Spawning and Survival Patterns of Larval Northern Anchovy, *Engraulis mordax*, in Contrasting Environments—A Site-Intensive Study

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ABSTRACT: During the 1985 spawning season of the northern anchovy, *Engraulis mordax* Girard, off southern California, a serial field study at contrasting sites linked measurable environmental characteristics with parameters of larval anchovy growth and survival and determined a range of environmental conditions over which northern anchovy had recently spawned. Surface and water column characteristics were measured while following surface drifters at each site, and their relation to corresponding measurements of larval anchovy production, growth, mortality, and starvation are reported.

The nearshore site was eutrophic with low current speeds, low wind speeds, and high forage levels which are characteristic of coastal spawning areas. The offshore site, by contrast, was relatively oligotrophic and had higher surface mixing rates, a deeper mixed layer, reduced stability in the pycnocline, and lower forage levels.

Among the measured characteristics of the ichthyoplankton, only one, the larval production rate, was markedly different at the two sites. Although habitat suitability for adult anchovies was different, survival probability for larval anchovies was more equivalent at the two sites than inspection of single parameters of the environment suggested. In contrast with the view that the northern anchovy spawns indiscriminately, the results of this study suggest that components of the adult northern anchovy population tend to spawn under conditions and at levels that yield consistent survival probabilities for their offspring.

Since Lasker's (1975, 1978, 1981) pioneering work on causes of larval fish mortality, recent developments have made techniques available to assess age-specific larval growth, mortality, and physiological condition. These developments have piqued interest in field studies that link environmental processes to survival probabilities for larvae of broadcast spawners. Here we present the results of a site-intensive shipboard study that combined newly available measures of larval condition with a suite of physical and biotic measures of their environment in the Lagrangian setting provided by near-surface drifters to determine local variations of a few days duration. Our results are intended to guide the design and execution of programs that address the recruitment process and its relation to the spawning environment.

Conditions under which northern anchovy, *Engraulis mordax* Girard, spawn and under which their eggs and larvae survive presently are known mainly from cruises of the CalCOFI program, which are quasi-synoptic surveys of broad areas of the spawning domain during which limited sets of environmental observations and measurements have been made (cf. Reid 1988). Owing to limits imposed by time and resources, such surveys do not yield knowledge of the local fate of spawned products because the methods that characterize survival likelihood of larval fish have only recently been developed and verified, and because local changes (those embedded in the surface flow) are not knowable by the survey approach.

METHODS

Site Selection

Criteria for selection of the two study sites were that each must 1) show evidence of recent spawning by anchovy, 2) contrast with the other site in macroscopic setting and environmental character, and 3) exhibit no local gradients indicative of smaller scale (0.1–10 km) environmental

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heterogeneity. The study followed a routine survey by the California Cooperative Fisheries Investigations (CalCOFI Cruise 8502) of the northern anchovy spawning domain. Visual inspection of plankton catches made on this survey yielded estimates of northern anchovy egg abundance at 4–10 nmi intervals. Within areas of high egg abundance, the ship's survey records of 3 m temperature and in vivo phytoplankton pigment fluorescence were scanned for evidence of local gradients. Low variations of pigments and temperature in the vicinity of possible sites were verified by inspection of available satellite images of sea surface temperature and surface layer color, and several sites were then targeted for this study.

At sea, we verified that our criteria held at each site by inspection of plankton tows to confirm recent (and therefore sustained) spawning activity, and by inspection of underway records for local homogeneity of temperature and pigment fluorescence at 3 m depth. We occupied sites shown in Figure 1.

Procedures on Site

Upon verification that a site met the three criteria, we launched a radio-transmitting surface drifter. The ship then moved several nmi to launch a second drifter. Thereafter, we alternated our station pattern between the two drifters, locating each drifter by radio direction-finding equipment and visually. Each site was thus defined, in the Lagrangian sense, to be the water corpus that was moving along with the two drifters. We assumed that both drifters at each site were implanted in macroscopically homogeneous water with respect to physical and biological character. We examine the limits of this assumption by contrasting variations within and between drifters at the same site.

