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Pattern in Space and Time of Clupeoid Fish Eggs in the California Current Region

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy in Oceanography

by

Katherine Alexandra Curtis

Committee in charge:

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2003
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[Signatures of committee members]

Chair

University of California, San Diego
2003
To my family

Herta K. Curtis and Celia A. Curtis

and to Preeti Chalsani, who understands me

and

In Memory of

Kent Krueger Curtis

and

Mark Andrew Acaley
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The text of Chapter 2, in part or in full, is a reprint of the material as it appears in *Fisheries Oceanography*. I was the primary researcher and author.
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Curtis, K.A. (in press) Fine scale spatial pattern of Pacific sardine (Sardinops sagax) and northern anchovy (Engraulis mordax) eggs. Fisheries Oceanography.
ABSTRACT OF THE DISSERTATION

Pattern in Space and Time of Clupeoid Fish Eggs in the California Current Region

by

Katherine Alexandra Curtis
Doctor of Philosophy in Oceanography
University of California, San Diego, 2003

Professor David M. Checkley, Jr., Chair

This dissertation examines spawning behavior and habitat in Pacific sardine (Sardinops sagax) and northern anchovy (Engraulis mordax) in the Southern California Bight (SCB). The fine-scale horizontal and vertical distributions of anchovy and sardine eggs are characterized and their potentials for interaction with the predator Euphausia pacifica are assessed under varying environmental conditions.

In Chapter 2, fine-scale horizontal pattern of sardine and anchovy eggs is characterized. Variograms for anchovy eggs have a higher nugget effect than those for sardine eggs, indicating that spatial structure of the distribution of sardine eggs is better resolved at the scales sampled. In light of other spatial studies of eggs of Sardinops sagax and Engraulis spp., I propose that the pattern is a function of species-specific life history, population size and age structure, spawning intensity, and physical scales of the spawning habitat.
Chapter 3 presents a model for vertical distribution of anchovy and sardine eggs, based on vertical mixing and ascent velocities of the eggs. The vertical mixing model that best predicts observed vertical distributions of anchovy eggs is different than that for sardine, and addition of a random error term to the terminal ascent velocity affects predictions of anchovy eggs, but not sardine eggs. Observed vertical distributions of sardine eggs are highly variable, perhaps due to horizontal patchiness or true vertical variability. The model does not improve prediction of integrated abundances from samples at 3-m depth over a simple regression of 3-m on integrated abundances.

In Chapter 4, distributions of sardine and anchovy eggs and adult and juvenile Euphausia pacifica, an abundant euphausiid predator on ichthyoplankton, are examined in geographic and T-S space in the SCB for 1953-1959 and 1995-2002. Variability in the relative distributions of the three species shows concordance with environmental change. Occurrence of significantly complementary distributions of anchovy eggs and E. pacifica provides supporting evidence for interaction between anchovy and euphausiids.

Spatial pattern in sardine and anchovy eggs is shown to be relevant to relationships between spawning behavior, spawning habitat, and population size. The potential importance of the dominant euphausiid species in influencing recruitment and spawning habitat selection is also supported.
Chapter 1

Introduction to the Dissertation

... the fact that it became technologically more feasible to study larval feeding than, say, predation on juveniles has lent the premise [that the supply of food for the youngest larvae is both variable and crucial] a certain pragmatic momentum. We often tend to continue longer than necessary the studies we already have developed the techniques to do, because development of new techniques to test other hypotheses, including pilot studies in the field, is frequently time-consuming and unrewarding.

- Michael M. Mullin, 1993, *Webs & Scales*

Clupeoids and climate change

Efforts by fisheries oceanographers to understand the variable recruitment of marine fish populations have particular significance in coastal boundary currents and upwelling systems, which account for a disproportionate amount of annual global landings. Clupeoid species alone, which include herrings, sardines, and anchovies, constituted 30% of the global annual marine fish catch in recent years (FAO, 2003). The small, planktivorous clupeoids are key species that exert bottom-up and top-down control on upper and lower trophic levels in these “wasp-waist” ecosystems (Cury et al., 2000).

Populations of sardine (*Sardinops sagax* and *Sardina pilchardus*) and anchovy (*Engraulis* spp.) undergo large decadal variations, often fluctuating out of phase (Kawasaki, 1991; Schwartzlose *et al.*, 1999) and in concert with large-scale climate regime shifts (MacCall, 2001). The recoveries or declines of these populations may often be initiated by one or more years of strong or poor recruitment, rather than by
direct competitive interaction with the other genus or by intraspecific density-dependent effects (Jacobson et al., 2001; Schwartzlose et al., 1999). Changes in the environment may catalyze the formation of a strong year class by increasing the amount of suitable habitat for above-average spawning and survivorship (Lluch-Belda et al., 1992). The obvious question that arises is:

*What differences between anchovy and sardine cause the disparity in their reaction to environmental change?*

In the California Current System, the dominant clupeoid species are the northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*). Records from the past two millennia, in the form of anchovy and sardine scales in the anaerobic sediments of the Santa Barbara Basin, indicate that the populations of these two species have fluctuated over still greater ranges previously than those observed during the relatively short history of their exploitation by humans (Baumgartner et al., 1992). Interestingly, low-frequency (centennial) periodicity in anchovy and sardine scale deposition appears to be in phase. The out-of-phase decadal fluctuations observed since the early 20th century appear to be in synchrony with decadal climate regimes that have been identified in the North Pacific (Mantua et al., 1997). In the Southern California Bight region, these alternating climate regimes are expressed as warm conditions, during which upwelling is suppressed and the California Current moves farther offshore, and cold conditions, characterized by enhanced upwelling and an inshore shift of the California Current (Bograd and Lynn, 2003).
Northern anchovy is a small, coastal pelagic species, rarely more than 180 mm in length and four years of age (Baxter, 1967). The fish reach sexual maturity at one to two years of age. Females are serial batch spawners, releasing about 5000 pelagic eggs as often as every 7 to 10 days over the spawning season (Hunter and Macewicz, 1980). Spawning is most intense during winter and early spring (December – April; Hernandez-Vasquez, 1994). The spawning center for the central subpopulation is nearshore in high-salinity, upwelled waters in the Southern California Bight (Checkley et al., 2000; Hewitt, 1980; Kramer and Ahlstrom, 1968), but the spawning range expands northward and offshore with increasing population size (MacCall, 1990). Losses of anchovy larvae that have been proposed to influence recruitment variability include ideas from all three traditional schools of thought in fisheries oceanography: starvation, particularly due to the disruption of thin layers of concentrated food organisms by storms (Lasker, 1978; Peterman and Bradford, 1987); loss from the population due to offshore transport in the Ekman layer during upwelling-favorable wind events (Methot, 1983; Parrish et al., 1981); and predation, including cannibalism (Hunter and Kimbrell, 1980; Lillelund and Lasker, 1971; Theilacker et al., 1993). None of these mechanisms have been related to climate change to explain why the anchovy population tends to increase during cold periods and decrease during warm periods.

Pacific sardine is a cosmopolitan species, occurring in upwelling systems around the world. The subpopulation off California ranges from Baja California to Alaska. Adults of a well-established population frequently reach eight years or more
and 250 mm in length (Murphy, 1966), but the population is skewed toward much younger age classes when it is rapidly increasing (Butler et al., 1996). Females of sardine are also serial batch spawners, releasing an average of 24,000 eggs every seven to 15 days (Macewicz et al., 1996). The dominant life history mode of sardine changes between large and small population sizes, becoming larger, longer-lived, and highly migratory as the population increases. The change in life history mode is accompanied by an apparent switch in spawning habitat, which moves from south of Point Conception and nearshore, mostly off of Baja California, to north of Point Conception and offshore, in the cool water at the inshore edge of the California Current (Checkley et al., 2000; Kramer, 1970; MacCall, 2001). This switch in spawning habitat is in contrast with the stationary expansion exhibited by anchovy, an interspecific difference that likely holds part of the explanation for the out-of-phase nature of the fluctuations in population size as seen in the 20th century. The switch in life history modes observed in sardine off of California may reflect an alternation of dominance between a northern and a southern subpopulation in this region (Felin, 1954; MacCall, 1979; Murphy, 1966), a phenomenon that has also been suggested to occur off of Japan (Kuroda, 1991). Less is known about mortality of sardine larvae than anchovy, since the sardine population has been low for most of the history of fisheries oceanography research in the region, led by the California Cooperative Oceanic Fisheries Investigations (CalCOFI). The offshore shift of sardine spawning habitat at large population size prompts another key question:
What advantage does offshore spawning habitat confer to sardine larvae?

Logerwell and Smith (2001) inverted the traditional approach to mortality sources in fish larvae and examined the distribution of surviving larvae. They found that a disproportionately large number of late larvae occur in mesoscale eddies in offshore habitat. Logerwell et al. (2001) calculated prerecruit production from temperature, prey, and abundance data and found that prerecruit production in a model mesoscale eddy was four times greater than in all other regions combined. This provides a promising mechanism for linking recruitment to climate variability (MacCall, 2001). However, Logerwell et al. (2001) determined that the relationship between eddy frequency and individual reproductive success of sardines is not linear, but domed, indicating that a more complex set of interacting processes determine recruitment. Importantly, Logerwell and Smith (2001) additionally found that the eggs of sardine, along with chlorophyll and zooplankton volume, were highest inshore, rather than in the offshore "survivors' habitat." The offshore shift of maximal abundances of sardine larvae relative to sardine eggs may reflect offshore transport (Logerwell and Smith, 2001) or greater mortality of sardine eggs and early larvae in inshore regions.

Predation is an important source of mortality in the early life history of marine fish larvae (Bailey and Houde, 1989) and, along with disease and parasitism, defensibly the dominant one in the earliest life history stages that depend on yolk for nutrition. If zooplankton biomass is higher inshore, then the potential for predation
mortality may be higher inshore as well. Butler (1987) concluded that due to their greater motility, sardine larvae are more vulnerable to predation than anchovy larvae, but less prone to starvation. This disparity in the relative risk of starvation and predation mortality in anchovy and sardine larvae may well be relevant to the differences between the two species in both their spawning habitat at large population size and their response to climate change.

This Dissertation

The initial objective of this thesis was to compare inshore and offshore mortality of sardine eggs with a Lagrangian patch-tracking approach. Spatial patchiness complicates mortality estimates of pelagic fish eggs because it introduces large errors to abundance estimates of the eggs. The primary system for abundance measurements of eggs in this study was the Continuous Underway Fish Egg Sampler (CUFES; Checkley et al., 1997). CUFES is a pumped system that can sample fish eggs at 3-m depth both underway and on station, and can integrate the high variability associated with the contagious distributions of pelagic fish eggs. CUFES thus permits greater precision in abundance estimation for pelagic fish eggs, but knowledge of their vertical distribution is additionally required for accuracy. Therefore, another goal of the study was the characterization of fine-scale horizontal and vertical distribution of sardine eggs, both for the practical purpose of improving abundance estimates, and to allow spatially explicit consideration of two factors controlling the change in
distribution and abundance of sardine eggs with time: predation and physical processes.

For several reasons, the comparison of mortality rates in inshore and offshore habitats did not succeed. Most importantly, limitations of the available ship (R/V Robert Gordon Sproul) did not allow sampling in offshore sardine spawning habitat in inclement weather, which predominates in spring in the California Current. This restriction was magnified by the greater caution required due to the installation of the Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS; Wiebe et al., 1985) package on the aft deck, where it was subject to wave damage. One possible solution to reaching offshore habitat in inclement conditions would be to eliminate vertically stratified sampling, instead combining CUFES sampling with a large number of vertically integrated tows on a grid for abundance estimation.

The other major obstacle to mortality estimation in the dynamic environment of the California Current is the separation of physical and biological factors influencing egg abundance. Delimitation of a patch to be surveyed completely and repeatedly in an adaptive manner would be ideal, but unlikely, given the apparently continuous distribution of sardine eggs in the offshore habitat during peak spawning season (see Checkley et al., 2000). Instead, a collaborative effort with a physical oceanographer to parameterize the advective and diffusive field at the scale of sampling would be the optimal solution. A dye-tracking approach to estimate diffusion in this study failed in several ways because inadequate time and resources were spent on this aspect during preparation for an already involved cruise. The Acoustic Doppler
Current Profiler was not functioning properly either, which was not determined until after completion of the cruise. Accounting for physical processes in such a mortality study will be a challenge in any case, but a more informed, collaborative effort with greater dedicated resources would be more likely to succeed and worth pursuing. Given the difficulties with weather and the physical oceanographic work, the dissertation was modified to focus on the comparison of anchovy and sardine egg distributions.

The large-scale distributions of sardine and anchovy eggs in the California Current System have been characterized in terms of spawning habitat in geographic and temperature-salinity space (Checkley et al., 2000; MacCall, 1979; MacCall, 1990). A comparative description of the spatial organization of sardine and anchovy eggs on fine scales may further illuminate the differences between spawning behavior and spawning habitat selection in these two species. In Chapter 2, the fine-scale horizontal distributions of sardine and anchovy eggs in the patch-tracking study are characterized and compared. Variograms are calculated for the horizontal distributions of the eggs, which were sampled on grids at a resolution of 0.75 km with CUFES. This analysis addresses an unexplored spatial scale, intermediate to those of preceding studies, and it provides a rare direct comparison of spatial pattern of sardine and anchovy eggs.

Knowledge of the vertical distribution of pelagic fish eggs is necessary for the consideration of ecological interactions with vertically migrating predators, and for abundance estimates when using a system that only samples at one depth, as is the
case with CUFES. Comparison of the vertical distributions between anchovy and sardine may also provide additional insight into interspecific differences in spawning behavior. Chapter 3 presents a model to predict the vertical distribution based on physical mixing parameters and characteristics of the eggs that determine their ascent rate. The model is tested on observed vertical distributions of the eggs and on its ability to predict integrated abundances measured in vertical egg tows from CUFES abundances at 3-m depth.

Finally, I tapped the considerable historical record, amassed by the CalCOFI program and a number of dedicated researchers, of the geographic distributions of sardine and anchovy eggs relative to their potential predators and environmental variables. These records may lend insight into the potential for and realization of ecological interactions between abundant predatory members of the zooplankton community and sardine and anchovy eggs. Euphausia pacifica is a dominant species in the California Current System and tends to reach maximal abundances in coastal waters (Brinton, 1976). E. pacifica has been identified as a potentially important predator on anchovy eggs and larvae (Theilacker et al., 1993), and complementary abundances of euphausiids and eggs of anchovy and sardine have been observed in CUFES survey samples (Checkley et al., 2000). In Chapter 4, the distributions of sardine and anchovy eggs are examined in geographic and temperature-salinity space relative to E. pacifica, over a range of environmental conditions and population sizes of the two clupeoid species.
References


Chapter 2

Fine-Scale Spatial Pattern of Pacific Sardine (*Sardinops sagax*) and Northern Anchovy (*Engraulis mordax*) Eggs

Abstract

Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) eggs exhibited different spatial structure on the scale of 0.75 to 2.5 km in two egg patches sampled in the Southern California Bight in April 2000. Plankton samples were collected at 4-minute intervals with a Continuous Underway Fish Egg Sampler (CUFES) on 5 x 5 km grids centered on surface drifters. Variograms were calculated for sardine and anchovy eggs in Lagrangian coordinates, using abundances of individual developmental stages grouped into daily cohorts. Model variograms for sardine eggs have a low nugget effect, about 10% of the total variance, indicating high autocorrelation between adjacent samples. In contrast, model variograms for anchovy eggs have a high nugget effect of 50-100%, indicating that most of the variance at the scales sampled is spatially unstructured. The difference between observed spatial patterns of sardine and anchovy eggs on this scale may reflect the behavior of the spawning adults: larger, faster, more abundant fish may organize into larger schools with greater structure and mobility that create smoother egg distributions. Size and mobility vary with population size in clupeoids. The current high abundance of sardines and low abundance of anchovy off California agree with the greater
autocorrelation of sardine egg samples and the observed tendency for locations of anchovy spawning to be more persistent on the temporal scale of days to weeks. Thus the spatial pattern of eggs and the persistence of spawning areas are suggested to depend on species, population size and age structure, spawning intensity, and characteristic physical scales of the spawning habitat.
Introduction

Clupeoid species, including sardine (*Sardinops sagax* and *Sardina pilchardus*) and anchovy (*Engraulis* spp.), occur in coastal boundary currents and upwelling systems around the world and are known for their large decadal variations in population size (Kawasaki, 1991; Schwartzlose *et al.*, 1999). The clupeoids' low trophic position and young age at first reproduction allow them to reach tremendous abundances and link them closely to the physical forcing mechanisms that control primary production. In regions where sardine and anchovy co-occur, such as off Japan, California, Peru, and South Africa, the two populations often fluctuate out of phase. The populations' recoveries or declines may often be initiated by one or more years of strong or poor recruitment, respectively, rather than by either a direct competitive interaction with the other species or intraspecific density-dependent effects (Jacobson *et al.*, 2001; Schwartzlose *et al.*, 1999). Changes in environmental conditions may catalyze the formation of a strong year class by creating suitable habitat for above-average spawning and survivorship (Lluch-Belda *et al.*, 1992).

