (demographics − kinematic fluxes), $m/r - F$; (*b*) demographic (natality, mortality) to kinematic fluxes (passive drift, active locomotion), r/F; (*c*) demographics, r_b/r_d; and (*d*) kinematic fluxes, F_{loc}/F_{fl}.

year 2) exceed those due to active or passive flux out of the brood box. The value of the ratio is greater than one.

The demographics rate diagram (figure 3c) depicts a ratio less than one at the scale of a brood cycle. Changes in biomass due to mortality over a biannual residence period will exceed those due to "natality" of juveniles from the spawning area.

The continuous presence of juvenile hake in the brood area over large temporal scales implies that absolute changes in biomass due to active flux exceed those due to drift out of the area with the California Current (figure 3d). Episodic events (e.g., upwellings) and large-scale water movements (e.g., currents) will change the value of the ratio to less than one over shorter temporal scales throughout the brood area.

In summary, processes that influence changes in hake biomass switch between the spawning and brood areas at the scale of a spawning season. Changes in larval hake biomass are dominated by mortality and drift with prevailing currents. Location of adult spawning is therefore

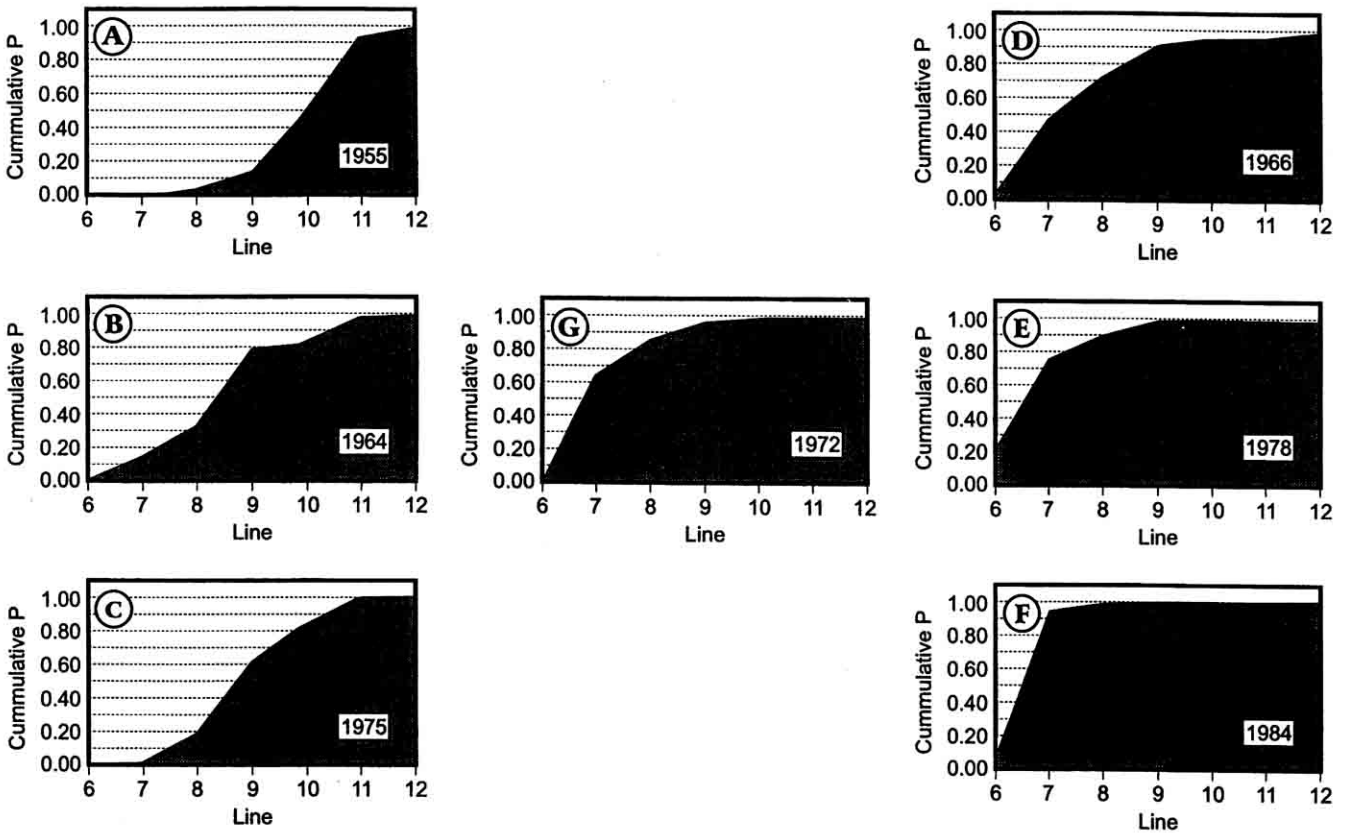

Figure 4. Cumulative frequency distributions of hake spawning location as a function of latitudinal zone. Colder than average (<10°C) water temperatures at 100-m depth at Point Conception occurred during 1955 (*A*), 1964 (*B*), and 1975 (*C*). Warmer than average temperatures occurred during 1966 (*D*), 1978 (*E*), and 1984 (*F*). In 1984, hake spawning was reported north of the CalCOFI sampling grid off the coast of Oregon (Hollowed 1992). Fisheries analysis indicates that the largest year class on record recruited from 1984. The cumulative diagram from 1972 (*G*) shows an exceptional year in which hake spawning appeared to show a Southern Hemisphere El Niño response even though the surface temperature in the Northern Hemisphere eastern boundary did not (see text).