Stations were patterned around each drifter, in turn, at cardinal points 2 km from the drifter. Vertical plankton tows, "CalVETs" (Smith et al. 1985), were made with 150 μm mesh nets from 50 m depth at all four stations to catch fish eggs and larvae to determine age-specific anchovy production and mortality. Oblique bongo tows were made to and from 50 m depth with 333 μm mesh nets and, after we lost the 333 μm mesh nets, with 505 μm mesh nets to catch northern anchovy larvae for estimation of starvation incidence and recent growth rate. At two of the four stations, paired vertical tows similar to CalVETs were made from 50 m depth with 75 μm mesh and 333 μm mesh nets to estimate composition and quantity of larval food rations and of other small plankton, respectively. CTD/Niskin casts were made to 100 m depth at one station, per drifter visit, to measure physical structure of the water column and to get water samples at 10 depths to determine concentrations of particulates, chlorophyll-a and phaeopigments. Secchi depth was determined at one station (daylight permitting) at each drifter to estimate thickness of the euphotic layer. Standard weather observations were made once per drifter visit.

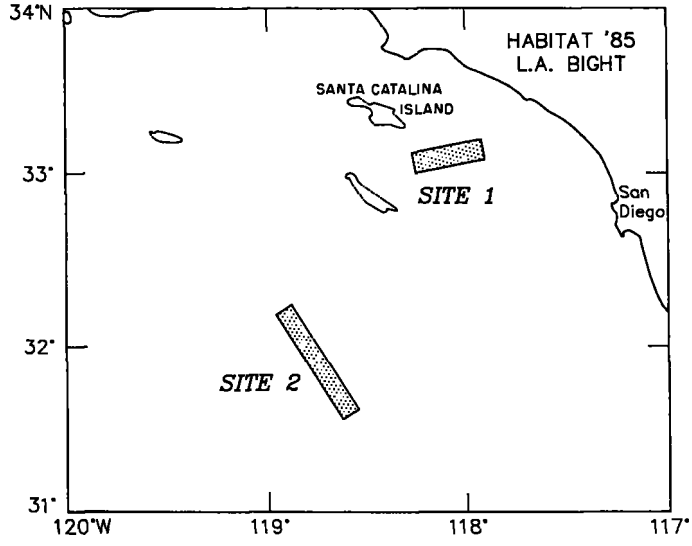


FIGURE 1.—Study site locations in the Southern California Bight.

Environmental Characteristics

Surface Drift

Drifter positions were determined by a combination of satellite navigation, Loran-C, and Decca radar over the course of the study, and were precise within 0.1 km. The drifters were designed as described by Davis et al. (1982) to minimize the effects of wave motion and of wind drag on exposed surfaces, both of which cause deviations of drifter motion from that of water parcels. The 2 km station spacing around each drifter was large compared with precision of drifter position and with deviation of the drifter's motion from surrounding water motion.

Vertical Temperature and Salinity Profiles

Temperature, conductivity, and pressure were recorded with a Neil Brown CTD, following methods used by NOAA/Southwest Fisheries Center.[1] Briefly, 0.25 s scans of temperature, conductivity, and pressure were recorded as the CTD profiled at 20–40 m/min. Conductivity and temperature records corrected for temperature lags are smoothed by a 5-point weighted running mean with binomial coefficients of 1, 4, 6, 4, 1. Salinity was computed using the Practical Salinity Scale of 1978. Salinities and temperature were compared and justified with salinity and temperature values from a hydrographic bottle tripped in the near-surface layer during each cast. Final data were enumerated at 2 m depth intervals.

Phytoplankton Pigments

Chlorophyll-a and phaeopigment-a concentrations were determined from fluorescence readings on a Turner 111[2] Fluorometer before and after acidification of 24 h extractions in 90% aqueous acetone of material retained on Whatman GF/C glass filters after filtration of 140 mL water samples.

Particles

Particle concentration and size distribution (16–160 μm equivalent diameters) were determined with a Coulter model Ta counter with a 280 μm pore configured to count particles in a 20–200 mL sample volume. Counts usually exceeded 40,000 per sample. These determinations stopped part way through the study owing to equipment malfunction at the second site.

Microplankton

Microplankton samples were aliquoted prior to counting. A 0.5 mL Stempel pipette was used 10–40 times to withdraw a subsample from the well-stirred original sample after adjusting the original volume to 750 mL. When 10 Stempel subsamples yielded too many plankters to enumerate, the sample was divided with a Folsom splitter to yield a countable fraction from at least 10 Stempel subsamplings.