Most knowledge of spawning behavior in clupeoids comes from studies of their egg distributions. The spawning season for Pacific sardine (*S. sagax*) in the Southern California Bight is bimodal, with a primary peak from February through June, and a secondary peak from July through September (Hernandez-Vasquez, 1994; G.A. Rebstock and D.M. Checkley, Jr., Scripps Institution of Oceanography, USA, unpub.). Spawning of northern anchovy (*Engraulis mordax*) off California historically peaked from December to April (Hernandez-Vasquez, 1994). Springtime (February to
April) spawning habitats for Pacific sardine and northern anchovy in the California Current System have distinct temperature-salinity characteristics: sardine eggs occur primarily in the cool water of the frontal region at the shoreward edge of the California Current, while northern anchovy eggs are most abundant in high-salinity, nearshore waters (Checkley et al., 2000; G. A. Rebstock and D. M. Checkley, Jr., Scripps Institution of Oceanography, USA, unpub.). Over decadal time scales, the spawning habitat of anchovy expands and contracts with population size, but the centroid of the egg distributions always remains contiguous with the coast (MacCall, 1990). In contrast, the centroid of springtime sardine spawning activity moves offshore at large population size (MacCall, 2001). Anchovy habitat may be more restricted to nearshore areas than sardine habitat due to the smaller size and inferior swimming ability of anchovy (Dotson and Griffith, 1996; MacCall, 2001).

Research has also been directed towards quantifying the spatial distribution patterns of the eggs of small pelagic fishes. Variogram analyses (explained in Methods) of large-scale survey data for sardine eggs off California, South Africa, and Australia indicate that the distribution of sardine eggs is highly structured (high autocorrelation at small scales) with decorrelation length scales of 15-30 km (Fletcher and Sumner, 1999; Lo et al., 2001; van der Lingen et al., 1998). Bez (2000) found similar structure for eggs of Bay of Biscay anchovy (Engraulis encrasicolus) collected at 6-km intervals. Finer scale studies, using vertical egg tows, characterized the decorrelation lengths for eggs of E. mordax and E. encrasicolus at the scales of tens to hundreds of meters and 2 to 7 km respectively (Smith and Hewitt, 1985; Uriarte and
Motos, 1998). Fine- and population-scale studies of the distributions of pelagic fish eggs indicate at least two possible levels of organization for spawning adults: schools and shoals (many contiguous schools over kilometers to tens of kilometers; Smith, 1973).

The combination of the Continuous Underway Fish Egg Sampler (CUFES; Checkley et al., 1997) and modern Global Positioning System (GPS) technology permits the collection of samples that integrate egg abundance over a well-defined distance and are paired with precise spatial and environmental information. Both of these characteristics are valuable in characterizing the highly contagious spatial distributions of pelagic fish eggs, especially at small scales. I am aware of only one published direct comparison of the quantitative spatial structure of sardine and anchovy eggs (S. sagax and E. capensis), sampled in vertical egg tows at 9 km intervals in the Benguela Current region (Barange and Hampton, 1997). Since typical decorrelation scales are on the order of 20 km, most spatial structure will be found at the least-studied scales of a few kilometers or less.

The spatial pattern of sardine and anchovy eggs is central to understanding the spawning behavior of these species and its relationship with spawning habitat. This study makes a direct comparison of spatial patterns of northern anchovy and Pacific sardine eggs at the scale of 0.75-2.5 km, using CUFES samples from two locations in the Southern California Bight. The ultimate goal is to address the relationship of spawning behavior to spawning habitat and the dramatic fluctuations in population size exhibited by sardine and anchovy species. These changes in population size are
accompanied by changes in life history that are likely to affect the behavior of spawning adults. Consequently, spatial autocorrelation analyses of sardine and anchovy eggs sampled at the scales relevant to spawning schools and shoals (tens to thousands of meters) have the potential to reveal interesting relationships between spawning behavior, population size, and concurrent environmental conditions.
Materials and Methods

Sample Collection and Processing

A fine-scale, Lagrangian study on the mortality of Pacific sardine and northern anchovy eggs was conducted on the R/V Robert Gordon Sproul from 18 to 27 April 2000 (SP0004). This cruise began 11 days after the April 2000 California Cooperative Oceanic Fisheries Investigations (CalCOFI 0004) survey cruise on the NOAA R/V David Starr Jordan.

Ichthyoplankton data for this study were collected with CUFES, an underway system that pumps sea water from 3-m depth at 0.64 m³ min⁻¹ while the vessel is stationary or underway (Checkley et al., 1997). Particles in the sea water were concentrated and collected in discrete, sequential samples in the cod ends of the sample collector. The mesh size of the concentrator and the cod ends was 505 μm. The samples were counted at sea, prior to preservation, for a near-real-time estimate of egg abundance. A small portion of the pre-concentrator flow was diverted through the Environmental Data Acquisition System (EDAS; Checkley, 2000) for concurrent measurements of temperature and salinity at 3 m.

CUFES data communicated from the R/V Jordan guided the R/V Sproul's CUFES search for abundant sardine and anchovy eggs. A sardine egg patch located near Butterfly Bank in the Southern California Bight (Patch 1), was followed from 0400 PST 20 April to 1800 PST 21 April, from starting position 32° 19' N 118° 17' W (Fig. 2-1a), with bottom depths ranging from 400 m to 1100 m. Subsequently, abundant anchovy eggs (Patch 2) were found northeast of Santa Catalina Island and
followed from 1600 PST 25 April to 1630 PST 27 April from starting position 33° 34' N 118° 36' W (Fig. 2-1b), with bottom depths ranging from 200 m to 900 m. The starting positions were the locations of maximum egg abundance of the target species along the ship's course. Egg maxima were pinpointed by increasing the resolution of underway CUFES sampling from 30-min intervals to 4-10-min intervals. A differential Global Positioning System (DGPS)-equipped surface drifter (George and Largier, 1996) was then deployed, and a sampling protocol was initiated and repeated every 10 to 12 hours. This sampling protocol consisted of (1) executing two vertical tows from 65 m depth with a PAIROVET net (Paired Vertical Egg Tow, 150-μm mesh; Smith et al., 1985; Uriarte and Motos, 1998) and a CTD cast in proximity to the drifter, (2) collecting approximately 50 4-min CUFES samples on a roughly 5 x 5 km survey grid of four equidistant parallel lines centered on the drifter, (3) repeating the PAIROVET and CTD deployments in proximity to the drifter, and (4) collecting eight vertically stratified samples from 70 m to the surface with a 1-m² Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS-1, 333-μm mesh; Wiebe et al., 1985). All plankton samples were preserved in a solution of 5% buffered Formalin in filtered sea water. Since the ship was steaming at 7.5-11 km hr⁻¹ (4-6 knots) during the grid, the resulting resolution for the 4-min CUFES samples was roughly 0.5-0.75 km. The volume filtered for each 4-min sample is approximately 2.6 m³, but since extrusion of anchovy eggs is known to occur through 505-μm mesh in plankton nets (Lo, 1983), the egg abundances for both species are expressed in eggs min⁻¹ for this study.
The 4-min CUFES samples were preserved immediately, without enumeration, and were processed after the cruise. Each preserved sample was sieved through a 200-μm mesh and resuspended in tap water for examination. Anchovy and sardine eggs were counted under a dissecting microscope and assigned a developmental stage (Moser and Ahlstrom, 1985; Lo et al., 1996). Disintegrated eggs, too damaged to be even roughly staged, were assigned proportionally to the stages counted in that sample. Disintegrated eggs accounted for an average of 2% of the total sardine eggs and none of the anchovy eggs.

Data Analysis

The distribution of developmental stages in the CUFES grid samples reflects discrete daily cohorts with some variability in developmental rates (Fig. 2-2a,b), so for each 4-min sample, the counts for the individual stages that comprised each cohort were combined. The range of mean expected ages for the stages in each cohort at the ambient sea surface temperature were also tabulated, and agree with the inference that cohorts were being followed through time (Tables 2-1,2-2). These cohort abundances for anchovy and sardine eggs were matched with temperature and salinity at 3-m depth and GPS position, acquired by EDAS and averaged over the corresponding 4-min sample interval. Lagrangian coordinates were calculated for each CUFES sample by subtracting the coordinates of the surface drifter from the ship's position. Judging by straightness of the isolines, Lagrangian maps of the most conservative property, salinity, represent a better synoptic picture than maps in Eulerian coordinates (Fig.
2-3), so Lagrangian coordinates were used for all further spatial analyses. The displacement of the surface drifter during each grid survey was also calculated (Tables 2-1,2-2).

The Variogram

The variogram represents the semivariance between data points as a function of the spatial distance between them. The experimental variogram is calculated using

$$\gamma^e(h) = \frac{1}{2n(h)} \sum_{i}^{n(h)} (f(x_i) - f(x_i + h))^2$$

[1]

where $\gamma^e(h)$ represents the experimental variogram for distance $h$, $n(h)$ is the number of point pairs separated by displacement $h$, and $f(x_i)$ is the value at data point $x_i$ (Petitgas, 1996). All grid samples in a data set were included in the variogram calculation, unless positive samples occupied only a contiguous subspace of the sample grid to be analyzed, in which case only the data within that polygon were used in the analysis (e.g. Fig. 2-4). Displacement $h$ represents direction and magnitude ($h$), also called lag. An anisotropic variogram exhibits directional behavior.

The model variogram is obtained by fitting one of a number of acceptable functions, including exponential, gaussian, spherical, and power functions (Armstrong et al., 1992), to the experimental variogram. If the model variogram is discontinuous at the origin, the discontinuity, or nugget effect, indicates what part of the overall variance appears unexplained by spatial structure at the sampling scale. The functional form of the model, particularly the slope near the origin, is related to the spatial continuity of the studied variable. Most variogram models reach a horizontal
asymptote at the decorrelation length scale, where the $h$- and $\gamma$-values are referred to as the range and sill, respectively.

The S-Plus library Geostatistics for Estimating Fish Abundance (GEFA), written by Nicolas Bez and Jacques Rivoirard (Centre de Géostatistique, Fontainebleau, France), was run in S-Plus 2000 for all geostatistical analyses. All other statistical analyses presented here were also done in S-Plus 2000. Experimental variograms were computed for individual cohort abundances and for total eggs for the three sardine egg grids in Patch 1 and five anchovy egg grids in Patch 2. Variograms were also computed for one cohort of anchovy eggs observed in Patch 1 and for temperature and salinity in Patch 1 and Patch 2, for comparison with variograms of the eggs. Multiple directional variograms were calculated for each data set to detect anisotropy. Anisotropic variograms were recalculated using different angles until the difference between the slopes near the origin was maximized for two perpendicular directions. Model variograms were fit to the experimental variograms using the GEFA software. Experimental and model variograms were divided by the total variance to scale them to 1, thereby enabling identification of trends with egg age and species.
Results

Temporal Persistence of Spawning Areas

The agreement between the large-scale egg distributions delineated by CUFES samples taken from the R/V Jordan and then from the R/V Sproul roughly two weeks later was greater for northern anchovy than for Pacific sardine (Fig. 2-1a,b). In addition, no new cohort of sardine eggs was observed from the R/V Sproul on the second day of sampling at Patch 1 (Fig. 2-2a). Anchovy spawning also apparently ceased in Patch 1, where three cohorts of anchovy eggs were observed upon arrival, but no new cohort was observed in the samples collected the following day. Anchovy continued to spawn in Patch 2 both nights of the study (Fig. 2-2b).

Fine-Scale Spatial Structure

Tables 2-1 and 2-2 summarize the data sets and the nugget effects of their variograms. The sardine egg patch was followed for 1.5 days, allowing three repeats of the fine-scale CUFES sampling grid centered on the drifter. The anchovy egg patch was followed for 2 days, allowing five CUFES grid surveys. Expected ages of the eggs were estimated from temperature-development relationships described for northern anchovy and Pacific sardine (Lo, 1985; Lo et al., 1996).

In all, 10 variograms were calculated for the sardine egg data, including three for total sardine eggs in each grid. The variograms for sardine eggs have low nugget effects, ranging from 2 to 19% of the variance (Tables 2-1,2-2), and they are anisotropic. Two representative examples of experimental and model variograms for
sardine eggs are shown alongside the original egg data (Fig. 2-4). No consistent pattern between developmental stage and percent nugget effect was found across grids for individual cohorts or across cohorts within a grid.

A total of 15 variograms was calculated for the anchovy egg data in Patch 2, including 5 for total anchovy eggs in each grid. The examples of distributions of anchovy eggs and their respective variograms in Fig. 2-5 show little spatial structure. The experimental variograms for anchovy appear to be isotropic, so they were modeled accordingly. All the variograms for anchovy egg data have high nugget effects, ranging from 62 to 100% of the variance (Tables 2-1,2-2). No consistent relationship between developmental stage and percent nugget effect was found within cohorts or within grids. Experimental variograms were not calculated for the two data sets in which Stage II eggs were included, because they had too few positive samples (Fig. 2-6), and a large number of contiguous zero values in the data leads to an artificially low nugget effect. Contiguous positive values in these data range from one to four samples in length, equal to <0.5 to 2 km in distance.

Two variograms were calculated for anchovy eggs in Patch 1. The first variogram was calculated for the only cohort of anchovy eggs (Stages IX-XI) with enough positive samples in Grid 1 to justify this analysis (Fig. 2-7a,b). This variogram has a nugget effect of 32%, which is intermediate between the sardine variograms and the Patch 2 anchovy variograms. The second variogram was calculated for total anchovy eggs, and has a nugget effect of 7% (Fig. 2-7c,d), comparable to the nugget
effects of variograms for sardine eggs in Patch 1. Later grids in Patch 1 did not contain enough positive anchovy samples to support variogram analysis.

Experimental variograms for the physical properties of temperature and salinity in Grid 1 of both Patch 1 and Patch 2 show very low values at the first lag (Fig. 2-8).

One average variogram was calculated for each cohort of sardine in Patch 1 and anchovy in Patch 2, and these variograms were tested for a significant difference between the spatial patterns of sardine and anchovy eggs. The single anchovy variogram for Patch 1 was not included in this analysis, since a sample size of 1 does not allow statistical comparison. Each experimental variogram was first normalized to a variance of 1. Every data set (one cohort in one grid) is represented by multiple directional variograms, so an average lag value and variogram value at the first lag was calculated from the directional variograms for each data set, weighting each point by the number of point pairs that it represented in the original data set. This normalized variogram value at the first lag (experimental variogram) and the normalized nugget effect (model variogram) for each cohort in each species were averaged across all the grids for which variograms were calculated for that cohort (Tables 2-1,2-2,2-3). The overall mean distance at the first lag was 0.7 km for anchovy and 0.9 km for sardine. The overall mean nugget effect and variogram value at the first lag were both significantly larger for anchovy (0.78, 0.83) than for sardine (0.07, 0.28) (t-tests, p < 0.001).
Vertical Sampling

Comparisons from the April 2000 cruise of anchovy egg abundances in PAIROVET samples with CUFES samples taken during approach to the PAIROVET stations indicated a significant positive relationship (linear regression, p < 0.00001) with a high $r^2$ of 0.70 (Fig. 2-9). Plots of density from CTD data show that the surface mixed layer in Patch1 reached 16-20 m depth, while the mixed layer in Patch 2 was generally less than 5 m (Fig. 2-10).
Discussion

Variograms for the fine-scale distribution of anchovy eggs in one patch in the Southern California Bight in April 2000 are different from those for sardine eggs in another patch. The difference is particularly marked in the nugget effect, which is much higher in anchovy than in sardine. This difference in the nugget effect for sardine and anchovy eggs could be explained by sampling error, differences in physical mixing regimes, biological differences in the spawning behavior that produced the two egg patches, mortality processes, or a combination of these factors. These are discussed in detail below.

If random error is added to spatially structured data with a low nugget effect, the nugget effect increases by the error variance. If a random error with constant variance occurs across both species, the lower abundance of anchovy eggs (Tables 2-1,2-2) would result in a greater relative degradation of the underlying structure in the data. But even at abundances as low as those in the anchovy data, sardine egg data still show spatial structure (Fig. 2-4c,d). Thus, the error would have to be unique to the anchovy eggs to manifest itself in the anchovy variograms alone. One possible source of error affecting anchovy eggs, and not sardine eggs, in CUFES samples is extrusion: the CUFES system employs 505-μm mesh, which allows significant extrusion of anchovy eggs from plankton nets (Lo, 1983). However, there are two reasons to doubt that this is the underlying cause for the high nugget effect in the anchovy variograms. First, field experiments comparing egg concentrations in CUFES samples and quantitative vertical tows with a 150-μm-mesh CalVET net (CalCOFI Vertical Egg
Tow, a single net version of the PAIROVET; Smith et al., 1985) gave similar $r^2$ values for northern anchovy and Pacific sardine (Checkley et al., 1997). A significant relationship with a high $r^2$ value was also found for PAIROVET and CUFES samples from the April 2000 cruise (Fig. 2-9). Secondly, variograms for eggs of Bay of Biscay anchovy (*E. engracicolus*) collected using CUFES with a 505-µm mesh had a very low nugget effect and were structurally comparable to variograms for eggs collected in CalVET nets during the same survey (Bez, 2000), supporting the validity of CUFES for the assessment of spatial structure of anchovy egg distributions.

The data used in this analysis are two-dimensional, while the ocean's dynamics are four-dimensional, so physical mixing and mortality processes over time must also be considered in the explanation of the different nugget effects for northern anchovy and Pacific sardine. The abundance of eggs at 3-m depth relative to the depth-integrated abundance changes with vertical physical mixing conditions and developmental stage of the positively buoyant eggs (e.g. Sundby, 1983; Coombs et al., 2001). However, the use of CUFES data without conversion to vertically integrated abundance should not bias the spatial analyses presented here for two reasons: (1) the data included in any one variogram were collected over a period of only 3-4 hours (Tables 2-1,2-2) and reflect discrete cohorts (Fig. 2-2a,b), so neither change in developmental stage nor physical mixing is expected to alter the vertical distribution of the eggs during the period of the grid survey; (2) variograms of egg abundance measured at 3-m depth are expected to be consistent with spatial patterns of depth-integrated abundances because any single conversion factor applied would be a linear
transformation of the data, and thus would not affect the normalized variogram. If hydrography varied greatly across the grid and necessitated the application of a more complex conversion algorithm, it would be unlikely to change so sharply between adjacent samples that it would affect the value of the experimental variogram at the first lag, though the slope might have an upward bias. The consistency between variograms for CalVET versus CUFES samples of *E. encrasicolus*, collected over a large survey grid with widely varying conditions, supports this argument (Bez, 2000).

