

Spatial dynamics of anchovy, sardine, and hake pre-recruit stages in the California Current

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Three genera, *Engraulis*, *Sardinops*, and *Merlucciu* have coincident spawning and juvenile brood areas in most eastern and western boundary currents throughout the world. The CalCOFI survey program has amassed a 50-year data series on location and timing of spawning and the resultant recruitment of anchovy, sardine, and hake in the California Current region. Use of existing Lefkovich matrix population projection models for these three species allows evaluation of the spatial and temporal scales that govern the biological and physical interactions. We present rate diagrams for hake and construct comparable diagrams for anchovy and sardine in a common, variable environment. Rate diagrams depict the relative importance of demographic (natality and mortality), growth, and kinematic (passive and active movement) processes to a quantity of interest as a function of spatial and temporal scale. Results confirm that the scale of observations will have to be manipulated to expose the importance of any combination of processes for life history stages among these species. Field sampling systems have not yet responded adequately to mesoscale features (50 km) persisting over months.

Keywords: anchovy (*Engraulis mordax*), sardine (*Sardinops sagax*), hake (*Merluccius productus*), whiting, fish larvae, juvenile fish, rate diagrams, dimensionless ratios, Eulerian, immigration, emigration, somatic growth, demographics, kinematics.

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Introduction

The relationships among time and space scales of a phenomenon and the observations designed to interpret them are nowhere more intimate than in the life cycle of pelagic schooling fishes. Reproduction begins with external fertilization of eggs at the scale of micrometers and minutes and cycles of reproductive success at the scale of thousands of kilometers and decades. For Pacific sardine (*Sardinops sagax*) (Ahlstrom, 1965) and northern anchovy (*Engraulis mordax*) (Smith, 1981; Methot, 1983; Peterman *et al.*, 1988), it has been noted that the annual abundance of large larvae does not match recruitment success. In Pacific hake (*Merluccius productus*), recruitment success may be indicated earlier in development (Hollowed, 1992). These findings are based on pelagic surveys aimed at the assessment of the

adult spawning biomass rather than of the survival and growth of the ensuing year class. Recruitment prediction must incorporate features of transport, the immediate feeding environment, and growth and mortality rates of the pre-recruits to evaluate the areas from which recruits are likely to come. Since recruitment surveys will involve different sampling gear, dynamic analysis of environmental data at several scales, and extended ship time, the added costs should be minimized by first getting a sense of time and space scales of the recruitment process.

Studies of recruitment processes have accelerated with the increase in numbers, types, and locales of fisheries that are subjected to stock assessments and management, and with the expansion of the available time-series (Myers and Mertz, 1998). For the most part, the emphasis in analysis has been temporal dynamics

[see Riffenburgh (1969) for an early synthesis for anchovy, sardine, and hake]; (Collie and Spencer, 1994; Paulik, 1973). The importance of spatial pattern can be seen in the classic description and analysis of 58 stocks by Hollowed *et al.* (1987), who showed that basin- and regional-scale patterns in recruitment of extreme year classes of many fish species are apparently driven by some common feature of the environment. We now need spatially explicit models and designed observations of the recruitment process (Harris, 1997; Nonacs *et al.*, 1998) to compare the response of overlapping populations to exploitation and a cascade of environmental events at several scales. Recent technological advances make spatially explicit analysis of recruitment dynamics feasible.