important to survival of individual hake. Changes in juvenile biomass are influenced more by changes due to somatic growth and to active locomotion.

Latitudinal Spawning Variation

The latitudinal distribution of hake larvae exhibits readily observable interannual changes (figure 4). Logistic constraints on survey frequency and latitudinal coverage probably underestimate the extent but not the nature of the variance in larval hake distribution and, by inference, adult spawning position. For example, in 1955, 1964, and 1975 (figure 4A–C) appreciable spawning activity occurred between lines 11 and 12. This suggests that there could have been considerable spawning south of the fully sampled area. By the same reasoning, in 1966, 1978, and 1984 (figure 4D–F) there is an indication that spawning occurred poleward of the CalCOFI survey. Spawning poleward of the survey area may have increased since 1984, but there are too few samples north of line 8 to quantify the trend.

The bootstrap time series of the midpoint of hake spawning is shown in figure 5. The best sampled segments of the time series (1951–61) show appreciable interannual continuity in changes of the center of spawning toward the equator (1952–55) and toward the pole (1955–59). Other latitudinal trends toward the pole occurred during 1964–69 and toward the equator during 1980–83. It is particularly notable that adjacent years are relatively similar and that no extreme northern spawning years are followed by extreme southern spawning years. Extreme changes in position of spawning never occurred in less than a three-year period. The overall trend of the time series is a poleward movement of approximately 444 km (240 nautical miles) over 34 years (1951–84). Standard errors of bootstrap estimates increase over time because of reduced sampling effort in both time and space.

Neither the time series of absolute recruitment of age-two hake (figure 6) nor the time series of hake recruitment per unit of female spawning biomass (figure 7) parallels trends observed in the hake latitudinal spawning position time series (figure 5). Single year spikes, defined as a doubling of recruitment in preceding and succeeding years, occurred in 1961, 1970, 1977, 1980,