On the horizontal plane, more intense, smaller-scale mixing in Patch 2 or smaller-scale mortality processes could result in the near-random distribution of anchovy eggs in that location. If turbulent mixing in the hydrodynamic shadow of Santa Catalina Island were the culprit, one would expect the salinity and temperature data at 3 m to show as little structure as the egg data. Also, in the case of either mortality or physical mixing acting on the eggs over time, spatial structure would be expected to decrease with age. However, variograms calculated for temperature and salinity data in Patch 2 (Fig. 2-8c,d) have low nugget effects, and no consistent pattern was found between nugget effect and stage of development in either species.

The vertical distribution of recently spawned eggs is relevant to the discussion of physical mixing processes. A frequently asked question is whether the low abundances and high patchiness observed in early-stage anchovy and sardine eggs in CUFES (e.g. Fig. 2-6) result solely from a horizontal sampling bias that misses small patches of highly concentrated eggs before they are rapidly diffused (Smith, 1973), or also from a vertical sampling bias due to spawning at depth, which would delay the
availability of eggs to CUFES at 3 m. The abundance and continuity of the distribution observed for Cohort 3 changed markedly from Grid 2 (Fig. 2-6a) to Grid 3 (Fig. 2-5c). The dominant developmental stages representing Cohort 3 in Grid 2 and in Grid 3 are on the order of 10 and 20 hours old, respectively (Table 2-2), at 17 °C, the sea surface temperature at Patch 2. The ten-hour age difference is consistent with the process of spawning at depth and subsequent concentration of the eggs at the surface (Cambalik et al., 1998). If the eggs are indeed spawned at depth, a more 3-dimensional physical mixing process must also be considered, in which the nearshore anchovy and offshore sardine eggs may rise through different flow fields after spawning. Unfortunately, the Acoustic Doppler Current Profiler was not functioning properly on this cruise, but CTD data show that vertical density structure was quite different at the two sites (Fig. 2-10).

The most parsimonious explanation for the difference between anchovy and sardine egg patterns in this study is biological. For reasons discussed above, these observed differences are not considered likely to be due only to sampling error or physical and mortality processes. In a broad sense, then, it is reasonable to speak of systematic differences between distributions of sardine and anchovy eggs as reflections of the behavior of spawning adults, the source of the original pattern of the eggs. The adult fish that spawned the eggs may have been organized spatially to different extents or at different scales, and they may have swum at different speeds during spawning. Smith and Hewitt (1985) inferred that the anchovy eggs they sampled had likely been spawned in patches of tens of meters before diffusing to
hundreds of meters. The upper limit of Smith and Hewitt's (1985) observed scale of
tens to hundreds of meters for anchovy egg patches in the Southern California Bight is
similar to the sampling resolution in this study. This spatial scale also corresponds to
the length of runs of consecutive positive values noted in the distributions of early-
stage anchovy eggs (Fig. 2-6). Consequently, one would expect the spatial structure of
anchovy eggs to remain largely unresolved, producing variograms with high nugget
effects. In contrast, the superior swimming ability of sardine (Dotson and Griffith,
1996) may allow organization at larger scales and greater movement during spawning,
both of which should produce the greater spatial autocorrelation of egg abundances
that was observed at the scales sampled. The greater mobility of adult sardines is
consistent with the observation of greater spatiotemporal variability of spawning areas
of sardine compared to those of anchovy both on the April 2000 cruise and in
comparison with distributions observed from the R/V Jordan (Fig. 2-1a,b). This latter
observation is probably also related to the location of the observed spawning areas of
sardine on the inshore periphery of their current spawning habitat (Checkley et al.,
2000), in contrast to the location of Patch 2 well within the inshore spawning habitat
of anchovy.

Additional differences between the two genera are also likely to influence the
spatial pattern of their pelagic eggs. Barange et al. (1999) suggested that sardine
schools may become more densely packed as their population increases, while
anchovy maintain the same density and expand their range. Greater packing density
may increase the structure of the distributions of spawned eggs. This effect would
work in synchrony with the disparity in fecundity between the two species: estimated batch fecundity of northern anchovy, about 5,000 (Picquelle and Stauffer, 1985), is much less than that of sardine, averaging 25,000 (Macewicz et al., 1996).

However, a review of the literature on variograms for sardine and anchovy eggs demonstrates that the distinction between the spatial patterns for Pacific sardine and northern anchovy eggs in this study cannot be explained simply as a difference between genera (Table 2-4). One facet of MacCall's (2001) unifying hypothesis on the common mechanism for decadal-scale biological regimes in Pacific boundary current systems states that when the boundary current is strong, anchovy populations grow, their spawning habitat expands in the offshore direction, and they switch to a longer-lived, later-maturing life history approaching that of sardine. As noted above, variograms for *Engraulis* spp. sometimes do reflect a high degree of spatial autocorrelation, as in the data from the Bay of Biscay (Bez, 2000). Northern anchovy eggs collected in Patch 1 in this study, at the offshore periphery of the current spawning habitat for anchovy, also show a high degree of autocorrelation (Fig. 2-7b,d), which agrees with the idea that larger adults may occur farther offshore and organize at a larger scale. Indeed, Cape anchovy (*Engraulis capensis*) in the Benguela current region has also been found to expand its range at larger stock sizes, with older fish occurring farther offshore (Barange et al., 1999). The tendency for larger, older fish to occur farther offshore may be confounded with the organization of the spawners on the same scales as the characteristic physical scales, which are probably
also larger offshore (P. Smith, Southwest Fisheries Science Center, USA, pers. comm.).

A final note emphasizes the critical importance of appropriate sampling resolution to the accurate characterization of spatial pattern in pelagic fish eggs. Barange and Hampton (1997) described the spatial organization of adults and eggs of Cape anchovy and sardine in the Benguela Current region with data from acoustic returns integrated over intervals of 1.85 km and net hauls at intervals of 9 km. Their analyses produced variograms with higher nugget effects and shorter ranges for sardine than for anchovy, though neither of the species had egg variograms with low nugget effects. Van der Lingen et al. (1998) elucidated these results with the analysis of CUFES survey data collected in September 1996. They found that variograms for sardine eggs in on-station CUFES and CalVET samples spaced 9 km apart were similar to those of Barange and Hampton (1997). However, variograms for sardine eggs in underway CUFES samples at a finer resolution of 2 to 4 km were highly structured and had low nugget effects (van der Lingen et al., 1998), demonstrating the influence of sampling resolution on the observed spatial pattern of pelagic fish eggs.

From this analysis and a review of the literature, it appears that spatial pattern in clupeoid eggs corresponds to the organization and behavior of spawning adults, which may be governed by several interacting variables that include population size and age structure, characteristic physical scales of the spawning habitat, swimming ability, and time of year relative to peak spawning season. As sardine or anchovy population sizes increase, the accompanying demographic shift towards larger, older
fish allows the formation of more extensive, faster-moving schools, which in turn results in a greater level of structure in the observed distributions of the spawned eggs.

Many interesting questions are sparked by this analysis. An obvious next step is a rigorous spatial analysis of existing ichthyoplankton and acoustic survey data from global upwelling regions to extract a better understanding of how the spatial organization of anchovy and sardine spawners varies with population size and the physical environment. This may require standardization of methods for ichthyoplankton collection and subsequent data analysis. Technological development will also create new opportunities to research the spatial distribution of fish eggs. In the near future, automated counting of fish eggs in the CUFES flow will permit resolution of egg distributions at the scale of meters. Automated counting will also vastly increase the effectiveness of standard surveys in addressing much finer scales than the present survey resolution. This will close the gap between the standard survey resolution for pelagic fish eggs and the scale of individual spawning schools seen on sonar, permitting the formation of a cohesive, synoptic picture of all scales of organization in at least one dimension.

The value of further study along these lines is magnified by the genetic structure of northern anchovy and Pacific sardine populations, which suggests that the historic population variability includes extinction and recolonization events (Grant and Bowen, 1998). Although the threat of extinction due to overfishing is small, poor resource management can disrupt ecosystems by temporarily depleting the target species (Beverton, 1990). Ultimately, a better understanding of the relationship of
spawning behavior to spawning habitat and environmentally driven fluctuations in population size may help identify anthropogenic effects on these highly variable populations, improving long-term management of the resources for species and ecosystem health.
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The text of this chapter, in part or in full, is a reprint of the material as it appears in Fisheries Oceanography. I was the primary researcher and author.
Table 2-1. Summary statistics for all grid-cohort data sets for Pacific sardine (*Sardinops sagax*), including the drifter displacement during the grid survey (the net movement of the drifter); the nugget effect, normalized by total variance; the mean, standard deviation, and range of the egg abundance; and the number of samples included in each data set (N, often a subset of all grid data points, because only points within polygons enclosing positive values were included in the analysis).

<table>
<thead>
<tr>
<th>Location</th>
<th>Grid</th>
<th>Date/Time Drifter displacement</th>
<th>Cohort</th>
<th>Stages/Expected Ages (hrs)</th>
<th>Nugget (normalized)</th>
<th>Mean (SD) (eggs min(^{-1}))</th>
<th>Range (eggs min(^{-1}))</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Patch 1</td>
<td>1</td>
<td>20 April 0900-1236 PST 1.9 km</td>
<td>1</td>
<td>X-XI (53-59)</td>
<td>0.02</td>
<td>2.0 (2.1)</td>
<td>0 - 8</td>
<td>49</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20 April 1910-2258 PST 4.3 km</td>
<td>2</td>
<td>VI-VII (30-36)</td>
<td>0.10</td>
<td>7.0 (8.7)</td>
<td>0 - 34.5</td>
<td>47</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>III-IV (12-18)</td>
<td>0.15</td>
<td>30.2 (21.3)</td>
<td>0.3 - 76.5</td>
<td>44</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Total</td>
<td></td>
<td>0.19</td>
<td>34.0 (28.2)</td>
<td>2.5 - 111.8</td>
<td>52</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>20 April 1910-2258 PST 4.3 km</td>
<td>2</td>
<td>VIII-IX (42-48)</td>
<td>0.04</td>
<td>1.5 (1.8)</td>
<td>0 - 7.4</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>V-VI (24-30)</td>
<td>0.09</td>
<td>13.8 (15.7)</td>
<td>0 - 54</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Total</td>
<td></td>
<td>0.10</td>
<td>14.1 (16.6)</td>
<td>0 - 58</td>
<td>43</td>
</tr>
<tr>
<td>3</td>
<td>3</td>
<td>21 April 0939-1252 PST 2.8 km</td>
<td>2</td>
<td>X-XI (53-59)</td>
<td>0.14</td>
<td>1.3 (1.5)</td>
<td>0 - 6.1</td>
<td>21</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>VI-VII (30-36)</td>
<td>0.02</td>
<td>8.5 (8.1)</td>
<td>0 - 24.2</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Total</td>
<td></td>
<td>0.06</td>
<td>9.2 (9.1)</td>
<td>0 - 25.9</td>
<td>27</td>
</tr>
</tbody>
</table>
Table 2-2. Summary statistics for all grid-cohort data sets for northern anchovy (*Engraulis mordax*), including the drifter displacement during the grid survey (the net movement of the drifter); the nugget effect, normalized by total variance; the mean, standard deviation, and range of the egg abundance; and the number of samples included in each data set (N, often a subset of all grid data points, because only points within polygons enclosing positive values were included in the analysis).

<table>
<thead>
<tr>
<th>Location</th>
<th>Grid</th>
<th>Date/Time Drifter displacement</th>
<th>Cohort</th>
<th>Stages/Expected Ages (hrs)</th>
<th>Nugget (normalized)</th>
<th>Mean (SD) (eggs min(^{-1}))</th>
<th>Range (eggs min(^{-1}))</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Patch 1</td>
<td>1</td>
<td>see above</td>
<td>1</td>
<td>IX-XI (49-57)</td>
<td>0.32</td>
<td>0.4 (0.3)</td>
<td>0 - 1.3</td>
<td>42</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total</td>
<td>1</td>
<td></td>
<td>0.07</td>
<td>1.0 (1.6)</td>
<td>0 - 7.2</td>
<td></td>
</tr>
<tr>
<td>Patch 2</td>
<td>1</td>
<td>25 April</td>
<td>1</td>
<td>VIII-X (37-44)</td>
<td>0.63</td>
<td>0.7 (0.6)</td>
<td>0 - 2.3</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1719-2023 PST</td>
<td>2</td>
<td>V-VI (22-27)</td>
<td>0.65</td>
<td>1.5 (1.2)</td>
<td>0 - 5.5</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.1 km Total</td>
<td></td>
<td></td>
<td>0.72</td>
<td>2.2 (1.4)</td>
<td>0 - 6.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>26 April</td>
<td>1</td>
<td>IX-XI (41-47)</td>
<td>0.94</td>
<td>0.4 (0.4)</td>
<td>0 - 1.5</td>
<td>49</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0208-0612 PST</td>
<td>2</td>
<td>VI-VII (27-32)</td>
<td>0.75</td>
<td>1.5 (1.0)</td>
<td>0 - 4.3</td>
<td>59</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.3 km Total</td>
<td>3</td>
<td>II-III (6-11)</td>
<td>N/A</td>
<td>0.1 (0.2)</td>
<td>0 - 0.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>26 April</td>
<td>2</td>
<td>VII-IX (32-37)</td>
<td>1</td>
<td>0.9 (0.5)</td>
<td>0 - 2.3</td>
<td>60</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1242-1649 PST</td>
<td>3</td>
<td>III-V (11-22)</td>
<td>0.83</td>
<td>0.7 (0.7)</td>
<td>0 - 3.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>4.4 km Total</td>
<td>1</td>
<td></td>
<td>1</td>
<td>1.6 (1.0)</td>
<td>0 - 4.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>26-27 April</td>
<td>2</td>
<td>IX-XI (41-47)</td>
<td>0.67</td>
<td>1.1 (0.8)</td>
<td>0 - 3.3</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2143-0107 PST</td>
<td>3</td>
<td>V-VI (22-27)</td>
<td>1</td>
<td>0.7 (0.6)</td>
<td>0 - 2.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.7 km Total</td>
<td>4</td>
<td>II (6)</td>
<td>N/A</td>
<td>0.1 (0.2)</td>
<td>0 - 1.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>27 April</td>
<td>3</td>
<td>VII-IX (32-41)</td>
<td>1</td>
<td>0.6 (0.5)</td>
<td>0 - 2.1</td>
<td>46</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1104-1416 PST</td>
<td>4</td>
<td>III-V (11-22)</td>
<td>0.62</td>
<td>0.5 (0.5)</td>
<td>0 - 1.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.0 km Total</td>
<td></td>
<td></td>
<td>0.82</td>
<td>1.1 (0.7)</td>
<td>0 - 3.2</td>
<td></td>
</tr>
</tbody>
</table>
Table 2-3. Average variogram parameters for each anchovy cohort in Patch 2 and sardine cohort in Patch 1. The normalized experimental variogram at the first lag and the normalized nugget effect were averaged across grids for each cohort. *Null hypothesis that means of anchovy and sardine values are equal is rejected (t-test, p<0.001).

<table>
<thead>
<tr>
<th>Cohort</th>
<th>Mean experimental variogram at first lag (normalized)*</th>
<th>Mean nugget effect (normalized)*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sardine</td>
<td>Anchovy</td>
</tr>
<tr>
<td>Cohort 1</td>
<td>0.24</td>
<td>0.89</td>
</tr>
<tr>
<td>Cohort 2</td>
<td>0.31</td>
<td>0.85</td>
</tr>
<tr>
<td>Cohort 3</td>
<td>0.30</td>
<td>0.86</td>
</tr>
<tr>
<td>Cohort 4</td>
<td>--</td>
<td>0.73</td>
</tr>
</tbody>
</table>
Table 2-4. Compilation of published variograms for eggs of *Engraulis* *spp.* and *Sardinops* *sagax*. In systems where both genera are present, a population is considered large if it exceeds the biomass of the population of the other genus. Acoustic estimates of spawning biomass off South Africa provide only relative, not absolute, abundances (Barange *et al*., 1999), so the population trends are listed instead. The normalized nugget effect (divided by total variance) is considered small if it is less than 50% of the total variance, and large if it is greater than 50% of the total variance.