The shortage of spatial analyses can now be remedied by using existing information to design new observational systems at defined spatial scales. The habitat of pelagic spawning fish can be defined by remote sensing by satellite and acoustics, and by trawling and pumping of eggs (Checkley *et al.*, 1997). Rates of expatriation can be estimated from knowledge of the depth of distribution, acoustic Doppler current profilers, and radar estimates of surface drift. Buoy observations of the juvenile habitat and eddy-scale oceanographic models with data assimilation in growth models (Brandt *et al.*, 1992; Mason and Brandt, 1996) provide powerful new tools in recruitment observation, analysis, and eventually prediction. Underwater mapping instruments (Rusby *et al.*, 1973; Soria *et al.*, 1996) can track herring schools as small as five tons over ranges of 13 km. Long-range buoy-mounted acoustic imaging (Nero and Huster, 1996) can count juvenile fish, and absorption spectroscopy (Weston and Ching, 1970; Diachok, 1999) can characterize the size distribution of fish over 20+ km sectors of the ocean over months using buoy-mounted multi-frequency arrays. At small scales, feeding encounters at the 10-m scale can be recorded optically and acoustically from towed instruments (McGehee and Jaffe, 1996) and use can be made of imaging ambient noise scattered from fish and plankton (Buckingham *et al.*, 1992).

Population data on a species complex like anchovies, sardines, and hake can be used as a "laboratory" for development of spatial analytical practices. In most temperate coastal habitats in the world, these species share decadal time scales and basin and regional spatial scales. They feed on similar prey for a period of their life cycle (Hand and Berner, 1959; Sumida and Moser, 1980; Loukashkin, 1970). In the California Current habitat, recruitment of anchovy during the period of monitoring has ranged 30-fold (Jacobson and Lo, 1994), of Pacific sardine 60-fold (Barnes *et al.*, 1997), and of hake 100-fold (Dorn and Saunders, 1997). Recent analytical innovations like rate diagrams and population projection matrices allow interpretation of spatially explicit

information. It is likely that persistent field evaluation of pre-recruit abundance and individual growth rates would eventually aid early detection of recruitment changes of this magnitude.

We here use spatially explicit rate diagrams of hake (Horne and Smith, 1997; Horne *et al.*, 1999) to make comparable diagrams for anchovy and sardine. We add to the usual use of dimensionless ratios of growth and reproduction (Beverton, 1992; Charnov and Berrigan, 1991) the use of drift and locomotion to spatially explicit rate diagrams of hake to make comparable diagrams for anchovy and sardine. The three species feed, spawn, and brood juveniles in the same regions. Existing Lefkovich population matrix models provide the demographic ratios for use in space-time explicit models of the life stages and habitats of anchovy and sardine (Lo *et al.*, 1992, 1995) and hake (Smith, 1995).

Materials and methods

The comparisons are based on "skeletal" Lefkovich (1965) stage-based models of anchovy, sardine, and hake populations (Tables 1 and 2). They are derived by collapsing the population information into embryonic, larval, juvenile, and adult stages. The models use rates of maternity (F: female eggs female⁻¹ d⁻¹), mortality (M: daily instantaneous rate), and stage duration (D in days). The demographic output summarizes the production at the beginning of each stage (i.e. natality and growth) and losses during the stage (i.e. mortality).

Larval production rates across the continental shelf were computed as in Horne *et al.* (1999). Briefly, the slope and intercept of an exponential fit to the sizes of larvae in each station grouping were used to establish the instantaneous production and mortality of each species.

We use several procedures to formulate the problem of comparative recruitment variability of the species. One procedure is the rate diagram (Horne and Schneider, 1994; Horne and Smith 1997), which uses a graphic summary of time and space scales that are annotated to exhibit biomass concentrations of larval (Bl) and juvenile (Bj) anchovy, sardine, and hake. Hake results are essentially repeated from Horne and Smith (1997), but slightly modified based on new growth data (Butler and Nishimoto, 1997; Cass-Calay, 1997). The demographic term (r) summarizes the production at the beginning of each stage (r_b : birth) and losses during the stage (r_n : natural mortality; r_h : harvest mortality). The growth term includes information on the somatic growth (m) of individuals within the stage. The volume term (V) and the flux term (F) characterize the changes in the biomass concentration (B_o) due to passive drift (F_{Π}) with the surrounding fluid and active swimming (F_{loc}) due to locomotion.

Table 1. Postulated population parameters (F: fecundity in female eggs per female; M: daily instantaneous mortality in d^{-1} ; D: stage duration in days; W_0 : initial weight in g; L-range: length range in cm).