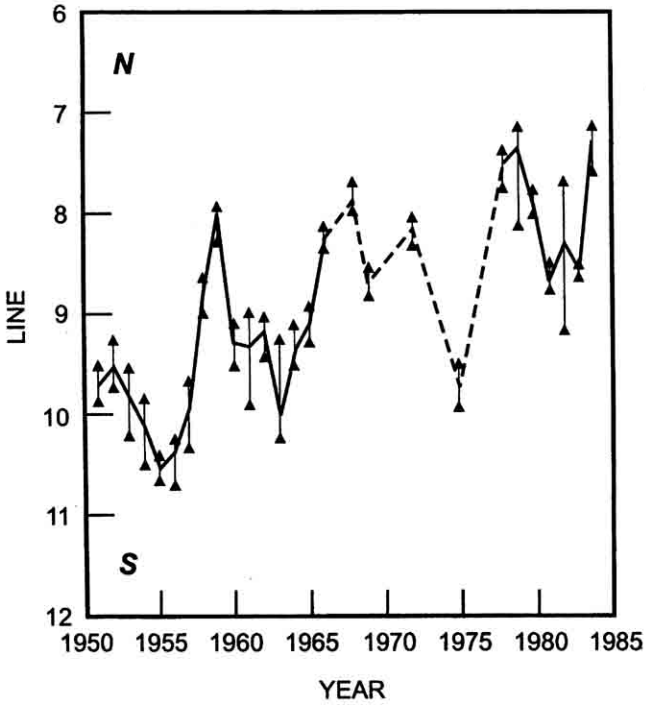

Figure 5. Bootstrap time series of hake larvae position (mean ± 2 SE). The numbers on the ordinate refer to positions along the coast (figure 1), with lower line numbers at the northern end (*N*) and higher numbers at the southern end (*S*). The *broken line* from 1965 to 1978 indicates years when annual surveys were not conducted. Surveys of larval hake were conducted two to four times during the spawning season in 1951–60, and triennially from 1966 to 1984. Larval surveys were not conducted in 1967, 1970–71, 1973–74, or 1976–77. Single surveys covering most of the latitudinal extent shown in figure 1 were conducted in 1968, 1979–80, and 1982–83. Quarterly larval surveys since 1985 have covered only the southern one-third of section 7, all of section 8, and the northern two-thirds of section 9, and therefore are not comparable.

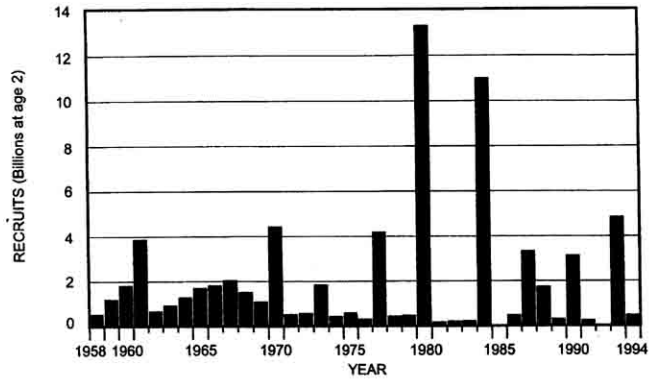

Figure 6. Estimates of absolute age-2 recruitment (billions) of hake, based on appendix table 9 in Dorn 1996.

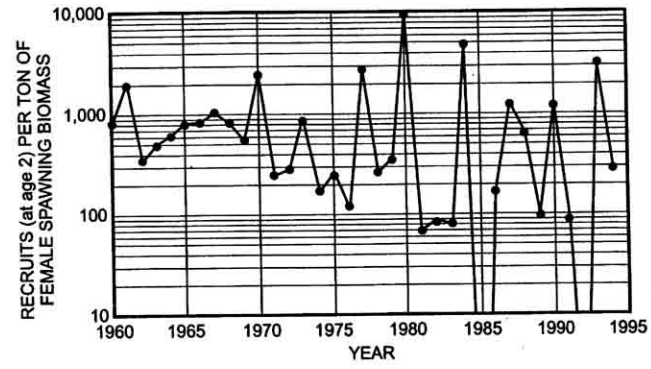

Figure 7. Recruitment rate of hake as recruits per ton of female spawning biomass, based on appendix table 9 in Dorn 1996. Hake recruits from the cohorts of 1985 and 1992 were virtually undetectable.

1984, 1987, 1990, and 1993. It appears that two to three years of poor recruitment follow each year of highly successful recruitment.

DISCUSSION

Identifying sources of variability in the recruitment of commercially important aquatic resources continues as a dominant theme in fisheries research. Variability in the survival of pre-recruit animals is accepted as a major influence on the size of adult population. Recruitment variability studies have examined biological (e.g., Ricker 1954; Beverton and Holt 1957), physical (e.g., Cushing 1980; Smith and Eppley 1982; Koslow 1984), or a combination of biological and physical (e.g., Lasker 1975; Sissenwine 1984; Rothschild 1986) processes that influence mortality and survival of larval and juvenile life stages.