<table>
<thead>
<tr>
<th>Region/Species</th>
<th>Population size</th>
<th>Nugget effect (normalized)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northeast Pacific</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. mordax</em></td>
<td>Small</td>
<td>Large</td>
<td>(this analysis)</td>
</tr>
<tr>
<td><em>S. sagax</em></td>
<td>Large</td>
<td>Small</td>
<td>(Lo <em>et al</em>., 2001; this analysis)</td>
</tr>
<tr>
<td>Northeast Atlantic</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. encrasicolus</em></td>
<td>Large</td>
<td>Small</td>
<td>(Bez, 2000; Uriarte and Motos, 1998)</td>
</tr>
<tr>
<td>Southeast Atlantic</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. capensis</em></td>
<td>Decreasing</td>
<td>Intermediate</td>
<td>(Barange and Hampton, 1997)</td>
</tr>
<tr>
<td><em>S. sagax</em></td>
<td>Increasing</td>
<td>Small</td>
<td>(van der Lingen <em>et al</em>., 1998)</td>
</tr>
</tbody>
</table>
Figure 2-1. Cruise tracks with egg concentrations at 3-m depth from CUFES (vertical bars, eggs min\textsuperscript{-1}) for SP0004 (solid line with black bars) and for CalCOFI 0004 (dashed line with gray bars). (a) Sardine egg abundance and inset of drifter track at Patch 1, with drifter positions marked for 0422 PST 20 April (starting position, star), 0422 PST 21 April, and 1722 PST 21 April (circles). (b) Anchovy egg abundance and inset of drifter track at Patch 2, with drifter positions marked for 1548 PST 25 April (starting position, star), 1548 PST 26 April, and 1513 PST 27 April (circles).
Figure 2.2. Histograms of mean concentration (eggs min$^{-1}$) of (a) sardine and (b) anchovy eggs by stage in each grid, with the date and start time of each grid shown.
Figure 2-3. Eulerian (a) and Lagrangian (b) maps of salinity at 3-m depth for Patch 1, Grid 1, 0900-1236 PST 20 April, with the starting position marked by white pentagram. Eulerian coordinates are GPS position of ship track. Lagrangian coordinates are GPS position of ship track minus GPS position of drifter track.
Figure 2-4. Sardine egg distributions and variograms. Two examples of staged sardine egg distributions overlaid on temperature at 3-m depth (a, c), with dashed lines delimiting the points included in the variograms. The corresponding directional variograms (b, d) were normalized by total variance. Symbol size in the variogram plots is proportional to the number of point pairs included in the variogram value at that lag. Zero degrees equals east-west. The experimental variograms were fitted to (b) an anisotropic spherical function and (d) an anisotropic linear function.
Figure 2-5. Anchovy egg distributions and variograms. Two examples of staged anchovy egg distributions in Patch 2 overlaid on temperature at 3-m depth (a, c). The corresponding directional variograms (b, d) were normalized by total variance. Symbol size in the variogram plots is proportional to the number of point pairs represented by the variogram value at that lag. The experimental variograms were fitted to isotropic linear functions.
Figure 2-6. Abundance maps of the two youngest anchovy egg cohorts on the first grids in which they were sampled, overlaid on temperature at 3 m. (a) Cohort 3, Grid 2, 0208-0612 PST 26 April. (b) Cohort 4, Grid 4, 2143 PST 27 April - 0107 PST 26 April.
Figure 2-7. Anchovy egg distributions and variograms for Patch 1, with dashed lines delimiting the points included in the variograms (a,c). The corresponding isotropic variograms (b, d) were normalized by total variance. Symbol size in the variogram plots is proportional to the number of point pairs represented at that lag. The experimental variograms were fitted to (b) a spherical function and (d) a linear function.
Figure 2-8. Directional variograms for temperature and salinity at 3-m depth in Patch 1, Grid 1 (a,b) and Patch 2, Grid 1 (c,d). The variograms were normalized by total variance. Symbol size in the variogram plots is proportional to the number of point pairs represented at that lag.
Figure 2-9. Comparison of abundances of anchovy eggs in CUFES (eggs min$^{-1}$) at 3-m depth (taken during station approach) and in PAIROVET (eggs 0.05m$^{-2}$) samples (linear regression, $r^2 = 0.70$, $p < 0.00001$).
Figure 2-10. Vertical profiles of potential density anomaly (sigma-theta, kg m\(^{-3}\)) from CTD casts in Patch 1 and Patch 2.
References


Chapter 3

Predicting the Vertical Distribution of Pelagic Fish Eggs: a Lesson in Patchiness

Abstract

The vertical distribution of pelagic fish eggs has been the subject of numerous modeling efforts. Here, I attempt to simulate the vertical distributions of northern anchovy (Engraulis mordax) and Pacific sardine (Sardinops sagax) eggs in the California Current region. Buoyancy of the eggs of both species was measured experimentally. Four different vertical mixing profiles, based on wind speed, mixed layer depth, and density profile, were combined with estimated terminal ascent velocities of the eggs to simulate the vertical distributions of the eggs. Model results were compared to data from vertically stratified net tows for both species, and tested on paired data for abundances of sardine eggs sampled at 3-m depth and in vertically integrated tows. Different vertical mixing models best predict the observed vertical distributions of anchovy and sardine eggs. Addition of a random error term to the terminal ascent velocity affects predictions of anchovy eggs, but not sardine. The model did not improve prediction of integrated abundances from samples at 3-m depth over a regression of 3-m on integrated abundances. Observed vertical distributions of sardine eggs are highly variable, and model development and verification may be impeded by horizontal patchiness or true vertical variability.
Introduction

Understanding the distribution of organisms in space is fundamental to reliable population estimates and to considerations of ecological interactions and life history processes. For the purpose of biological studies, space in the three-dimensional oceanic habitat is often broken down into horizontal and vertical components to simplify sampling methodology and theoretical approaches. It is important to remember that this separation is artificial, and that physical and biological processes in one dimension cannot be fully considered without reference to the other. Traditional net sampling is inadequate for separating vertical and horizontal elements of spatial structure. Variability in the vertical may strongly influence our ability to accurately assess the horizontal distribution of an organism, and vice versa, with temporal processes adding another layer of complication to this picture (e.g. Okubo, 1967). Interactions between vertical and horizontal processes present a particularly difficult problem for characterizing the spatial distribution of highly patchy organisms, such as pelagic fish eggs.

Let us assume for now a separation between vertical and horizontal processes. Variability at a given length scale is usually much greater in the vertical than in the horizontal. Knowledge of the vertical distribution of pelagic fish eggs is thus crucial to considering the spatial ecological processes that control mortality, including vertical overlap with predator populations and vulnerability to environmental stressors such as ultraviolet light (Hunter et al., 1979). Process studies on pelagic fish eggs, particularly those involving projections of development time and transport, also require knowledge
of vertical distribution. Finally, an inadequate understanding of the vertical
distribution of pelagic fish eggs compounds the challenge that horizontal variability
presents to determining their abundance.

Particular attention has been directed toward the abundance estimation
problem for eggs of clupeoid fishes, including sardine (Sardinops sagax and Sardina
pilchardus) and anchovy (Engraulis spp.), whose variable population size in
upwelling and boundary current regions is of interest to both ecologists and managers.
Population assessments for these species frequently use the Daily Egg Production
Method (Lasker, 1985), which requires abundance measurements of their early life
history stages. The positively buoyant eggs of sardine and anchovy occur
predominantly in and near the surface mixed layer, so sampling for these species is
generally confined to the top 70 m of the water column. Limited resources result in a
tradeoff between spatial coverage and horizontal resolution using accurate but low-
precision point estimates of depth-integrated abundances from vertical net hauls
(California Cooperative Oceanic Fisheries Investigations Vertical Egg Tow, CalVET;
Smith et al., 1985; Uriarte and Motos, 1998). The Continuous Underway Fish Egg
Sampler (CUFES; Checkley et al., 1997) is a high-volume pumped sampling system
that can sample on station or underway. CUFEs can integrate small-scale horizontal
variability, thereby increasing precision (van der Lingen et al., 1998), and
simultaneously allows efficient, high-resolution horizontal sampling of pelagic fish
eggs at a depth of 3 m. However, the utility of the new technology is limited by a lack
of the knowledge about the vertical distribution of eggs, which is needed for accurate
extrapolation from abundance measured at one depth to vertically integrated abundance.

Ichthyoplankton ecologists have approached the question of the vertical distribution of pelagic fish eggs with methods ranging from empirical to theoretical. Assuming relatively minor influence of horizontal processes, the time-dependent vertical distribution of pelagic fish eggs is determined by spawning depth, time since spawning, depth-dependent mortality, terminal ascent velocity, and the vertical diffusivity profile in the water column (Sundby, 1997). If vertical diffusivity is assumed to be constant in the mixed layer, positively buoyant eggs are expected to accumulate at the surface and decrease in concentration exponentially with depth (Sundby, 1983). Empirical studies of vertical distributions of clupeoid eggs include work on *Engraulis encrasicolus* and *Sardina pilchardus* in the Bay of Biscay (Motos and Coombs, 2000; Boyra *et al.*, 2003), *Engraulis mordax* off California (Moser and Pommeranz, 1999), *Engraulis japonicus* in Wakasa Bay (Tanaka 1992a), and *Sardinops sagax* (Silliman, 1943; Tanaka 1992b). Several one-dimensional spatial models of vertical egg distributions have been developed, including both steady-state and time-dependent models that vary in their parameterization of vertical diffusivity. The first of these was Sundby’s (1983) simple, steady-state solution balancing terminal ascent velocity and vertical diffusivity, where vertical diffusivity was derived as an empirical constant from observed vertical egg distributions. Page *et al.* (1989) elaborated the model by allowing ascent velocity to vary with depth, which permitted simulation of subsurface maxima. Time-dependent analytical solutions based on
elaborations of Sundby's basic model (Sundby, 1997; Westgård, 1989) and on models of mixed-layer physics (Cambalik, 1993; Westgård, 1989) have also been developed.

When extrapolating underway measurements at 3 m to integrated abundances, knowledge of the history of the water column in that location is generally not available. Therefore, two useful simplifications for the simulation of vertical distributions are to model in only one dimension and to assume steady state. The optimal model should be able to predict the vertical distribution of eggs given a few physical parameters that can be measured underway or interpolated between stations. These are major simplifications, considering the complexity of clupeoid egg distributions in space and time. This paper presents a model that can be applied to underway egg abundance data to predict integrated abundance from expected vertical distribution of Pacific sardine (Sardinops sagax) and northern anchovy (Engraulis mordax) eggs in the California Current region.
Materials and Methods

Field Collections and Data

The data for testing the model were collected on several cruises and in shore-based laboratory work. Vertical distributions of anchovy and sardine eggs were determined from R/V Robert Gordon Sproul 20 to 27 April 2000 (SP0004) and from NOAA R/V David Starr Jordan 19 to 25 March 1997 (JD9703) (Fig. 3-1). For each SP0004 collection (one for sardine; five for anchovy), eight 5-min vertically stratified samples were taken over roughly equidistant depth intervals in an oblique tow from 70 m to the surface with a 1-m² Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS-1, 333-μm mesh, Wiebe et al., 1985). MOCNESS collections from JD9703 (six for sardine eggs) each consisted of nine 1-min samples from 70 m to the surface, including one targeted for 3-m depth. Hydrographic data for the tows on both of these cruises were taken from the environmental package on the MOCNESS. On JD9703, the conductivity probe malfunctioned, so the surface salinity values from the ship’s conductivity-temperature unit for those stations were used and assumed to be constant over the depth of the profile (density is primarily determined by temperature in the California Current region). Wind data for SP0004 were taken from the ship’s MET package and averaged over 6 hours prior to the retrieval time for the MOCNESS, since the ship was within a few km of the positions for the tows over that time period. For JD9703, the ship was not on station before the tow, so the instantaneous wind for each tow was taken from the most proximate hourly observation on the ship’s bridge.
Observations of abundances of sardine eggs sampled at 3 m (CUFES) and in an integrated haul from 70 m to the surface (CalVET) were collected on six cruises on NOAA R/V David Starr Jordan, including JD9703 and the April 1998-2002 California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises. CUFES samples water at roughly 0.64 m$^3$ min$^{-1}$ (Checkley et al., 1997), while CalVET collections sample a volume of 3.5 m$^3$ and determine the abundance of eggs under 0.05 m$^2$ of sea surface. Stations with both a CalVET sample and a CTD profile were paired with either a CUFES sample collected simultaneously with the net tow (ca. 2-min duration) or the average of pre- and post-station CUFES samples (ca. 10- to 30-min duration each). A total of 90 paired observations met these criteria and were included in this analysis. CalCOFI winds were taken from on-station data, whereas the winds for JD9703 were taken from the most proximate hourly bridge observations. CTD profiles provided the hydrographic data for each station.

All plankton samples were preserved in a solution of 5% buffered Formalin in filtered seawater. MOCNESS samples were subsampled with a Folsom plankton splitter or a Stempel pipette such that either all the eggs or a minimum of about 100 eggs of the targeted species (anchovy or sardine) were sorted and counted. All sardine eggs in CalVET samples were sorted and counted. Sorted eggs were assigned a developmental stage (Moser and Ahlstrom, 1985; Lo et al., 1996) or classified as disintegrated, and the total estimated number of eggs in the sample was prorated to stages according to the proportions in the subsample. Sorting, counting, and staging were done under a dissecting microscope.
A density gradient column (Coombs, 1981) was used for density measurements of sardine and anchovy eggs collected in surface net tows. Sardine experiments were run at sea on NOAA R/V David Starr Jordan on the April 2001 CalCOFI cruise (JD0104). Anchovy experiments were run in March 2002 with eggs collected from a skiff off the Scripps Institution of Oceanography pier. After measuring density in the column, each egg was individually preserved in 5% buffered Formalin for later staging and measurement. The diameter (for spherical sardine eggs) or long and short axes (for ellipsoid anchovy eggs) of each egg were measured under a dissecting microscope with an ocular micrometer. Eggs measured fresh and again one month after preservation did not show a significant change in size (pers. obs., R/V Roger Revelle, April 2003). The buoyancy of the eggs is determined by the salinity of the environment rather than the temperature, since their thermal expansion coefficient is similar to that of water (Coombs, 1985). Thus, the density results are treated in terms of equivalent salinities.

**Simulations of Vertical Egg Distributions**

The simulations used the steady-state analytical solution for vertical egg distribution in the VertEgg software package (Ådlandsvik, 2000) in Matlab, which is based on Sundby’s original model (1983). Inputs are integrated abundance of eggs (eggs m\(^{-2}\)) and profiles of vertical diffusivity and of ascent velocity of the eggs. The model returns a vertical profile of the eggs over the binned depths specified in the initializing phase. 1-m depth bins were used for all the simulations presented here.
Eggs were assumed to travel at terminal ascent velocity throughout the water column. The salinity of seawater, which determines the buoyancy of the eggs when they have equilibrated to ambient temperature, usually changes relatively little in the upper 70 m in the California Current region, and far less than the inter-individual variation in equivalent salinity measured for each species. Therefore, the terminal ascent velocity was assumed to remain constant over the water column and was calculated, after Sundby (1983), for each set of environmental conditions from egg size and buoyancy. The buoyancy of the eggs was calculated as the density difference, at the ambient sea surface temperature, between seawater of the ambient sea surface salinity and seawater of the mean equivalent salinity of the eggs, as measured in the density gradient column. The permeable chorion of the egg allows the perivitelline fluid to equilibrate osmotically with the surrounding seawater (e.g. Davenport, 1981), so the equivalent salinity was corrected accordingly with

\[ S_{\text{egg}} = (1 - p) \times S_{\text{column}} + ps \times S_{\text{sw}} \]

where \( S_{\text{egg}} \) is the equivalent salinity used to calculate the terminal ascent velocity, \( S_{\text{column}} \) is the species-specific equivalent salinity of the egg measured in the density gradient column, \( S_{\text{sw}} \) is the sea surface salinity, and \( ps \) is the ratio of the perivitelline space to the total egg volume (0.05 for anchovy, 0.9 for sardine; Boyra et al., 2003). Anchovy eggs are ellipsoids, so their equivalent spherical diameter was used instead of diameter. The average dimensions of anchovy eggs lie within the theoretical shape limits that allow the equivalent spherical diameter to be used to calculate terminal velocity through a fluid at low Reynolds number without a correction factor (McNown
and Malaika, 1950) and Boyra et al. (2003) did not find that such a correction factor improved their model fit.

Model Variations

The vertical diffusivity profiles were parameterized in four ways (Fig. 3-2), which will be referred to as cubic, step, decay, and decay-50. In all cases, the background vertical diffusivity $K_0$ was set to $10^{-5}$ m$^2$ s$^{-1}$. The neutral wind stress $\tau$ at each station was calculated from shipboard wind observations after Large and Pond (1981), and the friction velocity $u^*$ from

$$u^* = \sqrt{\tau/\rho_0}$$

where $\rho_0$ is the density of seawater (set at 1025 kg m$^{-3}$). The mixed layer depth $m$ was set as the minimum depth at which the temperature was more than 0.2 °C less than the surface temperature.

Of the four diffusivity profiles, the cubic mixing profile (Pringle and Franks, 2001) most closely approximates the Mellor Yamada 2.5 turbulence closure scheme, a common turbulence parameterization in current, coastal-sea modeling (Jones, 2002). The profile of vertical diffusivity $K_z$ was calculated by

$$K_z(z) = K_0 + \kappa u^* \left( \frac{z}{m} - 1 \right)^2$$

where $\kappa$ is von Karman’s constant (0.41) and $z$ is positive and increases downwards. Since the cubic mixing profile goes to zero at the surface, a roughness length scale
was introduced to prevent the eggs from remaining stuck in the surface bin by setting \( K_z(0) \) equal to one half of \( K_z(1) \).

The step diffusivity profile, the simplest of the four profiles, was parameterized as

\[
K_z = \frac{k u^* m}{4}; \quad z \leq m \\
K_z = K_0; \quad z > m
\]

The decay profiles both have a surface vertical diffusivity equal to that in the step profile, which was allowed to decay to \( K_0 \) at some depth as the inverse of the change in density. For the decay profile, this depth was set to the minimum depth at which the temperature was more than 0.5 °C less than the surface temperature, while this depth was set at a constant 50 m in the decay-50 profile (Boyra et al., 2003). For simulations at shallow stations with sampling depths less than either decay model depth, the diffusivity profiles for the decay model(s) were allowed to decay to \( K_0 \) at the maximal depth of hydrographic sampling.