Stage	F	M	D	W_0	Basis	L-range
Anchovy						
Embryo	0	0.3058	6.5	3.0E-05	Dry	Egg-0.4
Larva	0	0.117	57	2.0E-05	Dry	0.4-3.5
Juvenile	0	0.02085	142	5.0E-02	Dry	3.5-8.5
Adult	245	0.0022	2537	9.0E-01	Dry	8.5-16
Sardine						
Embryo	0	0.3571	7	6.0E-05	Dry	Egg-0.4
Larva	0	0.1115	48	2.0E-05	Dry	0.4-3.5
Juvenile	0	0.01442	405	5.0E-02	Dry	3.5-13.5
Adult	997	0.0011	4009	4.0E+00	Dry	13.5-32
Hake						
Embryo	0	0.135	16	9.05E-04	Live	Egg-0.4
Larva	0	0.076	100	3.05E-04	Live	0.4-2
Juvenile	0	0.00417	602	1.21E-02	Live	2-33.3
Adult	120	0.00055	6570	2.63E+01	Live	33.3-62

Table 2. Background data.

	Anchovy	Sardine	Hake
Spawning season (d; 95%)	251	262	76
Mid-point of spawning	1 Mar	1 May	1 Feb
Larval mortality	0.127%	0.47%	0.05%
Juvenile mortality	5.2%	0.29%	8.0%
Natality	0.4%	0.4%	1.32%
Growth egg to metamorphosis	16 700%	83 333%	1 337%
Growth metamorphosis to maturation	1 800%	800%	217 355%
Current speed (cm/s)	25	25	
Current direction	S	SE	E

Results

Anchovy and sardine

Because the results for anchovy and sardine are similar, they are treated here together. The growth to population dynamics ratio in the larval rate diagrams [Figure 1(a)] indicates that changes in the concentration of biomass due to somatic growth exceed those due to demographic and flux processes at the scale of decades and at the scale of a spawning season. From the time that eggs are laid until larvae metamorphose to juveniles (Table 2), individual anchovy biomass increases by 16 700% and 83 000% of their birth weight, respectively. Annual recruitment is 100% of the cohort and any flux of larvae out of the study box by the California Current is replaced by an import of larval biomass from the north. The resulting value of the ratio is much greater than 1 in both species (16 700/100, 83 000/100, respectively). At daily scales during the spawning season (for duration,

see Table 2), changes in biomass due to somatic growth ($16\% d^{-1}$ for both species) still exceed those due to demographics and the net flux of larvae out of the study area. The ratio remains greater than 1.

Because the net flux of larvae into and out of the study box is set to zero, all values of the demographic to flux ratio [Figure 1(b)] are indeterminate.

Demographics can be examined over the largest range of scales [Figure 1(c)]. Spectral analysis of scale deposition rates of anchovy and sardine show that changes in biomass due to mortality can exceed those due to natality at a century scale (Soutar and Isaacs, 1974; Smith, 1978; Baumgartner *et al.*, 1992). At the scale of an annual spawning season, natality averages $0.4\% d^{-1}$ for both species and larval mortality is estimated at $11\% d^{-1}$ and $0.047\% d^{-1}$, respectively (Table 2). Because there is no flux of larvae out of the spawning area and survivors exist, the resulting value of the demographic ratio is greater than one. During any spawning event, natality exceeds mortality and the value of the ratio