Inferring causality from correlations between single environmental variables and biological responses deserves the bad reputation that Gulland (1953) gave it in the early days of fisheries hydrography. This problem has been accentuated by the massive availability of environmental data, personal computers, and exploratory statistical programs. It may become routine to explore many data series where at least one would contain a "significant" relationship at the 95% level. To illustrate using an example of hake and water temperature, the 1972 surface temperature in the Southern California Bight was the lowest since 1951. But surface temperature was not indicative of hake spawning activity, because the 100-m temperature at Point Conception was among the warmest recorded and coincided with the most northerly spawning of the Pacific hake (figure 4G).

An alternative to simple correlative analyses is to propose models of suitable complexity that reflect variability observed in biological quantities. To continue the hake and temperature example, the secular rise in California Current surface temperature could be characterized by sea level (Roemmich 1992), West Wind Drift (Chelton and Davis 1982), or coastally trapped waves (Enfield and Allen 1980; Pares-Sierra and O'Brien 1989; White 1994). If the usual range of the hake annual migration is 1,100 km and a linear regression model predicts a 375-km shift in the center of spawning distribution for each degree of change in water tempera-

ture at 100-m depth off Point Conception, then one could examine how variability in the California Current and the accompanying changes in water temperature affect hake spawning activity. One could also evaluate the consequences of variable coastal water flow during the southward and northward adult migrations. The adults could be swimming (1) against the current both ways, (2) with the current both ways, (3) with the current on the way to the spawning grounds and against it to the feeding grounds, or (4) against the current on the way to the spawning grounds and with it to the feeding grounds.

For this study we use rate diagrams to identify processes that influence the production, survival, and growth of hake larvae into juveniles from November through March when adults are in the spawning area. The relative importance of biological and physical processes to the survival and growth of adult hake is not evaluated. We surmise that the adaptive value of spawning at the southern limit of "hake habitat" is fast growth of embryos and larvae, and that the adaptive value of the northern end of the habitat is faster adult growth in the productive waters of the subarctic. Northward migration by adults after spawning is an attempt to seek larger and richer feeding grounds than those found off central California and Baja California. We infer support for this strategy from Robinson et al. (1993), who found that 90% of the productivity in British Columbian waters occurs during the upwelling months of April through October.

The use of rate diagrams avoids assumptions that single biological or physical processes are linked to observed patterns at any scale of interest and that biological and physical processes are coupled at characteristic spatial and temporal scales. Rate diagrams contain nominal values of dimensionless ratios that indicate the relative importance of two or more processes based on published knowledge, available data, and biological reasoning. Rate diagrams can be used to summarize current knowledge of spatial and temporal dynamics, to identify cogent space and time scales for any life-history stage in process-oriented research, and to identify processes that may influence distribution patterns over the range of scales where they dominate (Hatcher et al. 1987; Horne and Schneider 1994).

The application of rate diagrams to research design is best illustrated by example. It is relevant to ask, "Is drift important to the recruitment of hake, and if so, over what scales should drift be examined?" From hake life history we know that the adult spawning season lasts approximately 76 days each year and occurs offshore from the San Francisco area in the north to Baja California in the south. The northern and southern limits of spawning shift among years, but suitable spawning habitat is assumed along the length of the coast. If we assume that all initial larval movement inshore is net drift with currents, then potential larval transport is 3.87 cm s^{-1}, or 3.34 km day^{-1}. The spawning box covers an area of approximately 600,000 km^2. At the spatiotemporal scale of a spawning season, the rate diagram of larval growth to population dynamics ratio (figure 2a) indicates that demographic and kinematic processes are more important than growth processes. The ratio of demographic to kinematic rates (figure 2b) is less than one, although at smaller temporal scales demographic and kinematic processes may be important to the recruitment of hake. Further comparison shows that kinematic processes are dominated by flux out of the spawning area (figure 2d) and that mortality exceeds changes in biomass due to natality (figure 2c). When the focus is shifted to juvenile hake, changes in biomass due to somatic growth exceed those due to drift with currents (figure 3a). Over the course of a spawning season, research effort should focus on larval movement and mortality at scales of one day and more than one kilometer.