These four versions of the model were also modified by the addition of a normally distributed random error in the equivalent salinity of the eggs, with a standard deviation equal to that found in the experimental measurements. The addition of the error was achieved by running the model 100 times with 100 equidistant inputs for equivalent salinity spanning the one-percent confidence limits of equivalent salinity assuming a Gaussian distribution:

\[-2.57 * s \leq S_{column} \leq 2.57 * s\]
where $s$ is the experimental standard deviation for equivalent salinity of the eggs of that species. Each of the 100 resulting vectors of vertical egg distribution was multiplied by the value of the normal probability curve associated with the equivalent salinity used for that model run, then summed within equal depth bins to produce the final vector of vertical egg distribution.

**Validation**

The predictions of the vertical distribution simulations for sardine and anchovy were compared to the vertically stratified samples collected in MOCNESS tows. First, the abundance of eggs m$^{-2}$ was estimated from each MOCNESS tow to provide the simulation input, based on the assumption that each net represents an average of the depths over which it sampled. The concentration of eggs in each net was multiplied by the number of 1-m bins sampled by that net, and the sum of these provided an estimate of eggs m$^{-2}$. The simulations for the MOCNESS tows were run to 80-m depth, so that the simulated sampling of the water column would not encounter boundary effects. To compare the 1-m resolution output of the models to the MOCNESS net samples, which integrate over several meters, the depth and time records for each MOCNESS tow were used to simulate sampling of the depth bins of the modeled vertical distribution in the same proportions as the real tow.

A coefficient of determination was calculated to assess the fit of the models to each tow (Boyra *et al.*, 2003):
\[ R^2 = 1 - \frac{\sum (y_i - \hat{y}_i)^2}{\sum (y_i - \bar{y})^2} \]

where \( y_i \) is the observed egg concentration in net \( i \), \( \hat{y}_i \) is the predicted concentration, and \( \bar{y} \) is the mean observed concentration. All nets deeper than that with a simulated concentration of at least 0.025 eggs m\(^{-3}\) were summed for this comparison. The coefficient of determination in this sense can range from negative infinity to 1. It quantifies the fit of the model to the observed data, where 1 indicates perfect fit, and negative numbers indicate that the model fits the observed data worse than does the mean of the observed data, so they are reported as zeros.

The sardine models were further tested on the dataset of paired CUFES (eggs m\(^{-3}\)) and CalVET (eggs m\(^{-2}\)) observations. For these simulations, the models were run with inputs of 100 eggs m\(^{-2}\) and the shallower of 100 m or the station depth. The prediction of the vertically integrated abundance in CalVET from the observed CUFES concentration for that station was calculated by multiplying the CUFES concentration by the ratio of the summed model concentrations in each 1-m depth bin above the tow depth (usually 70 m) to the model concentration at 3 m. The performance of each model was evaluated with the coefficient of determination and compared to the prediction capability of a linear regression relating CUFES concentrations to CalVET abundances.

A few high-value points can easily influence the coefficient of determination. To account for this, the \( R^2 \) was recalculated 1000 times for bootstrapped sets of paired observations and model predictions (Efron and Tibshirani, 1993). In addition, the
simulations were rerun 100 times with bootstrapped sets of physical data inputs to see whether the models performed any better given the correct physical inputs as compared to random inputs.
Results

**Equivalent Salinities and Terminal Ascent Velocities**

Density measurements of sardine and anchovy eggs in the density gradient column are summarized as equivalent salinities in Fig. 3-3 and Table 3-1. Sardine eggs, for which stages II-XI were measured, showed significant increases in equivalent salinity at stages X and XI (Wilcoxon rank sum test with Bonferroni's correction, p<0.05). In anchovy eggs, for which stages IV-XI were measured, equivalent salinity appeared to fluctuate after stage IX, but no significant difference was found between stages. However, the median equivalent salinity of six unfertilized anchovy eggs was found to be significantly greater than the median of the both stage IV and all other stages (IV-XI) combined (Wilcoxon rank sum test with Bonferroni's correction, p<0.05).

Since the density changes that occur at later developmental stages may be related to increasing permeability of the vitelline membrane (Mangor-Jensen, 1987), the equivalent salinities of these older eggs in the density gradient column is unlikely to reflect that in the sea. Thus for the remainder of the analyses, only the statistics for stages II-IX are used. These stages were combined within each species, since there were no significant differences among them. Sardine eggs of these stages (n=208) have a median equivalent salinity (30.5) that is significantly less than that of anchovy (32.0, n=217; Wilcoxon rank sum test, p<0.05). The terminal ascent velocities of sardine (stages II-IX) and anchovy (stages IV-IX) eggs were calculated as a function of their equivalent salinities, dimensions, and the nominal ratio of perivitelline space...
to total egg volume for that species (Table 3-2). The null hypothesis that the medians of the calculated terminal ascent velocities for the two species are the same could not be rejected (Wilcoxon rank sum test, p = 0.6).

**Simulations: Sardine and Anchovy MOCNESS profiles**

Since the model is based on the buoyancies of stages IV-IX for anchovy and II-IX for sardine, and the depth of spawning is unknown, only stages III-IX were included in observed vertical profiles and estimates of eggs m\(^{-2}\) from MOCNESS sampling.

The standard deviation of the terminal ascent velocities calculated for the model with an error term in equivalent salinity was only 10% less than the standard deviation of velocities calculated for individual eggs. Thus the variance in equivalent salinity accounts for the majority of the variance in the calculated terminal ascent velocity for sardine and anchovy eggs.

The addition of an error term for equivalent salinity of sardine eggs to the models of the vertical distributions did not affect their predictions, so error was not included in the variations evaluated for sardine. Some of the model variations agreed reasonably well with three of the seven tows (Table 3-3; Fig. 3-4, upper panel), with the highest \(R^2\) usually exhibited by the cubic model, followed by the step model and the decay model. The decay-50 model had the lowest \(R^2\).

Error did affect the results of the models for anchovy eggs, so it was retained as a variable to be evaluated. The only parameterization of diffusivity that performed
well for anchovy eggs was decay-50, for which predictions compared favorably with all five tows (Fig. 3-4, lower panel), and the addition of error to the simulations further improved the fit (Table 3-4).

Simulations: Sardine CUFES and CalVET Data

The fit of predicted abundances of sardine eggs (eggs m$^{-2}$) from the four diffusivity parameterizations, given the concentrations measured in CUFES, temperature and salinity profiles, and wind speed, to the observed abundances in the CalVET collections were compared to the fit of predictions made using the slope from a linear robust regression, which is not sensitive to deviations from normality and outliers, of CUFES against CalVET ($m = 0.0317$, S-Plus 2000 robust MM regression; Table 3-5). The regression was forced through the origin to reduce the median residual and increase the proportion of variation in response explained by the model. The step and decay models performed about as well as the regression, with $R^2$ values near 0.2, while the cubic and decay-50 models had considerably lower $R^2$ values.

The mixed-layer-dependent mixing models (cubic and step) are expected to perform poorly under very low wind conditions, which can rapidly permit surface stratification. Due to the slow terminal ascent velocities of the eggs of both species (on the order of 1 m h$^{-1}$), they would be expected to occur deeper in the water column than would be predicted from these models as the mixed layer becomes shallower. Consequently, the data points for stations with winds less than 1 m s$^{-1}$ were removed and the $R^2$ values recalculated for the remaining 87 data points. Finally, since the
models are based upon buoyancies for stages II-IX and the eggs may take hours to reach the surface after spawning, the data points for CalVET samples containing less than 50% stages III-IX were excluded, leaving 65 data points for the $R^2$ calculations. For both of these reduced data sets, the cubic model performed somewhat better than the regression, the step and decay models performed similarly to the regression, and the decay-50 model continued to perform poorly (Table 3-5).

However, when examined visually, the spread of the cubic predictions, plotted against observed abundances, around a line of slope 1 (a perfect fit) appears as large as that of the regression predictions (Fig. 3-5). The data are log-transformed for visual presentation, but all statistics were calculated on untransformed data. The $R^2$ statistic can be strongly influenced by a few points, so the cubic model and regression results for the latter two data subsets were resampled with replacement by bootstrapping, and the $R^2$ values recalculated each time. The results indicate a large spread of $R^2$ values (Table 3-6a), as different sets of points are included in the calculations.

Finally, the physical oceanographic inputs to the cubic model were also resampled with replacement by bootstrapping, and the model run with 100 different sets of these resampled data. The $R^2$ values resulting from these model predictions made with mismatched physical data have a lower mean and a greater standard deviation than the $R^2$ values bootstrapped from the model predictions made with the matching physical data (Table 3-6b). The original $R^2$ values align with the upper end of the distribution for model runs with mismatched values.
Discussion

Several points can be taken from this analysis concerning life history design, the care necessary in model evaluation, and the interaction between patchy distributions and sampling design.

Equivalent Salinity and Terminal Ascent Velocity

The pattern in equivalent salinity of Pacific sardine and northern anchovy generally agreed with previous studies. Unfertilized eggs of anchovy had significantly higher equivalent salinities than fertilized eggs of all stages combined. Holliday (1965) found that unfertilized eggs do not osmoregulate, thus becoming isosmotic with surrounding seawater and losing their buoyancy. Coombs (1985) found that density of pilchard (Sardina pilchardus) eggs, like that of Pacific sardine here, remained relatively constant until the final developmental stages, when it increased rapidly. Accordingly, Mangor-Jensen (1987) reported an increase in permeability of the vitelline membrane of cod (Gadus morhua) eggs in late developmental stages, which he suggested reflects a tradeoff between buoyancy and an increase in exchange of gases and metabolites. However, northern anchovy eggs did not show a consistent pattern of increase in equivalent salinity with developmental stage in this study, while Tanaka (1990) did find a rapid increase in the final stages for Japanese anchovy (Engraulis japonicus). Tanaka used a series of beakers of different salinities rather than a density gradient column, so perhaps the column method adversely affects osmoregulation by late stages in anchovy. Since unfertilized anchovy eggs and late-
stage sardine eggs are denser than other stages, likely due to osmotic equilibration with the surrounding seawater (Holliday, 1965; Mangor-Jensen, 1987), they probably tend to occur deeper in the water column and may continuously sink due to the density of the chorion.

The comparative aspect of this study illuminated some interesting similarities and differences between propagule characteristics in Pacific sardine and northern anchovy. The maternal investment per egg in terms of the volume of the vitelline space is similar between these two species, as are the terminal ascent velocities for eggs collected at the sea surface. However, two very different egg designs arrive at the same terminal ascent velocity – the sardine has a more buoyant vitelline space but a much larger perivitelline space than the anchovy, highlighting the importance of taking the latter feature into account when determining the terminal ascent velocity from density measurements of the eggs.

The different ratios of perivitelline space to total egg volume also account for the greater effect on the predicted distributions of anchovy eggs of observed variation in equivalent salinity, although the observed variation is similar for sardine and anchovy (Table 3-2). The inclusion of the error term shifts the predicted distributions of anchovy eggs deeper, because a proportion of the eggs have terminal ascent velocities that approach zero, while the large perivitelline space in sardine eggs dampens the effect of variations in equivalent salinity. This difference may make biological sense when placed in the context of the springtime spawning habitats of the two species. Sardine spawn offshore at the inner edge of the California Current, while
anchovy spawn in nearshore waters (Checkley et al. 2000), which are typically much more stratified than the offshore waters during the stormy spring season. A tendency for anchovy eggs to occur deeper relative to the mixed layer may offset a difference in mixed layer depths typical of the spawning habitats and may also affect their transport.

Reasons for avoiding excessive accumulation at the surface include exposure to damaging ultraviolet radiation (Hunter et al., 1979; Vetter et al., 1999), concentration threshold effects in predators (Hunter and Dorr, 1982; Bailey and Houde, 1989). Butler’s (1987) identification of fundamental differences between the swimming behaviors of larval sardine and anchovy and the resulting opposite patterns in predation and starvation risks at this stage also suggests different optimizations of early life history strategies for these two species.

**Simulations: Sardine and Anchovy MOCNESS profiles**

The vertical profiles of anchovy and sardine eggs from MOCNESS sampling were best predicted by different diffusivity parameterizations. The cubic mixing profile, physically the most realistic, agreed best with three of the sardine MOCNESS tows, while the other four tows did not resemble any of the model predictions (Table 3-3, Figure 3-4). In contrast, the only mixing profile that agreed with the anchovy MOCNESS data was the decay-50 parameterization. This difference is unexpected, since the underlying dynamics should be the same for both species – a balance between egg buoyancy and physical mixing. Possible explanations for the disparity between sardine and anchovy simulations are unequal bias in the buoyancy...
measurements, strong shear-induced vertical mixing in the area where anchovy eggs were sampled, failure of the sardine MOCNESS tows to reflect the true vertical distributions, or different mortality rates with depth for the two species.

The buoyancy estimation of the eggs of both species is probably biased toward lower equivalent salinities because eggs for the experiments were collected in surface nets, so less buoyant eggs that occur deeper were not sampled. Since the addition of the error term has a greater effect on the predicted vertical distribution of anchovy eggs than sardine eggs, it is reasonable to conclude that the bias would be worse for anchovy. In this case, the decay-50 model can be thought of as implicitly incorporating a larger proportion of higher-density eggs, as is accomplished by adding the error term, rather than as the most correct physical model. However, it should be noted that the sardine eggs for the density measurements were collected in rougher conditions than were the anchovy eggs, so the inverse bias may also have been introduced. In either case, the likely bias in buoyancy measurements on eggs collected in surface tows renders suspect the approach frequently taken in other studies of inferring vertical diffusivity from known buoyancy and vertical distribution (e.g. Sundby, 1983) unless care has been taken to include eggs from all depths of occurrence in the experiments.

If strong vertical shear is present in the area where anchovy eggs were sampled near Santa Catalina Island, the vertical diffusivity profile would not be parameterized correctly by the simple mixed-layer dynamics that underlie the cubic and step profiles. This could cause a difference between the performances of different mixing profiles
for the two species, since it would violate the assumption that the underlying dynamics for the observed distributions of both species were the same.

Finally, the three sardine MOCNESS tows that were fit well by simulations may not be representative of the true vertical distribution of the eggs. In the tows for which the model did not perform well, the majority of the sardine eggs were collected below the thermocline (Fig. 3-4, upper panel). These data may be interpreted as an artifact of the horizontally patchy nature of the eggs and the horizontal movement during the oblique tow, with the inference that the ship had left the egg patch by the time the MOCNESS package sampled the mixed layer. But the tows that were matched well by the simulations may have likewise been the result of the net being towed into such a patch, so that the opposite problem occurred, with proportionally fewer eggs sampled below the mixed layer than is true at any one given spot. In this case, the real profiles of egg concentrations would be expected to lie between the two extremes, producing distributions that look much like those found for anchovy eggs (Fig. 3-4, lower panel).

Why are the observed vertical distributions of anchovy eggs from MOCNESS tows less variable than those of sardine? If the variability in the sardine distributions is purely due to horizontal patchiness, the 1-min net samples in the six sardine tows from JD9703 may coincide with some scale of horizontal variability, while the 5-min net samples in anchovy tows may average over that scale of variability. This explanation is reinforced if anchovy eggs are spawned in smaller patches (10s to 100s m) than sardine (100s m to km) (Smith and Hewitt, 1985; Lo et al., 2001; Curtis, in press).
Spawning in more numerous, smaller patches may also result in a more homogeneous distribution of eggs from the interaction between vertical and horizontal mixing processes (see below), so anchovy may in fact have more manageable three-dimensional distributions than sardine do for the purpose of predicting vertical distribution.

**Simulations: Sardine CUFES and CalVET Data**

The three explanations discussed for the difference in model performance between the two species have different implications. If greater bias exists in buoyancy measurements of anchovy eggs or the physical mixing model does not adequately represent mixing profiles in the coastal region where the anchovy eggs were sampled, then the relative performance of the different mixing profiles for sardine eggs should remain the same in the test with the paired CUFES and CalVET data set. On the other hand, if the true sardine profiles look like anchovy profiles and would also be better explained by the decay-50 profile, this profile should perform better than the others in the CUFES/CalVET test. The cubic model tends to perform the best of the four in the CUFES/CalVET data simulations (Table 3-5), but this result must be regarded with caution due to the high bootstrap standard error for the coefficient of determination (Table 3-6a).

The inaccuracy of the model in predicting integrated abundances from concentrations at 3-m depth may stem from three problems: 1) the application of a model based on stages III-IX to data that include all stages, 2) small numbers of eggs
in CUFES and CalVET samples (50 of the 90 CalVET tows have total egg counts less than 10), and 3) horizontal variability integrated by CUFES but not CalVET samples. Excluding samples containing less than 50% stages III-IX had a negligible effect on the performance of the model (Table 3-5), so the application of the model to samples with eggs of all stages is not likely the problem. The tendency for the cubic model predictions to lie closer to the 1:1 line with increasing value on a log-log plot (Fig. 3-5) supports the argument that small samples are a problem. Additionally, if factors other than the balance between vertical mixing and egg buoyancy strongly influence the vertical distributions of the eggs, they may be illuminated by efforts to optimize the prediction of CalVET abundances from CUFES samples with a Generalized Linear Model (C. van der Lingen, Marine and Coastal Management, South Africa, pers. comm.).