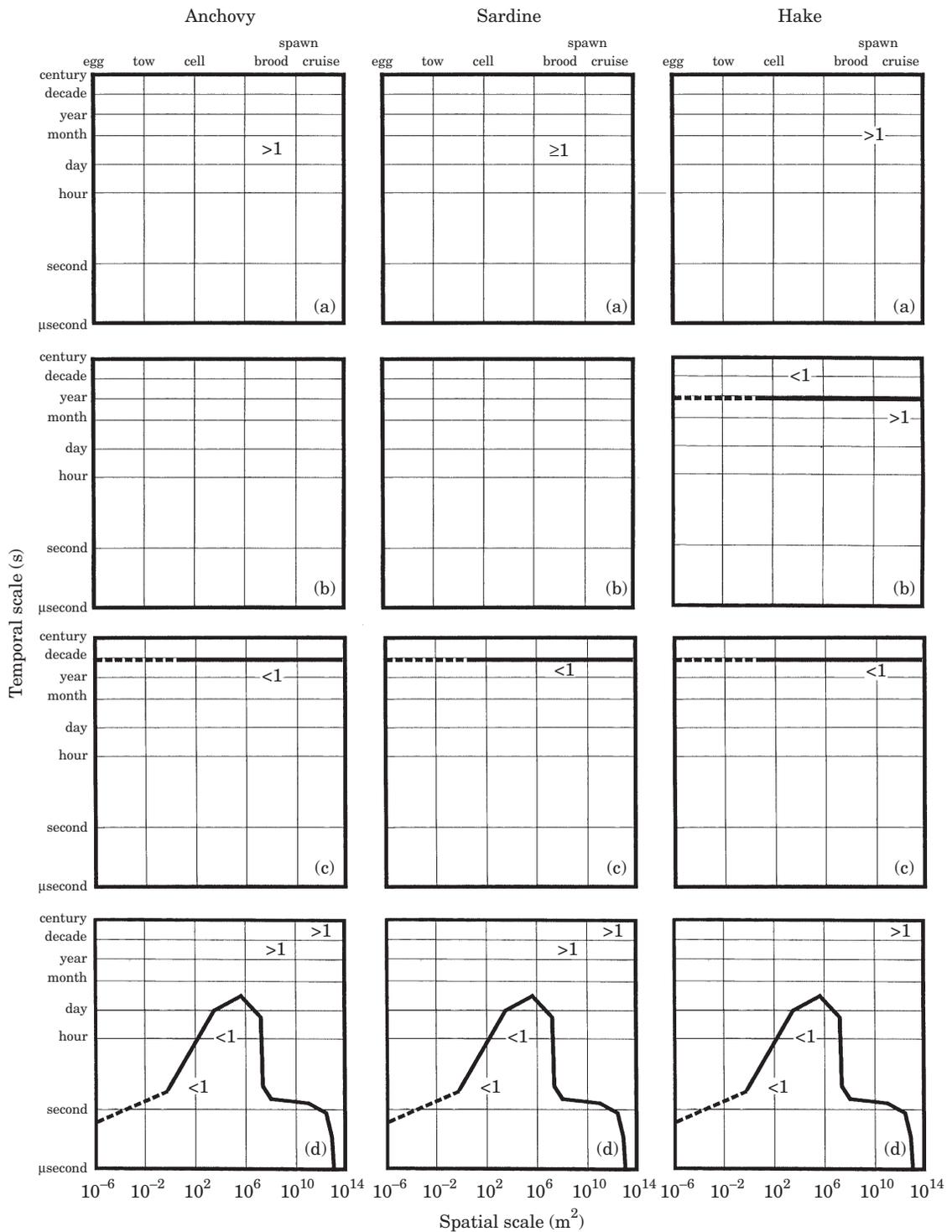


Figure 1. Rate diagrams of (a) somatic growth to population dynamics (demographics/kinematic fluxes; $m/(r \times F)$), (b) natality and mortality to passive drift and active locomotion (demographics/kinematic fluxes; r/F); (c) demographics (r_b/r_d); and (d) kinematic fluxes (F_{loc}/F_n) for larval anchovy, sardine, and Pacific hake biomass distribution in the Eastern Pacific. Ratio values >1 and <1 are contoured. Broken lines extend contours across scales where data are lacking.

exceeds 1. Ratio values are less than 1 at spatio-temporal scales of an individual organism dying (seconds, mm^2).

The rate diagram of the kinematics ratio for larvae [Figure 1(d)] indicates a zero flux into or out of the study box and all values of the ratio are zero.