It is also important to realize what rate diagrams do not provide. Examining relative rates of biological and physical processes as a function of spatial and temporal scale results in dimensionless ratio values that are independent of geographic location and clock time. Dimensionless ratio values are not predictors of organism distribution patterns resulting from physical or biological processes. Rate diagrams have yet to be incorporated into models for predicting abundance or recruitment but can be used to identify important terms for inclusion across any range of scales.

Rate diagrams can be constructed from a Eularian (fixed) or Lagrangian (moving) perspective. The choice of perspective will influence terms that are included in the equation and terms used to form dimensionless ratios. Schneider (1991, 1993) and Horne and Schneider (1994) used a Lagrangian perspective to examine rates of change in aerial or volumetric distributions of marine bird, fish, and zooplankton biomass as a function of temporal and spatial scale. The difference in the Lagrangian formulation is that kinematic terms in the equation describing all potential variance-generating processes do not include fluxes of organisms or biomass. A moving perspective does not incorporate the crossing of outer boundaries by organisms within the volume of interest. Outer boundaries expand and contract to contain all organisms. The Eularian perspective used in this study allows us to quantify the flux of hake out of the spawning grounds, and the northern flux of juveniles into the feeding grounds. We arbitrarily set the outer limits of the spawning and brood areas to encompass all latitudinal variation in adult spawning due to variability in water temperature.

Water temperature is used as an index of important changes in absolute recruitment (figure 6) and recruitment rates per unit of spawning hake female (figure 7). Of the 61 billion recruits spawned during the 37 years from 1958 to 1994, 29 billion came from the three most successful years (1980, 1984, 1993) and less than 0.2 billion from the three least successful years (1981, 1985, 1992). Recruitment during the 16 years that were considered cold-water years averaged 0.8 billion recruits per year. An average 2.5 billion hake per year recruited during the 20 years considered warm-water years. Fishery yield models that use Los Angeles Bight surface temperatures have demonstrated that yields of 150,000 tons can be increased to 200,000 tons during higher-temperature years (Francis et al. 1982). Higher-temperature years were defined as those with annual average sea-surface temperature in the Southern California Bight between 15.67° and 16.81°C in the years 1931–79. The year 1970 was labeled warm at 15.46° because of the recruitment of a large hake year class from a small spawning biomass compared to small hake year classes at temperatures ranging from 13.5° to 15.59° (Francis et al. 1982). Unfortunately, predictions of hake recruitment based on water temperatures do not follow the same trend. Warm-water years tend to persist, but no large hake recruitment has consecutively followed a large hake recruitment (Smith 1995, appendix table 9; Dorn 1996). These order-of-magnitude changes in cohort success have been independent of the adult population size (Bailey 1981).

Present estimates of allowable Pacific hake catch are influenced by the success of hake recruitment since 1980. Extraordinary recruitment of the 1980, 1984, and 1993 cohorts coincides with the fundamental oceanic change in the Pacific (Venrick et al. 1987; Beamish 1995; Polovina et al. 1995). Before the 1975 transition, hake catches were more variable and ranged from 103,000 to 234,000 metric tons. Since 1975, catches have ranged from 90,000 to 359,000 metric tons (Wooster and Hollowed 1995; Dorn 1996).

It is uncertain what the effects of a return to the cold climate of 1950–56 would be in the presence of a fishery. The sustained harvest rates may have to be reduced if adult spawning shifted hundreds of kilometers to the south in response to colder waters or faster California Current flow along the coast. Catches above 10% of the adult spawning stock have only occurred since 1994. A longer migration path implied by cold water temperature may influence natural mortality rates of both adult and juvenile hake. Similarly, reductions in older age classes potentially reduce the occupancy of traditional spawning areas and may reduce the stabilizing factors that sustain the population in larger ocean areas.