Boyra et al. (2003) also found a high degree of variability in their success at predicting the vertical distribution of eggs in any one vertically stratified tow, analogous to the MOCNESS tows in this study, for eggs of Engraulis encrasicolus or Sardina pilchardus in the Bay of Biscay. Only when they averaged across tows, and thus horizontal variability, were they able to achieve reliably good fits for their optimized vertical distribution models. Their use of density rather than equivalent salinity makes their results difficult to compare to other studies, but their optimal models for sardine and anchovy were the same, both including an error term in buoyancy and a gradual decay profile of vertical diffusivity. As was the case here, they obtained a worse average fit to individual sardine tows than to anchovy tows.
Tanaka (1992a) seemed to experience somewhat better success with Japanese anchovy (*Engraulis japonicus*), but he sampled at several depths simultaneously. The aggregated nature of clupeoid eggs may complicate model selection and evaluation and the task of predicting their vertical distributions.

In a two-dimensional sense, the horizontal patchiness incorporated by the sampling methods used to date for vertical distribution studies of fish eggs may cause the observed vertical distributions to be inconsistent from one tow to the next, as patches are encountered, entered, or exited at different points along the tows each time. The pairing of CUFES and CalVET samples is equally prone to this problem, since the CUFES samples were collected pre- and post-station in most cases and integrate much more horizontal variability, while the CalVET net samples only a very small surface area. Van der Lingen *et al.* (1998) and Bez (2000) demonstrated for *S. sagax* and *E. encrasicolus*, respectively, that underway CUFES samples have a much lower variance and thus higher precision than either on-station CUFES samples or CalVET collections.

One challenge, then, is to study the vertical distribution of pelagic fish eggs without confounding the data with horizontal variability. Plankton pumps, used effectively as one-dimensional samplers in studies of vertical distribution in other zooplanktonic taxa, have not been of much use in studying ichthyoplankton, whose abundances are generally too small to be sampled in sufficient numbers by the pumps. An elaboration of CUFES under development that will allow it to sample water at different depths of up to 70 m may solve this problem and provide a better instrument
for testing the vertical distribution models presented here (D. Checkley, Jr., Scripps Institution of Oceanography, USA, pers. comm.).

However, it may be that, in addition to the issue of horizontal patchiness alone, researchers on clupeoids are also dealing with particularly strong effects of the interaction between horizontal and vertical processes on spatial pattern. If the eggs are initially spawned at or below the thermocline, where shear is high, the slow predicted terminal ascent velocities of the eggs may produce distributions that are patchy in all three dimensions and have a long memory of the shear flow processes in that region. This would be particularly true of the larger patches with length scales of 100s m to km, characteristic of sardine spawning offshore (Lo et al. 1996; Curtis, in press), because the vertical deformation from shear-induced diffusion at these scales persists for 10s h to days (Csanady, 1978), similar to the development time of the eggs. In this case, the variability seen in data from vertically stratified tows may reflect not only horizontal patchiness but also vertical variability.

One cannot discount the possibility that variable vertical distribution reflects variable depth of spawning combined with the slow, and possibly overestimated (see above), predicted ascent rate of the eggs. Interestingly, Coombs (1985) found good replication of vertical distributions of pilchard (Sardina pilchardus) eggs in two consecutive tows, but high seasonal variability.

The problem of predicting the vertical distribution of the eggs will be complicated greatly if the assumption that underlies one-dimensional models, that the dynamics of vertical distribution are dominated by processes in the vertical, is
violated. Further study of the relationship between horizontal and vertical patchiness in clupeoid egg distributions is merited, perhaps by combining vertically stratified sampling with underway sampling at a fixed depth. The difficulty of predicting the vertical distribution of sardine eggs underscores the importance of continuing unbiased, and thus accurate, CalVET sampling. However, the variance associated with the small, localized CalVET samples calls for considering integration of results of underway sampling into abundance estimates.

Modeling approaches are useful tools for the synthesis of information to develop hypotheses and a new level of understanding. Here, simulations of the vertical distribution of northern anchovy and Pacific sardine eggs prompt consideration of the adaptive value of different egg designs and of the effect of three-dimensional physical and biological processes on the predictability of the distributions of highly aggregated organisms. The importance of testing the robustness of model evaluation statistics is also reinforced, in this case using bootstrapping procedures, to better evaluate results and their limitations. Simulations with theoretically based physical parameterizations predict the integrated abundance of clupeoid eggs from their abundance at a fixed depth about as well as does an empirical relationship between the fixed-depth and integrated abundances. A more rigorous test of the model will become possible as new advances in sampling methods for pelagic fish eggs in the vertical dimension minimize confusion with horizontal variability.
Acknowledgements

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Table 3-1. Median equivalent salinities and number of eggs measured (n) by stage for sardine and anchovy eggs in the density gradient column. *Null hypothesis that median equivalent salinity of stage is equal to the median of the next (for stage XI, preceding) stage is rejected (Wilcoxon rank sum test with Bonferroni’s correction, p<0.05). Unf = unfertilized eggs.

<table>
<thead>
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<th></th>
<th>Unf</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>VI</th>
<th>VII</th>
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Table 3-2. Mean and standard deviation of calculated terminal ascent velocities (v). D = diameter, esd = equivalent spherical diameter, $S_{column}$ = equivalent salinities, N = number of eggs measured, and $ps$ = nominal ratios of perivitelline space to total egg volume for sardine stage II-IX eggs and anchovy stage IV-IX eggs.

<table>
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<th>d or esd (cm)</th>
<th>$S_{column}$</th>
<th>$ps$</th>
<th>N</th>
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Table 3-3. $R^2$ values for sardine for fit of four diffusivity model variations (step - S, cubic - C, decay - D, decay-50 – D50). Results were obtained for seven MOCNESS tows, with different estimated abundances of stage III-IX eggs m$^{-2}$. Negative values of $R^2$ are reported as zeros.

<table>
<thead>
<tr>
<th>Tow</th>
<th>Cruise</th>
<th>Eggs m$^{-2}$</th>
<th>Model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>S1</td>
<td>SP0004</td>
<td>243</td>
<td>0.89</td>
</tr>
<tr>
<td>S2</td>
<td>JD9703</td>
<td>1414</td>
<td>0</td>
</tr>
<tr>
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<td>JD9703</td>
<td>66</td>
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<td>S4</td>
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<tr>
<td>S7</td>
<td>JD9703</td>
<td>483</td>
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Table 3-4. $R^2$ values for anchovy for fit of four diffusivity model variations (step - S, cubic - C, decay - D, decay-50 – D50) with and without error (E). Results were obtained for five MOCNESS tows, with different estimated abundances of stage III-IX eggs m$^{-2}$. Negative values of $R^2$ are reported as zeros.

<table>
<thead>
<tr>
<th>Tow</th>
<th>Cruise</th>
<th>Eggs m$^{-2}$</th>
<th>Model</th>
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<tr>
<td></td>
<td></td>
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<td>SE</td>
</tr>
<tr>
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Table 3-5. Fit of predictions of sardine eggs m$^{-2}$ from CUFES concentrations by four diffusivity model variations and a regression of CUFES against CalVET to the actual observations of eggs m$^{-2}$ in CalVET tows. $R^2$ was calculated for all stations, stations with wind (w) $\geq$ 1 m s$^{-1}$, and stations with wind $\geq$ 1 m s$^{-1}$ and proportion of stages III-IX in CalVET $\geq$ 50% of the total egg abundance.

<table>
<thead>
<tr>
<th></th>
<th>N</th>
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<th>Step</th>
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<th>Decay-50</th>
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<td>All Stations</td>
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<td>0.25</td>
<td>0.22</td>
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<tr>
<td>w $\geq$ 1 m s$^{-1}$</td>
<td>87</td>
<td>0.25</td>
<td>0.22</td>
<td>0.34</td>
<td>0.21</td>
<td>0</td>
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<tr>
<td>w $\geq$ 1 m s$^{-1}$ &amp; III-IX $\geq$ 50%</td>
<td>65</td>
<td>0.32</td>
<td>0.31</td>
<td>0.41</td>
<td>0.27</td>
<td>0.01</td>
</tr>
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</table>
Table 3-6. Results of bootstrap resampling of the CUFES-CalVET simulations with cubic model and regression relationship. Bootstrap means and standard errors of $R^2$ values are given for a) bootstraps of the original results for the wind-selected (W) stations and the wind- and stage-selected (WST) stations, and for b) the repeated cubic model runs with bootstrapped physical inputs for those two data subsets (P).

<table>
<thead>
<tr>
<th></th>
<th>Regression</th>
<th></th>
<th>Cubic</th>
<th></th>
</tr>
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<tbody>
<tr>
<td></td>
<td>$\bar{x}$</td>
<td>s.e.</td>
<td>$\bar{x}$</td>
<td>s.e.</td>
</tr>
<tr>
<td>a. Bootstrap W</td>
<td>0.28</td>
<td>0.16</td>
<td>0.31</td>
<td>0.21</td>
</tr>
<tr>
<td>Bootstrap WST</td>
<td>0.37</td>
<td>0.14</td>
<td>0.39</td>
<td>0.22</td>
</tr>
<tr>
<td>b. Bootstrap P W</td>
<td>-</td>
<td>-</td>
<td>0.08</td>
<td>0.43</td>
</tr>
<tr>
<td>Bootstrap P WST</td>
<td>-</td>
<td>-</td>
<td>0.11</td>
<td>0.46</td>
</tr>
</tbody>
</table>
Figure 3-1. Locations of MOCNESS sampling for sardine (S1 – S7) and anchovy (A) on SP0004 (☆) and JD9703 (+).
Figure 3-2. Example of four vertical diffusivity profiles used in the simulations with the density profile for station S1, 20-April-2000.
Figure 3-3. Equivalent salinity of anchovy and sardine eggs from the density gradient column. Median values for each developmental stage measured, with vertical bars representing first and third quartiles. Unf = unfertilized.
Figure 3-4. Observed and predicted concentrations of stage III-IX eggs in MOCNESS tows for sardine (upper panel) and anchovy (lower panel), plotted with density anomaly (sigma-theta) profile. Cubic (*) and decay-50 (o) model predictions are shown for both species. Predictions for decay-50 with error (Δ) are shown for anchovy eggs (lower panel).
Figure 3-5. Predicted (from CUFES) versus observed (CalVET) abundances of sardine eggs m$^{-2}$ for empirical regression (o), model with cubic mixing profile for winds $\geq 1$ m s$^{-1}$ (+), and model with cubic mixing profile for winds < 1 m s$^{-1}$ (⋆). Solid line indicates 1:1 agreement.
References


Chapter 4

Distributions in Geographic and T-S space: Potential for Interaction between

Key Species in an Upwelling System

Abstract

The distributions of the pelagic eggs of *Sardinops sagax* (Pacific sardine) and *Engraulis mordax* (northern anchovy) in the Southern California Bight region were examined in geographic and temperature-salinity (T-S) space in relation to the dominant euphausiid species and potential predator, *Euphausia pacifica*. California Cooperative Oceanic Fisheries Investigations (CalCOFI) survey data from two periods, 1953-59 and 1995-2002, show that *E. pacifica* overlaps with spawning areas of both sardine and anchovy in the region inshore of the California Current. The habitats of the three species show differences between three periods within the data set that correspond to cold and warm climate regimes. The distribution of *E. pacifica* in T-S space is similar in all three periods, but the percentage of positive stations is greater in cold years. During cold years (1953-57 and 1999-2002), sardine eggs tend to occur in higher salinity, cooler water, quite similar to *E. pacifica*, while anchovy eggs occur in higher salinity, warmer water. During the warm phase (1995-98), anchovy eggs occur in cooler, fresher water, resembling the restricted, coastal distribution of *E. pacifica*, while sardine eggs shift to warmer, fresher water. A test for complementary distributions of sardine and anchovy eggs in comparison to *E. pacifica*
shows that four years have significant index values for anchovy and *E. pacifica* (1954, 1996, 1997, 2002), the latter three of which are coincident with the three highest mean sample abundances of *E. pacifica*. This local-scale result supports the potential for interaction between anchovy and *E. pacifica* that is suggested by their overlap in broader geographic and T-S space. High predation pressure inshore may contribute to the adaptive value of offshore spawning by sardine when the population size off California is high.
Introduction

Upwelling and other boundary current systems are characterized by abundant, highly variable populations of species at low trophic levels, including euphausiids and coastal pelagic fishes. Ecological interactions between these species create the potential for dynamic links that may at times have cascading effects on the rest of the community. In the Benguela Current region, euphausiids are both important prey items for and likely competitors with zooplanktivorous species, such as Cape anchovy (*Engraulis capensis*) and young hake (*Merluccius* spp.) (Pillar *et al.*, 1992). Euphausiids are also predators on early life history stages of northern anchovy off California (Theilacker *et al.*, 1993), anchoveta (*E. ringens*) off Peru and Chile (Krautz *et al.*, 2003), and walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska (Bailey *et al.*, 1993).

Predation is a major source of mortality for early life history stages of marine fishes (Bailey and Houde, 1989; Houde, 1987) and defensively the primary source of mortality for non-feeding egg and yolk-sac larva stages, although endogenous factors, disease, and parasites may also be important (Heath, 1992). The extraordinarily high abundances reached by some euphausiid species in coastal surface waters at night (Brinton and Townsend, 2003; Sameoto, 1983) make them likely candidates as major predators on many species of coastal pelagic fish eggs and larvae that are concentrated in the top 10s m of the water column (e.g. Moser and Pommeranz, 1999). Complementary distributions of pelagic fish eggs and euphausiids in underway, pumped samples from surveys off California provide additional evidence that
interaction exists between euphausiids and pelagic fish eggs (Checkley et al., 2000; R.C. Dotson and D. Griffith, Southwest Fisheries Science Center, USA, pers. comm.). The complementary distribution might be explained by direct predation on the eggs, avoidance of areas of high euphausiidi abundance by spawning adults, or predation on euphausiids by spawning schools.

*Euphausia pacifica* is generally the most abundant euphausiidi species in the California Current System and has the broadest range, occasionally reaching its greatest densities near the coast of California (Brinton, 1976; Brinton and Townsend, 2003). The upwelling center in the Southern California Bight serves as a reproductive refuge in warm-temperate waters for this temperate species, but a large portion of the population may be advected into the area from the north in the California Current. The adult and juvenile stages of *E. pacifica* migrate into the top 50 m at night (Brinton, 1967) and may account for a large portion of the natural mortality of eggs and yolk-sac larvae of northern anchovy (Theilacker et al., 1993). Juvenile and adult *E. pacifica* are opportunistic omnivores (reviewed in Mauchline, 1980; see also Dilling et al., 1998; Ohman, 1984), so they are probable predators on other species of pelagic fish eggs as well, although phytoplankton are likely to predominate in their diets (Ohman, 1984). *E. pacifica* may be an important member of a suite of predators affecting survivorship in the spawning habitat of coastal pelagic fishes. Characterizing the relative distributions of *E. pacifica* and the spawning habitats of key coastal pelagic species of fish is of interest, particularly for the highly variable and abundant northern anchovy and Pacific sardine.
Winter and spring (January to June) spawning habitats for Pacific sardine (Sardinops sagax) and northern anchovy (Engraulis mordax) in the California Current System occupy distinct regions in temperature-salinity (T-S) space, which reflect differences in their geographic distributions relative to dominant physical forcing mechanisms. Sardine eggs occur primarily in the cool water of the frontal region at the shoreward edge of the California Current, while northern anchovy eggs are most abundant in coastal, high-salinity, upwelled waters (Checkley et al., 2000; G. A. Rebstock and D. M. Checkley, Jr., Scripps Institution of Oceanography, USA, unpub.). The spawning habitats of both species expand and contract with population size over decadal time scales, but the centroid of anchovy spawning always remains contiguous with the coast (MacCall, 1990), while springtime sardine spawning activity is centered offshore at large population size (MacCall, 2001). The changes in spawning habitat and population size coincide and interact with ecosystem-wide state changes between cold and warm regimes (Mantua et al., 1997; Rebstock, 2003). During warm regimes, when the California Current moves offshore and upwelling is diminished in the Southern California Bight region (Bograd and Lynn, 2003), the sardine population increases. In contrast, the anchovy population increased during the cold regime that ended in 1976-77 (Smith, 1972; Smith and Moser, 2003). Superimposed on this decadal variability, El Niño events are a major source of interannual variability in the physical and biological components of the Southern California Bight (Bograd and Lynn, 2003; Hayward, 2000).
The interaction between geographic changes in spawning habitat and physical forcing mechanisms are likely reflected in the T-S distributions of the eggs and may also affect the strength of their interaction with euphausiids. This study characterizes the distributions of the pelagic eggs of two clupeoids, Pacific sardine and northern anchovy, in geographic and T-S space in the Southern California Bight region relative to the dominant euphausiid species (Brinton, 1976; Brinton and Townsend, 2003) and potential predator, *E. pacifica*. The time periods included encompass cold and warm regime conditions (Bograd and Lynn, 2003; Laveniegos and Ohman, 2003) and two strong El Niño events. Finer-scale, more direct evidence for interaction between clupeoids and euphausiids is also sought by testing for local correlation between their distributions. Euphausiids have been trophically linked to clupeoids in upwelling and boundary current systems as a key dietary component, probable competitor (Pillar *et al.*, 1992), and predator on their early life history stages. Strong ecological interactions between the abundant, variable populations of these taxa and physical forcing mechanisms likely contribute to the dynamic character of these ecosystems. Evidence of the potential for and realization of such interactions is thus of great interest to understanding these systems.
Materials and Methods

The distributional data for combined juvenile and adult *E. pacifica* and the eggs of sardine and anchovy were collected in plankton tows on CalCOFI cruises, which survey a grid of stations in the California Current System (Fig. 4-1). Sampling methods and gear are described in Kramer et al. (1972), Smith and Richardson (1977), Moser et al. (2003), Ohman and Smith (1995), and Brinton and Townsend (2003). Euphausiid data originate from the study of Brinton and Townsend (2003). All abundances are expressed as densities in number per 10 m² of sea surface. When available, temperature and salinity at 10-m depth from hydrocasts or conductivity-temperature-depth probes were combined with the euphausiid and egg data from each station. The data for this analysis were limited temporally to the periods 1953-59 and 1995-2002 in winter and spring (January – June), and geographically from lines 77 to 93 as far offshore as station 80 (Fig. 4-1). This area is largely southeast and inshore of the spawning habitat of sardine observed in recent years (Checkley et al., 2000) and north of the spawning area of sardine in the 1950s (Kramer, 1970). During 1953-1959, CalCOFI cruises were monthly, so the dataset for the period 1953-59 includes six cruises per year (five for 1957), as compared to two cruises per year during 1995-2002. Only night stations were used for euphausiids, including from approximately one hour after local sunset to one hour before local sunrise. Daytime tows often catch more than an order of magnitude fewer juvenile and adult *E. pacifica* than nighttime tows, due to a combination of avoidance and vertical migration (Brinton and Townsend, 1981). Gear and sampling changes between the 1950s and 1990s increased
the capture efficiency for juvenile and adult *E. pacifica* (Brinton and Townsend, 1981) and less so for anchovy eggs (Lo, 1983), but no correction factors were introduced in this analysis.