In the juvenile rate diagrams, the growth to population dynamics ratio [Figure 2(a)] is greater than 1 at the scale of the brood area. Changes in biomass due to somatic growth rate (1800% from metamorphosis to adult weight for anchovy; 800% for sardine) exceed those due to changes in recruitment (5.2% and 0.29% mortality, respectively) and we have arbitrarily set fluxes to zero. Because anchovy and sardine remain along the west coast of North America, we have set the net flux of juveniles into and out of the study box to zero, and all values of the demographic to flux ratio are indeterminate [Figure 2(b)].

The demographics rate diagram [Figure 2(c)] depicts a ratio less than 1 at the scale of the brood cycle. Changes in biomass due to mortality over a juvenile residence period will exceed those due to "natality" of juveniles from the spawning area. At larger scales, it is logical that persistence of adult fish indicates that changes in biomass due to recruitment must equal or exceed those due to mortality.

The continuous presence of juvenile anchovy and sardine within 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 within the California Current [Figure 2(d)]. Episodic events (e.g. upwelling) and large-scale water movements will change the value of the ratio to less than 1 over shorter temporal scales throughout the brood area.

Hake

The rate diagram of growth to population dynamics ratio [Figure 1(a)] indicates that changes in hake 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 laid until larvae are transported out of the spawning area, individual biomass increases by 1340% (Table 2). 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 of biomass to recruitment flux is much greater than 1 (1340/100). At daily scales, changes in biomass due to somatic growth are less than those due to demographics and the net flux of larvae out of the spawning area and the ratio is less than 1.

Changes in larval biomass due to demographics at temporal scales larger than an annual cycle are balanced by those due to kinematics in the spawning area [Figure 1(b)]. Over an annual cycle, changes in biomass due to active and passive flux ($\approx 100\%$) greatly exceed those

due to net recruitment ($\approx 2.21\%$, see below). On a daily basis during an average spawning season of 76 d, 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), which results 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 recruitment must equal or exceed mortality at the largest temporal and spatial scales. Because there is a net flux of hake out of the spawning area, the demographics ratio will exceed unity [Figure 1(c)]. At the scale of a spawning season (76 d), natality does not exceed $14\% \text{ week}^{-1}$ and larval mortality is $13\% \text{ d}^{-1}$ (Smith, 1995). The corresponding demographic ratio is less than 1. During a spawning event by an aggregation ($\approx 10^6 \text{ m}^2$ over a 24-h cycle) or a spawning pair ($\approx 10^{-1} \text{ m}^2$, min), natality exceeds mortality and the value of the ratio exceeds 1. Ratio values are less than 1 at spatio-temporal scales of an individual organism dying (sec, mm^2).

The rate diagram of the kinematics ratio [Figure 1(d)] indicates the dominance of passive flux over active locomotion across most spatio-temporal scales. Fluxes of larvae caused by drift with tides, currents, and upwelling exceed fluxes owing to active locomotion except over very short time scales. If an egg is released at the mid-point in the northern half of the spawning area, the net drift is 3.8 cm s^{-1} eastward. A total of 67.6 d would elapse for these larvae to drift 222 km to the boundary of the juvenile brood area. Residence times in the spawning area are 102 d (Smith, 1995), so an additional 34.4 d 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 only exceed unity at the scale of a larval swimming burst.

In the juvenile rate diagrams, the growth to population dynamics ratio [Figure 2(a)] is >1 at the scale of the brood area. Changes in biomass due to somatic growth rate (220 000% over a 602-d residence period) 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 spatio-temporal scales greater than a brood cycle, the rate diagram of the recruitment to flux ratio [Figure 2(b)] indicates that changes in biomass due to the flux of juveniles into and out of the brood area (100% in two