Observations of successive recruitment of a large cohort followed by a small cohort suggests that Pacific hake abundance may be regulated by both bottom-up and top-down mechanisms of population control. Since adult abundance, mortality, or growth do not influence cohort variability, massive success of a first cohort is probably due to egg production or high survival of early life stages. Survival of embryonic, larval, or early juvenile hake may depend on temperature and movement of ambient water. Spawning in southerly latitudes has been associated with cold (<10°C) water temperatures at a depth of 100 m off central California. Northward shifts in spawning have been attributed to warming water and the reduction of older hake cohorts (Smith 1972, 1975; Bailey 1980). Since zooplankton crops are higher in cold years relative to those in warm years (figure 23 in Reid et al. 1958), latitudinal shifts in spawning imply that success of a cohort depends on the matching of spawning activity and subsequent larval transport with high plankton production. The absence of suitable food, or expatriation from suitable food may lead to the recruitment of a "typical" rather than a large hake cohort. The failure to produce a large cohort under similar conditions in a subsequent year may be due to increased abundance of predators, including cannibalistic juveniles from previous cohorts. Although there has been insufficient study of intercohort cannibalism, stomach contents of 1+ and 2+ Pacific hake show that when cohorts co-occur, cannibalism is common (Bailey et al. 1982; Buckley and Livingston, 1997).

Cannibalism among successive cohorts may affect hake population dynamics in two opposing ways. The ultimate success of a cohort may depend on the arrival of the subsequent cohort to serve as a food source at the brood area. The ensuing biomass depletion of the younger cohort may be insignificant relative to the biomass of the entire stock, but numeric losses from the younger cohort may have a significant demographic effect on the cohort and, at a larger temporal scale, on the population. Density-dependent population regulation appears to cycle on a bi- or triennial scale. If juvenile hake limit recruitment of succeeding cohorts, it may be advantageous to institute an occasional fishery on juvenile hake. Juvenile fishing mortality on one cohort may increase recruitment of a subsequent cohort through a reduction in density-dependent cannibalism. This might also benefit the rest of the ecosystem by reducing the consumption of euphausiid shrimp and larval or juvenile fishes of other species.

Hake research efforts are often designed to quantify abundances and identify habitat preferences of egg through adult stages. To estimate abundance it is crucial to choose a sampling resolution that will ensure maximum independence of adjacent samples as dictated by the central-limit theorem. Surveys should be designed to improve the discriminating power (precision) by in-

creasing the effective number of samples. If the sampling resolution is less than the autocorrelation lag distance, then adjacent samples are not independent; the standard error of the response variable should be decremented as a function of the autocorrelation; and sampling effort has been wasted. Sampling resolution may change among life-history stages but should not change with location unless distribution patterns differ regionally.

Given the opportunistic history of hake research, it is advantageous to examine how rate diagrams can help design surveys sampling geographic areas or multispecies communities. A simple extension of single-species rate diagrams overlays sets of rate diagrams for all species of interest to determine appropriate sample range and resolution. In an examination of energy flux from prey to seabird predators, Schneider (1995) identified processes that were important at critical time and space scales for marine birds. For sampling cruises in the CalCOFI program, rate diagrams of anchovy (*Engraulis mordax*), sardine (*Sardinops sagax*), and hake could be compared to ensure that samples will detect change in critical processes and extend over the range of a critical process such as the temporal and geographic boundaries of hake spawning activity. The use of rate diagrams during cruise planning should make the allocation of sampling effort less contentious by explicitly defining sampling requirements and highlighting sampling constraints.

ACKNOWLEDGMENTS

We thank Arnold Mantyla and Ron Lynn for discussions relating physical oceanography to Pacific hake migration and recruitment, and John Butler and Geoff Moser for general discussions of hake biology. Thanks also to John Hunter for sustained interest in contrasting deeper-living Pacific hake recruitment series with those of shallow-living Pacific sardine and northern anchovy. Comments by two reviewers and editorial work by Anne Hollowed resulted in a more cogent text. Faults in interpretation remain those of the authors. This work was supported in part by the National Science Foundation (OCE-941-5740).

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