The arithmetic mean of the density of each species in each year is given as a proxy of abundance in the SCB region. Arithmetic means were used rather than multiplying each station density by the area around it to arrive at a total abundance for the area surveyed, since the number of stations included in the analysis varied between cruises. Back-transformed means and confidence intervals of log-transformed (ln[x+1]) values are given for comparison.

T-S diagrams with abundances of *E. pacifica* and sardine and anchovy eggs were plotted for each year and for sets of years that correspond to cold and warm regime conditions: 1953-59 (cold), 1995-98 (warm), and 1999-2002 (cold) (cf. Mantua *et al.*, 1997; Bograd *et al.*, 2000; Laveniegos and Ohman, 2003). These time periods encompass two El Niño events (1958-59, 1998) that produced particularly strong anomalies in zooplankton volume in the California Current region (reviewed in Hayward, 2000) and in observed species of fish off California (Lea and Rosenblatt, 2000), so these years were considered separately and are classified as "warm" years in the Results. For each set of years, the mean and standard deviation of temperature and salinity for sardine and anchovy eggs and euphausiids, weighted by their log-transformed densities in each sample, were calculated and plotted with the unweighted mean and standard deviation for all samples.
Distributions of sardine and anchovy eggs were also compared to those of juvenile and adult *E. pacifica* on a local scale. To test for complementary distributions of sardine and anchovy eggs with respect to *E. pacifica* on a sample-by-sample basis, a local index of complementarity *I* (i.e. local index of collocation, Bez and Rivoirard, 2000) was computed

\[
I = \frac{\sum (z_1 z_2)}{\sqrt{\left(\sum z_1^2 \sum z_2^2\right)}},
\]

where \(z_1\) and \(z_2\) are the abundances in each sample of the two populations being compared. \(I\) is a measure of correlation that ranges from zero to one and is not sensitive to the number of samples with zeros for both species. Since the index is calculated for paired samples, only nighttime samples were included for all three species. The significance level of \(I\) was determined by recalculating \(I\) for 1000 random permutations of the egg abundances within each cruise among the samples that were positive for either *E. pacifica* or eggs of the species of interest. \(I\) was considered significant, i.e. the distributions of the two species being considered were more complementary than expected by random chance, if fewer than 50 of the 1000 values of \(I\) calculated by random permutation were less than the index calculated for the actual distributions (\(p < 0.05\)).
Results

Geographic Distribution

*E. pacifica* adults and juveniles are widely distributed in the study area, with localized spots of high abundance (Fig. 4-2). An average of 87% of all night stations over all years in the dataset are positive for *E. pacifica* juveniles and adults, with higher percent positive stations in cold years (Wilcoxon rank-sum test, $p < 0.0005$; Tables 4-1,4-2). During El Niño years, the mean abundances of *E. pacifica* are lower (1958-59, 1998; Wilcoxon rank-sum test, $p < 0.05$; Table 4-1) and its geographic distribution is also contracted toward the coast (Fig. 4-2). Anchovy egg distributions are contiguous with the coast in all years, frequently extending southwest of San Clemente Island, with further offshore expansion in the late 1950s (Fig. 4-2). Sardine eggs tend to occur offshore, outside the Southern California Bight, but during warm years (1958-59, 1995-98), spawning is contiguous with the coast and overlaps with that of anchovy (Fig. 4-3). A higher percentage of stations are positive for sardine eggs in warm years (Wilcoxon rank-sum test, $p < 0.005$; Table 4-2). The geographic ranges of the eggs of both species in the study region coincide with that of *E. pacifica* due to its broad distribution.

T-S Distribution

The T-S distributions of anchovy eggs, sardine eggs, and *E. pacifica* juveniles and adults show changing relationships between the three species under different environmental conditions (Fig. 4-4a-e). The weighted means of temperature and
salinity (centroid) for *E. pacifica* follow the sample mean in all periods except the
1998 El Niño, shifting warmer and fresher with the sample mean during the warm
regime. In contrast, the centroids for sardine and anchovy eggs move relative to the
sample mean between warm and cold periods (Fig. 4-4a,c,e). During both 1953-57 and
1999-2002, the anchovy centroid is warmer and saltier than *E. pacifica*, but the sardine
centroid shifts from being similar to anchovy during 1953-1957 to an even cooler
position than that of *E. pacifica* during 1999-2002 (Fig. 4-4a,e). The weighted
standard deviations of salinity and temperature for anchovy eggs, *E. pacifica*, and all
samples are smaller in 1999-2002 than during the 1950s, and their centroids are saltier.

All three species have similar centroids during the 1958-59 El Niño (Fig.
4-4b), having shifted warmer and saltier by varying degrees to overlap with the sample
mean.

During warm regime years (1995-97), sardine eggs, *E. pacifica*, and sample
means closely overlap and are shifted warmer and fresher than in the cold periods,
while the anchovy centroid is shifted warmer, to a position slightly saltier than the
other species (Fig. 4-4c).

The 1998 El Niño looks quite different from that of 1958-59. Compared to
non-El-Niño years, the centroid for *E. pacifica* is shifted warmer and aligns with the
sardine centroid, which is similar to its position in 1995-97. *E. pacifica* and sardine
eggs are centered in fresher and cooler water than the sample mean, while the anchovy
centroid is saltier than the mean, and also saltier and warmer than its position in 1995-
97 (Fig. 4-4d). The four centroids appear to align along a pronounced diagonal axis from warm, salty water to cool, fresh water.

**Local Index of Complementarity**

Four of the p-values for the year-wise values of the local index of complementarity for anchovy eggs and *E. pacifica* adults and juveniles are significant (p < 0.05; Table 4-3). If Bonferroni’s correction for multiple testing is applied, the critical p-value for the same alpha-level is shifted to 0.05/15, or 0.003, so only 1997 remains significant. Three of the p-values less than 0.05 occur in the 1995-2002 period (1996, 1997, 2002) and coincide with the three highest mean abundances of *E. pacifica* (Table 4-1). No night samples are positive for sardine eggs in 1953, so the index was not calculated for that year. None of the values for the index of complementarity for sardine eggs and *E. pacifica* are significant (Table 4-3).
Discussion

Variability in the relative distributions of the pelagic eggs of Pacific sardine, northern anchovy, and adults and juveniles of *E. pacifica*, an abundant potential predator on ichthyoplankton, shows concordance with ecosystem changes occurring on multiyear time scales. The distributions of these three species were examined in geographic and T-S space in the Southern California Bight (SCB) region for 1953-1959 and 1995-2002, encompassing two El Niño events (1958-59, 1998) and three multiyear warm and cold periods in the California Current System (Bograd and Lynn, 2003; Lavanigos and Ohman, 2003).

*E. pacifica* occupies a larger percentage of stations in cold years (Table 4-2). *E. pacifica* has a lower mean abundance in El Niño years than other years (Table 4-1), so it may have had less potential impact on natural egg mortality in those years. Brinton and Townsend (2003) considered all life stages of *E. pacifica* and found that its abundance does not change significantly between cold and warm regimes (pre- and post-1976-77), but they noted large declines in abundance with El Niño events. During El Niño years, the geographic distribution of *E. pacifica* in the Southern California Bight region is also contracted closer to the coast (Fig. 4-2). The T-S centroid for *E. pacifica* aligns with the sample mean during warm and cold periods (Fig. 4-4). The lower percent positive stations in warm years suggests that the breadth of suitable habitat for *E. pacifica* is less than during cold years, but this difference in area of habitat does not appear to correlate with mean abundance (Table 4-2).
Anchovy eggs occur in nearshore waters, extending farther offshore in the 1950s than in 1995-2002 (Fig. 4-2). Smith and Moser (2003) found that abundances of anchovy larvae were increasing in the 1950s and smaller and decreasing in 1995-2000, which reflects changes in spawning biomass in the 1950s (Smith, 1972). Thus the offshore extension of the egg distributions in this study likely correlates with population size and agrees with MacCall's (1990) basin theory of expansion of spawning habitat with population size. The T-S distribution of anchovy tends to agree with previous nearshore, high-salinity characterizations (Checkley et al., 2000; G. A. Rebstock and D. M. Checkley, Jr., Scripps Institution of Oceanography, USA, unpub.) but shows changes over the period studied. The anchovy centroid is saltier and warmer than the sample mean in the two cold regimes (Fig. 4-4a,e), but the smaller weighted standard deviations in 1999-2002 likely reflect the contracted spawning habitat at small population size (Fig. 4-2). During the warm regime, the anchovy centroid is fresher, closely aligning with the other centroids. The potential for overlap between E. pacifica and anchovy eggs would be expected to be highest during warm years.

Sardine eggs tend to occur offshore of the anchovy egg distributions, outside the SCB, but they overlap with anchovy during warm years to become contiguous with the coast (Fig. 4-3). Sardine eggs occur at a higher percentage of stations during warm years (Table 4-2). T-S diagrams for recent years agree with previous findings that sardine egg habitat is cooler and fresher than anchovy egg habitat (Checkley et al., 2000; G. A. Rebstock and D. M. Checkley, Jr., Scripps Institution of Oceanography, USA, unpub.). However, in the warm regime, the T-S diagram
diverges from that of Checkley et al. (2000) from the same period. This disparity results from the restriction of this analysis to the SCB region, so it is missing cooler, low-salinity values from north of Point Conception that are included in the analysis of Checkley et al. (2000). In the 1950s as well, sardine aligns closely with anchovy, which is puzzling since the two are clearly separated in geographic space. This may be in part because much of anchovy spawning occurs prior to the upwelling season in cool water of relatively low salinity. The sardine centroid shifts warmer and fresher during the warm regime (1995-97), reflecting the change in available habitat as the California Current moves offshore and the influence of upwelling decreases, as is manifest in the T-S diagram (Bograd and Lynn, 2003). The sardine centroid in 1999-2002 is cooler than in the 1950s during the first cold regime (Fig. 4-4a,e). This may be related to the population size of Pacific sardine, which is smaller in the 1950s than in 1999-2002 (MacCall, 1979; Conser et al., 2002). MacCall (1979) also suggested that the sardine spawning in the SCB region in the 1950s may be from a different, southern stock off Baja California, which is supported by maps of sardine eggs and larvae in the 1950s (Kramer, 1970) that show the eggs in the SCB region as the northern extent of a spawning distribution that is centered off Baja. During 1999-2002, on the other hand, the spawning in the SCB region appears to be the southeastern extreme of a distribution that is centered offshore and north of Point Conception (Checkley et al., 2000; R. Charter, Southwest Fisheries Science Center, USA, pers. comm.; N.B. data south of the SCB region are not available for 1995-2002). The sardine centroid during both 1995-1997 and El Niño events is in close proximity to that of E. pacifica (Fig. 4-
4b-d). This proximity in T-S space as well as coastally contiguous geographic distribution of sardine eggs during warm years suggest that the potential for overlap and interaction between these two species in the SCB region is also maximized in warm years.

Different responses to the two El Niño events are seen in the centroids for sardine and anchovy eggs and *E. pacifica* (Fig. 4-4b,d). The explanation for these differences seems to lie in month-to-month variability in 1998 in the distributions of the variables involved. The strong diagonal axis in the upper right quadrant of the T-S diagram in 1998 is due to an intrusion of subtropical water in February (Hayward, 2000). Sardine eggs only become abundant in April, so their centroid is fresher and cooler than the sample mean for both months. *E. pacifica* is patchily distributed during both El Niño events, but in 1998, few positive samples occur in the subtropical intrusion in February, so its centroid is also shifted cooler and fresher than the sample mean for this year. Anchovy eggs are concentrated in the salty, nearshore waters in both months of 1998, shifting their centroid saltier than the mean. In contrast, during both the 1958-1959 El Niño and the 1995-1997 warm years, the centroids for all three species and the sample mean are similar, suggesting that the habitat in the Southern California Bight is homogeneous in most warm years, relative to cold years, by the weakness of the influence of nearshore upwelled water, barring a subtropical intrusion as in 1998.

The local index of complementarity provides a means of assessing more directly whether the distributions of sardine or anchovy eggs appear to interact with
those of *E. pacifica*. Four years have a significant index of complementarity for anchovy and *E. pacifica* (Table 4-3), of which three coincide with the three highest mean abundances of *E. pacifica* among the years in the dataset, and two coincide with the warm regime, during which interaction between these two species is expected to be maximized. None of the years have a significant index of complementarity for sardine and *E. pacifica*.

Three explanations exist for the observed complementary distributions of anchovy eggs and *E. pacifica*: the euphausiids may be eating "holes" in the anchovy eggs distributions (in the sense of Genin *et al.*, 1988), adult anchovy may be avoiding spawning in areas of high euphausiid abundance, or selectively feeding adult anchovy may be eating "holes" in the euphausiidi distributions (Koslow, 1981). The latter explanation is not supported by the coincidence of three of the significant index values with the three years of greatest euphausiid abundance in the dataset, as it would seem more likely that anchovy feeding would have an impact on a smaller population of euphausiids. The lack of interaction between sardine eggs and *E. pacifica* makes the first explanation of direct predation on the eggs less likely, though anchovy and sardine may interact differently with *E. pacifica* when their habitats respectively coincide maximally: during maximal coincidence for anchovy, anchovy and *E. pacifica* are restricted to a smaller area and may thus experience stronger interactions. Since sardine spawning in the SCB region is peripheral to the primary spawning grounds of the species, the lack of interaction between sardine eggs and *E. pacifica* may be due to lack of adaptation by sardine to local processes in the SCB. This last
idea supports the explanation that adult anchovy choose not to spawn in areas of high abundance of *E. pacifica*.

Logerwell and Smith (2001) found that late sardine larvae ("survivors") are found mostly offshore in mesoscale eddies. The offshore spawning habitat that sardine exploit at large population sizes likely has several advantages. Evidence for local interaction between anchovy eggs and *E. pacifica* suggests that high predator concentrations in nearshore habitat may interact with sardine on a global, evolutionary scale as part of the driving force to reproduce in offshore habitat under favorable conditions. This idea is supported by the greater susceptibility of sardine larvae than anchovy larvae to predation, due to the greater proportion of time spent in motion, which also makes them capable of surviving at lower food concentrations (Butler, 1987).

This analysis examines the interaction between the distributions of sardine and anchovy eggs and *E. pacifica* both in broad terms in geographic and T-S space and at the local scale of paired sample-by-sample abundances. The results suggest that the potential for ecological interactions between the abundant, variable populations of euphausiids and clupeoids in the SCB changes with large-scale, long-term patterns in physical forcing. Interactions between these key species and the influence of variable physical forcing on them, as seen in geographic and T-S distributions, may contribute to the dynamic character of these ecosystems and influence the evolutionary adaptations of the organisms involved.
Acknowledgements

I thank Edward Brinton for permission to use his euphausiid data and the SIO Pelagic Invertebrates Collection, especially Annie Townsend and Mark Ohman, for furnishing them. Richard Charter of the Fisheries Resources Division at the Southwest Fisheries Science Center, the CalCOFI program and staff, and Ginger Rebstock provided data on egg distributions and hydrography. Dave Checkley, my advisor, provided encouragement, insight, and feedback. Valuable feedback was also supplied by my committee members, Mark Ohman, Rob Pinkel, Kaustuv Roy, and Paul Smith. This work was supported by the National Sea Grant College Program of the U.S. Department of Commerce’s National Oceanic and Atmospheric Administration under NOAA Grant #NA06RG0142, project #86-F-N, through the California Sea Grant College Program.
Table 4-1. Percent positive (pp) and mean abundances for anchovy and sardine eggs (night and day stations) and *E. pacifica* (night stations only) for each year. W = warm, C = cold. * marks years with a significant index of complementarity. Back-transformed means and 95% confidence intervals (± 2 standard errors) of log-transformed values (\ln(x+1)) are given for comparison.