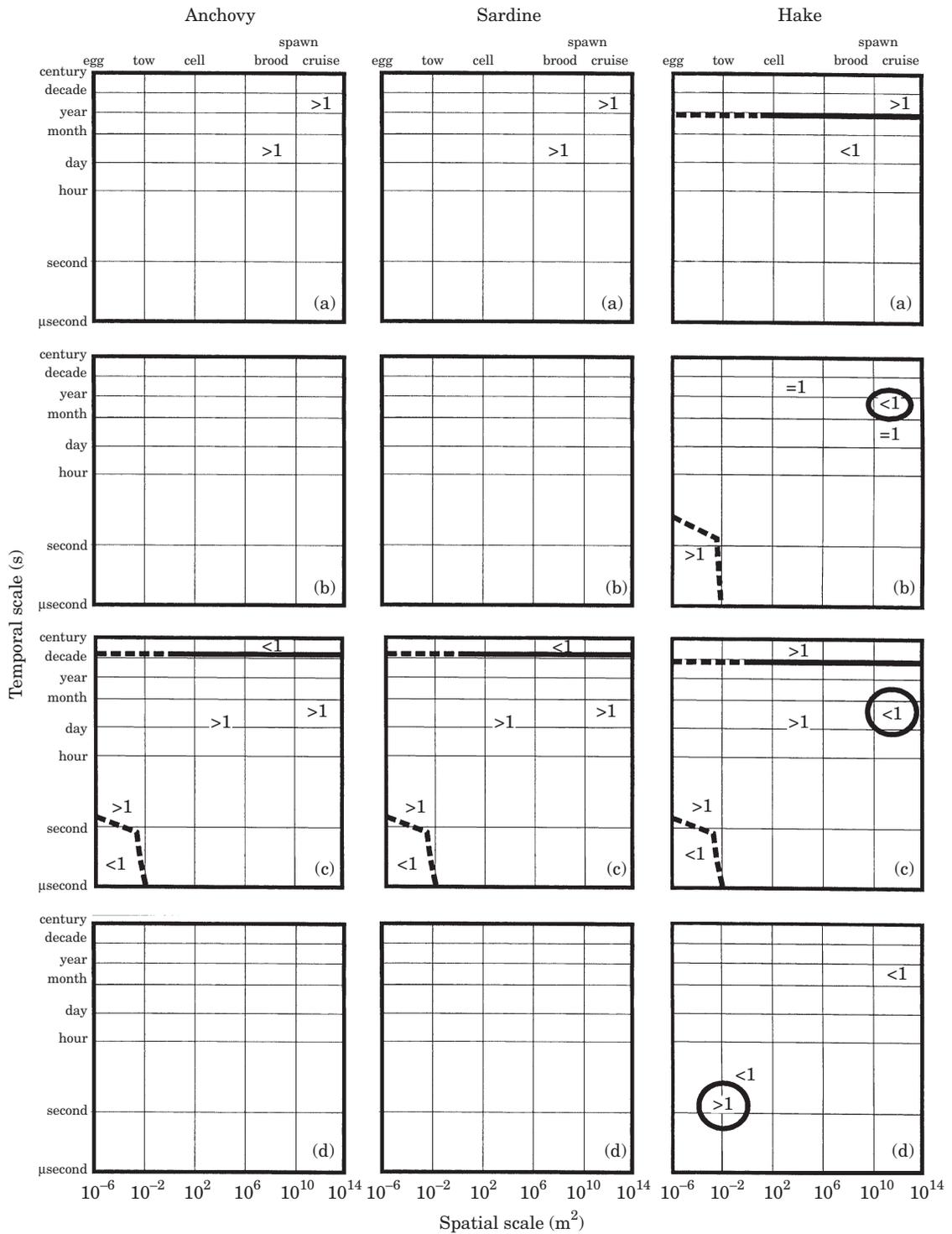


Figure 2. Rate diagrams for juvenile anchovy, sardine, and hake biomass distribution in the eastern Pacific. See Figure 1 for details.

years) exceed those due to recruitment (58% mortality by age 2; Smith, 1995). Even if the flux of larvae into the brood area is considered juvenile “natality”, changes in

biomass due to natality and mortality do not exceed the net flux of biomass out of the brood area. A newly recruited juvenile hake weighs 0.0121 g when leaving the

spawning area and 26.3 g at the end of the second year of life (Smith, 1995). At temporal scales less than a year, biomass changes due to mortality (41% in year 1, 30% in year 2) exceed those due to active or passive flux out of the area. The value of the ratio is greater than 1.