<table>
<thead>
<tr>
<th></th>
<th>Anchovy Eggs</th>
<th></th>
<th>Sardine Eggs</th>
<th></th>
<th><em>E. pacifica</em></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>pp</td>
<td>(\bar{x})</td>
<td>Log Mean</td>
<td>Log C.I.</td>
<td>pp</td>
<td>(\bar{x})</td>
</tr>
<tr>
<td>1953</td>
<td>C</td>
<td>14</td>
<td>15.6</td>
<td>0.5</td>
<td>0.3-0.8</td>
<td>3</td>
</tr>
<tr>
<td>1954*</td>
<td>C</td>
<td>28</td>
<td>38.1</td>
<td>1.9</td>
<td>1.2-2.9</td>
<td>16</td>
</tr>
<tr>
<td>1955</td>
<td>C</td>
<td>35</td>
<td>85.6</td>
<td>3.2</td>
<td>1.8-5.2</td>
<td>19</td>
</tr>
<tr>
<td>1956</td>
<td>C</td>
<td>20</td>
<td>29.4</td>
<td>1.2</td>
<td>0.6-2.0</td>
<td>5</td>
</tr>
<tr>
<td>1957</td>
<td>C</td>
<td>39</td>
<td>1202.2</td>
<td>11.2</td>
<td>4.8-24.8</td>
<td>6</td>
</tr>
<tr>
<td>1958</td>
<td>W</td>
<td>58</td>
<td>329.2</td>
<td>11.9</td>
<td>7.1-19.5</td>
<td>19</td>
</tr>
<tr>
<td>1959</td>
<td>W</td>
<td>55</td>
<td>211.1</td>
<td>10.2</td>
<td>6.6-15.7</td>
<td>18</td>
</tr>
<tr>
<td>1995</td>
<td>W</td>
<td>36</td>
<td>393.8</td>
<td>4.2</td>
<td>2.5-6.5</td>
<td>18</td>
</tr>
<tr>
<td>1996*</td>
<td>W</td>
<td>25</td>
<td>412.5</td>
<td>3.1</td>
<td>1.7-5.2</td>
<td>38</td>
</tr>
<tr>
<td>1997*</td>
<td>W</td>
<td>28</td>
<td>359.5</td>
<td>3.8</td>
<td>2.2-6.3</td>
<td>30</td>
</tr>
<tr>
<td>1998</td>
<td>W</td>
<td>22</td>
<td>90.1</td>
<td>1.9</td>
<td>1.1-3.1</td>
<td>28</td>
</tr>
<tr>
<td>1999</td>
<td>C</td>
<td>18</td>
<td>162.0</td>
<td>1.4</td>
<td>0.8-2.3</td>
<td>17</td>
</tr>
<tr>
<td>2000</td>
<td>C</td>
<td>21</td>
<td>196.8</td>
<td>2.1</td>
<td>1.1-3.4</td>
<td>11</td>
</tr>
<tr>
<td>2001</td>
<td>C</td>
<td>25</td>
<td>4.4</td>
<td>0.8</td>
<td>0.5-1.2</td>
<td>17</td>
</tr>
<tr>
<td>2002*</td>
<td>C</td>
<td>31</td>
<td>2.6</td>
<td>0.8</td>
<td>0.5-1.1</td>
<td>7</td>
</tr>
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</table>
Table 4-2. Mean and standard error, for cold and warm years, of mean abundance ($\bar{x}$, $s_{\bar{x}}$) and percent positive stations ($pp$, $s_{pp}$). Values for anchovy and sardine eggs include night and day stations, *E. pacifica* includes night stations only.

<table>
<thead>
<tr>
<th></th>
<th>Anchovy Eggs</th>
<th>Sardine Eggs</th>
<th><em>E. pacifica</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{x}$</td>
<td>$s_{\bar{x}}$</td>
<td>$pp$</td>
</tr>
<tr>
<td>Cold</td>
<td>193</td>
<td>128</td>
<td>26</td>
</tr>
<tr>
<td>Warm</td>
<td>299</td>
<td>51</td>
<td>37</td>
</tr>
</tbody>
</table>
Table 4-3. P-values and values of local index of complementarity, calculated using night stations only (* p<0.05).

<table>
<thead>
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<tbody>
<tr>
<td></td>
<td>I</td>
<td>p-value</td>
</tr>
<tr>
<td>1953</td>
<td>0.029</td>
<td>0.399</td>
</tr>
<tr>
<td>1954</td>
<td>0.069</td>
<td>0.006*</td>
</tr>
<tr>
<td>1955</td>
<td>0.122</td>
<td>0.145</td>
</tr>
<tr>
<td>1956</td>
<td>0.279</td>
<td>0.941</td>
</tr>
<tr>
<td>1957</td>
<td>0.239</td>
<td>0.788</td>
</tr>
<tr>
<td>1958</td>
<td>0.027</td>
<td>0.725</td>
</tr>
<tr>
<td>1959</td>
<td>0.063</td>
<td>0.587</td>
</tr>
<tr>
<td>1995</td>
<td>0.097</td>
<td>0.255</td>
</tr>
<tr>
<td>1996</td>
<td>0.015</td>
<td>0.049*</td>
</tr>
<tr>
<td>1997</td>
<td>0.004</td>
<td>0.002*</td>
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<tr>
<td>1998</td>
<td>0.165</td>
<td>0.517</td>
</tr>
<tr>
<td>1999</td>
<td>0.310</td>
<td>0.747</td>
</tr>
<tr>
<td>2000</td>
<td>0.094</td>
<td>0.498</td>
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<tr>
<td>2001</td>
<td>0.130</td>
<td>0.339</td>
</tr>
<tr>
<td>2002</td>
<td>0.076</td>
<td>0.004*</td>
</tr>
</tbody>
</table>
Figure 4-1. Standard CalCOFI coverage included in analysis. CalCOFI line numbers are labeled.
Figure 4-2. Geographic distribution of anchovy (E.m., Δ) eggs and adult and juvenile *E. pacifica* (○) for all cruises in each year. (+) denotes night stations with zeros for all three species.
Figure 4-3. Geographic distribution of sardine (S.s., ▼) eggs and adult and juvenile E. pacifica (●) for all cruises in each year. (+) denotes night stations with zeros for all three species.
Figure 4-4. T-S diagrams of anchovy (E.m., Δ) eggs, sardine (S.s., ▽) eggs, and adult and juvenile E. pacifica (○) with crosses at weighted means, two weighted standard deviations wide, where weighting procedure uses natural-logarithm-transformed abundances. Black cross denotes unweighted sample mean and standard deviation. (+) denotes night stations with zeros for all three species. (.) denotes day stations with zeros for sardine and anchovy eggs. Diagrams are divided into quadrants at 33.5 and 15 °C.
References


Chapter 5

Conclusions

The questions that motivated this dissertation are 1) why anchovy (*Engraulis mordax*) and sardine (*Sardinops sagax*) respond differently to environmental change and 2) what advantage offshore spawning habitat confers to sardine larvae. The specific objectives were 1) to characterize and compare the fine-scale horizontal (100s m to km) and vertical (m to 10s m) distributions of anchovy and sardine eggs and 2) to assess their relative potentials for interaction with the potential predator *Euphausia pacifica*. The characterization of spatial pattern in sardine and anchovy eggs is shown to be relevant to understanding the relationships between spawning behavior, spawning habitat, and the variable population sizes of these commercially and ecologically important species. Assessing the potential importance of interactions between clupeoids and other key species, in particular euphausiids, in upwelling ecosystems also contributes valuably to our understanding of and ideas about the dynamics of these populations and ecosystems and the evolutionary adaptations of the organisms involved.

The spatial analyses and models in Chapters 2 and 3 show distinct differences between the fine-scale distributions of anchovy and sardine eggs in both the horizontal and vertical dimensions. In Chapter 4, the relative distributions of sardine and anchovy eggs and *E. pacifica* indicate strong potential for ecological interactions between the abundant, variable populations of these species. Moreover, the potential
strength of these interactions appears to change with large-scale, long-term patterns in physical forcing. These results are reiterated below in somewhat greater detail before extending them in more general terms and recommending directions for future research.

**Fine-scale distributions of anchovy and sardine eggs**

Chapter 2 and part of Chapter 3 are based on repeated horizontal and vertical sampling of two areas of high egg abundance, one sardine and one anchovy, which were tracked with a surface drifter. Chapter 2 provides a direct comparison of fine-scale horizontal spatial pattern of sardine and anchovy eggs as characterized by variograms. Horizontal distributions of pelagic fish eggs in the study areas were sampled at 0.75-km-resolution on grids centered on a drifter with a Continuous Underway Fish Egg Sampler (Checkley et al., 1997).

Variograms for anchovy eggs have a significantly higher nugget effect than those for sardine eggs, indicating that the spatial structure of the distribution of sardine eggs was better resolved at the scales sampled. After careful consideration of other possible explanations, this difference is attributed to the organization of the spawning adults. Fish that are larger, faster, and more abundant may organize into larger schools with greater structure and mobility that create smoother egg distributions. Age structure, and thus size and mobility, varies with population size in clupeoids. Although sardines in migratory life history phase are better swimmers than anchovies, several cases demonstrate that anchovy eggs show coherent pattern at fine- to
mesoscales in other species and regions. In light of other spatial studies of eggs of *Sardinops sagax* and *Engraulis* spp., I propose that spatial pattern of their eggs is explained by the interacting factors of species-specific life history, population size and age structure, spawning intensity, and characteristic physical scales of the spawning habitat.

In Chapter 3, a model is presented to predict the vertical distribution of anchovy and sardine eggs, based on vertical mixing and ascent rates of the eggs. Four different vertical mixing profiles, based on wind speed, mixed layer depth, and density profile, were combined with terminal ascent velocities of eggs, calculated from experimentally determined buoyancy and size. The model was evaluated by comparing predicted vertical distributions to observations in vertically stratified samples of sardine and anchovy eggs. An additional evaluation step for sardine eggs used paired observations of concentrations at 3-m depth in CUFES and vertically integrated abundances. The observed integrated abundances were compared to model predictions of integrated abundance from concentration at 3-m depth.

Vertical distributions of anchovy and sardine eggs are, unexpectedly, best predicted by different vertical mixing models. Furthermore, addition of a random error term to the terminal ascent velocity shifts the predicted vertical distribution of anchovy eggs deeper, but does not affect the model predictions for sardine eggs. These results suggest that a more fundamental difference, either in the physical forcing of vertical mixing between anchovy and sardine habitat or in the characteristics of eggs of anchovy and sardine, has not been captured in the experimental data or the model.
Additionally, profiles of sardine eggs from vertically stratified samples are quite variable in appearance, and the model does not improve prediction of integrated abundances from samples in CUFES at 3-m depth over a simple regression of CUFES against integrated abundances. Horizontal patchiness may influence the observed vertical distributions of the eggs, complicating model evaluation.

If horizontal patchiness obfuscates the observed vertical distribution of sardine eggs more than anchovy eggs in oblique tows, Chapter 2 is relevant to the interpretation of Chapter 3. The distribution of sardine eggs is more coherent than anchovy on the order of one km in variogram analyses. Most of the oblique, vertically stratified tows for sardine eggs were less than one km in length, while those for anchovy covered several km. If patch scales for anchovy are much less than for sardine, the longer tows may have integrated over patch variability, while the shorter tows coincided with a scale of variability in sardine eggs that was not resolved by the km-scale horizontal sampling.

This scenario poses two sampling challenges: sub-100-m horizontal and on-station stratified vertical sampling of pelagic fish eggs. A synoptic view of the distributions of anchovy and sardine eggs at scales less than a km has not been approximated to date. Smith and Hewitt (1985) and Uriarte and Motos (1998; studying Engraulis encrasicoles) sampled anchovy eggs in rapidly repeated vertical tows on station to assess their small-scale variability. These studies would be valuably extended by high-resolution, continuous sampling along a transect, which will be possible with the automation of egg identification and counting in CUFES (Iwamoto
et al., 2001). The confounding of horizontal and vertical variability suggests that on-station, vertically stratified sampling of fish eggs would be a valuable advance. Plankton pumps sample too small a volume of water for the quantification of pelagic fish eggs in most cases, but plans exist for the adaptation of CUFES for vertical sampling (D.M. Checkley, Jr., Scripps Institution of Oceanography, USA, pers. comm.). Thus, technology currently under development may prove useful in addressing the questions posed by the results of Chapters 2 and 3.

Another approach to further exploration of these results, which is possible without further technological developments, is a modeling exercise. An evaluation of the effects of initial abundances of eggs, school size, school motion, and depth of spawning on the resulting distribution of eggs, as it is affected by advection and diffusion, would be of great interest. The external fertilization strategy of these pelagic fish theoretically introduces limitations on the initial density of milt and eggs required for fertilization, and thus on the density and motion of spawning schools (P.E. Smith and J.R. Hunter, Southwest Fisheries Science Center, USA, pers. comm.). These limitations must affect the behavior and organization of the spawning schools, and a better understanding of them may help resolve the cause for the differences between the fine-scale spatial pattern of anchovy and sardine eggs.

Dynamics Cubed: Trophic Interactions, Populations, and Environmental Variability

In Chapter 4, distributions of sardine and anchovy eggs and adult and juvenile Euphausia pacifica, an abundant potential predator on ichthyoplankton, are examined
in geographic and temperature-salinity space in the Southern California Bight (SCB) region for 1953-1959 and 1995-2002. These years encompass two El Niño events (1958-59, 1998) and three longer-term periods of anomalous conditions, two cold and one warm, that have affected the California Current System. The complementarity of the distributions of euphausiids and eggs on a local scale was also assessed.

Variability in the relative distributions of sardine and anchovy eggs and *E. pacifica* shows concordance with environmental change on decadal and multiyear time scales. *E. pacifica* is broadly distributed, though it contracts toward the coast in warm years, causing it to coincide more with the range of anchovy spawning in geographic and T-S space. During cold years, when *E. pacifica* is more widespread in the SCB region, it overlaps more with the distribution of sardine eggs in geographic and T-S space. Occurrence of significantly complementary distributions of anchovy eggs and *E. pacifica* supports the idea of interaction between anchovy and euphausiids. None of the years have a significant index of complementarity for sardine eggs and *E. pacifica*.

The apparent interaction of the distribution of *E. pacifica* with anchovy eggs, but not sardine eggs, on the local level suggests that the two clupeoid species may interact with the abundant euphausiid on different temporal and spatial scales. Anchovy spawning is concentrated in the Southern California Bight (Hewitt, 1980; Kramer and Ahlstrom, 1968), which also serves as a southern reproduction refuge for the temperate *Euphausia pacifica*. Anchovy may either interact with *E. pacifica* directly by suffering high predation mortality from euphausiid swarms during early life history, or it may be adapted to avoid spawning in regions of particularly high
euphausiid abundance. Sardine may have responded to the inshore abundance of predators on an evolutionary time scale by spawning in offshore habitat, trading the presumably lower likelihood of offshore advection or starvation in the nearshore environment for a low-predation environment offshore. Sardine larvae are more vulnerable to predation and less vulnerable to starvation than anchovy larvae (Butler, 1987), matching the proposed evolutionary tradeoff in spawning habitat.

Alternations between recruitment-limiting processes also take place on an inter-annual basis. Logerwell and Smith (2001) found that the frequency of mesoscale eddies, which they identified as "survivors’ habitat," has a dome-shaped relationship to recruitment, rather than a linear one, indicating that the availability of eddy habitat is displaced by another recruitment-limiting process during years of frequent eddy occurrence. MacCall (2001) suggested that weaker flow during warm regimes may be more conducive to eddy formation.

The aggregate explanatory power of proposed sources of mortality and recruitment variability in anchovy, including high abundances of euphausiids, storm frequency (Peterman and Bradford, 1987), and offshore transport (Methot, 1983; Parrish et al., 1981), has not yet been investigated. Variation in these loss terms with decadal environmental variability also has not been addressed. Peterman and Bradford (1987) determined that storm frequency is the dominant source of observed mortality of anchovy larvae in a multiple regression of mortality rate as a function of indices for storm frequency, cannibalism, and offshore transport. However, observed mortality rate of larvae does not always reflect recruitment success for that year (Methot, 1983),
because different temporal scales are involved for each loss term of larvae. For instance, losses due to offshore transport are not reflected in short-term mortality rates, while predation and starvation losses are.

As further components of larval mortality and recruitment variability are identified and their variability with decadal environmental change evaluated, it will be interesting to see how suites of components affecting anchovy versus sardine mortality and recruitment affect the level of variability and persistence seen in the populations. Sinclair (1988) proposed that the evolutionary success of marine populations is determined by their persistence rather than their abundance. The sardine population off California is more variable and less persistent than anchovy on decadal and evolutionary time scales (Grant and Bowen, 1998; Soutar and Isaacs, 1974). However, sardine is almost an order of magnitude more productive per unit spawning area (Jacobson et al., 2001). Likewise, Logerwell et al. (2001) calculated an order of magnitude greater potential production of sardine larvae in offshore eddy habitat than in other habitats. Thus the offshore spawning habitat that sardine exploits appears to have extraordinarily high potential for production in good conditions, perhaps by combining low predation risk (as discussed in Chapter 4) and Bakun's (1996) fundamental triad of enrichment, concentration, and retention. The differences in the fine-scale horizontal patterns of sardine and anchovy eggs (observed in Chapter 2 and hinted at in Chapter 3) appear to be fundamentally related to the same factors - abundance and swimming ability - that determine the geographic distribution of sardine and anchovy eggs and the ability of the majority of the population of sardines,
but only a fraction of anchovies, to exploit this productive offshore habitat. However, the variability of eddy habitat translates into an ephemeral presence of the sardine population off of California. The strategy of sardine thus seems to be at variance with the evolutionary extension of Sinclair's member/vagrant hypothesis.

This dissertation characterizes patterns of sardine and anchovy eggs on the fine scale and in geographic and temperature-salinity space, relating these patterns to the distribution of an abundant euphausiid predator and to variability in populations and environment. The results provide useful input for future models, such as of the interaction of patches of ichthyoplankton prey and euphausiid predators in horizontal and vertical space, and the influence of different parameters of the spawning process on the distribution of pelagic fish eggs. This dissertation also stimulates many further questions and ideas about the relationships between the dynamic trio of the populations of these three species, their trophic interactions, and their environment.
References