The demographics rate diagram [Figure 2(c)] depicts a ratio less than 1 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 [Figure 2(d)]. Episodic events (e.g. upwelling) and large-scale water movements (e.g. currents) will change the value of the ratio to less than 1 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 important to survival of individual hake. Changes in juvenile biomass are influenced more by changes in somatic growth and active locomotion.

Discussion

This primary description of the embryonic and larval stage transport phenomena would support the observation of larger numbers of older larvae averaged over the whole region for sardine and anchovy because the offshore contingent shows lower than average mortality indices and persistence in time. On the contrary, the expatriated hake appears to have accelerated mortality rates on the offshore side of the spawning area. So, even though the relationship of abundance of larvae to juveniles is weak, it supports the idea of a more important role of larvae in recruitment variability of hake over a 100-d period than for sardine and anchovy, in which this stage lasts only about 50 d.

While there are increasing opportunities for use of spatio-temporal information about recruitment, there has not been enough formal and sustained work towards assembling this information at the appropriate spatial scales (Schneider *et al.*, 1999). There is not a general appreciation for the dominant scales controlling recruitment for any pelagic species [but see Walsh *et al.* (1980) for anchoveta transport]. Existing data have often been taken for a variety of reasons on a convenient set of platforms at convenient times: conclusions drawn from analysis of haphazard data must be tempered by this fact. Findings derived from retrospective analysis must be labelled speculative until hypotheses can be tested at

more appropriate time and space scales. Fortunately, extreme recruitment rates appear to be regional or basin scale environmentally driven and sufficiently massive for easy detection (Hollowed *et al.*, 1987). Unfortunately, detection of recruitment failure is usually delayed for a generation of the species involved; so the cause of recruitment failure is embedded in inadequate observations.

The earlier advances in time-scale dynamics can now be augmented by spatial-scale dynamic analyses (Horne and Schneider, 1994). Gulland (1982) rejected the use of the cycle “with its implication of regularity and predictability”: in the spatial domain, it may not be useful to look for “characteristic” length scales either. Instead of analogs of “frequency” and “length” scale, the existing data appear to show rather broad bands of the time/space grid interspersed with large indeterminate areas. This would lead one to look across broad bands in both domains in historical and paleo-oceanographic data. While we have compared three species with considerable biomass (anchovy, sardine, and hake) there is no evidence at the recruitment level that they react to a joint carrying capacity, foster the growth or aggregation of common predators, or even react to common physical and oceanographic events in a similar fashion. One would have to agree with Riffenburgh (1969) that fisheries on one or the other of these three species would not influence the population growth rate of the other species at all.

The populations of these three planktivorous species at the larval and juvenile stage are maintained by occasional high recruitment rates that require high egg production and high embryonic and larval survival. While these features are required, they are not sufficient to guarantee high recruitment (clupeoids: Smith, 1985; hake: Hollowed, 1992) in the California Current habitats. Because the recruitment of these species is not coordinated (Hollowed *et al.*, 1987), the regional and basin scale changes in temperature and productivity are not driving the differences in annual reproductive success. Because dependence of reproductive success on spawning biomass is weak, density-dependent factors are overridden by ocean physics. By comparison of the anchovy–sardine–hake complex, we can see that more physical measurements are required at the mesoscale in the California Current system. Examination of the results of Peterman *et al.* (1988) would lead to discounting the larval stage and microscale as the controlling scales and stages for reproductive success. While the capability to measure, visualize, and analyze mesoscale physics and the biological response has grown, field studies have not yet responded suitably to this scale (50 km) and persistence (four months) of change over the late larval and juvenile period.

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