Microplankton samples were enumerated in covered chambers with a Wild dissection microscope (at 250 magnification) to determine mean concentrations of larval anchovy food organisms in the upper 50 m. Food organisms are here assumed to be those having ingestible dimensions (20–160 μm width), no pronounced spines or processes that would interfere with ingestion or with gut wall integrity, and, except for ingestible eggs, some degree of motility (Rojas de Mendiola 1974; Arthur 1976). Food concentrations and rations given here are underestimated because larvae are known to take organisms smaller than were retained by the meshes of the 75 μm mesh net used (Rojas de Mendiola 1974; Arthur 1976). The sampled food fraction probably represents the major part of available food rations; although less in number, this fraction is greater in volume than the unfiltered fraction and is captured selectively by larvae (Lasker and Zweifel 1978; Theilacker and Dorsey 1980). The food retained by the net is assumed here to be the majority of, and proportional to, the total rations available to larvae over the 50 m layer sampled.

Zooplankton

Zooplankton counts were made on all organisms collected in the 333 μm mesh vertical tows. Samples were not aliquoted. The net tow method used precluded quantitative representation of faster or rarer organisms, including some types of potential predators on fish larvae. Determined for each sample were number of species, number of specimens of each species, and sex ratios (where applicable) for the following major tax-

[1]K. Bliss, Oceanographer, Southwest Fisheries Center, La Jolla, CA, 92038, pers. commun. May 1985.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

onomic groups: Medusae, Siphonophorae, Ctenophora, Chaetognatha, Cladocera, Ostracoda, Amphipoda, Copepoda, Euphausiidae, crustacean larvae, other invertebrate larvae, pelagic Mollusca, Polychaeta, Tunicata, Radiolaria, and Foraminifera. Anchovy eggs and larvae, sized to the nearest 0.25 mm, were also enumerated from these collections. Zooplankton enumerations are given in detail in Alvariño and Kimbrell (1987).

Larval Characteristics

Larval Growth

Growth of larvae was estimated from 224 larvae collected in 15 tows at Site 1 and from 116 larvae collected in 30 tows at Site 2. Samples for otolith ageing of larval anchovies were taken from the portside net of bongo tows and were preserved after removal of gelatinous zooplankters in 80% ethanol buffered with 20 mM tris [hydroxymethyl] aminomethane. Larvae were sorted from the plankton and stored in the same preservative.

Standard lengths of larvae were measured prior to removal of their otoliths. Preserved standard lengths were converted to live lengths using a correction factor for net shrinkage (Theilacker 1980). At Site 1, tow duration was six minutes and each sample was fixed within five minutes of tow completion. Length of the inshore larvae were corrected by a net shrinkage factor of eight minutes. Tow duration at Site 2 was also six minutes, but because of the large number of salps collected offshore, time before preservation increased to about 10 minutes. Lengths of offshore larvae were corrected for 13 minutes of net shrinkage.

Daily increments in the otoliths were counted using a compound microscope equipped with a closed-circuit television system, a video coordinate digitizer, and a microcomputer (Methot and Kramer 1979). Age from hatching was determined from the number of daily rings in the otoliths. Because the initial ring is deposited at the time of first feeding, at about five days from hatching, time since hatching is 5 days more than the ring count (Brothers et al. 1976).

Laird-Gompertz growth curves were fit to the length at age using nonlinear regression. To compare differences in growth rates between the two sites, analysis of covariance was performed on segments of the data so that the assumption of linearity was reasonable.

Larval Production and Mortality

Age-specific larval anchovy production rates were computed from counts of larvae in 1 mm size classes to 9 mm preserved standard length (SL) from bongo tows and in 0.5 mm size classes to 7 mm SL from CalVETs. Counts of larvae were corrected for volume of water filtered, for net avoidance, and for losses owing to extrusion through the net meshes (Zweifel and Smith 1981). Larval production at each age was estimated by dividing size-specific larval abundance by time spent at each size. Duration at size was specfied from Laird-Gompertz growth curves (Methot and Hewitt 1980; Lo 1983).

Larval mortality curves were based on the Pareto decay function (Lo 1985):

$$z(t) = \beta/t$$

where $z(t)$ is the instantaneous mortality rate (IMR), β is the IMR coefficient, and t is age (days) since spawning. Daily production is given by

$$P_t = P_0(t/t_0)^{-\beta} \quad t_0 < t < 20\ d$$

where P_t is daily larval production at age t, P_0 is initial larval production (at hatching), t_0 is age at hatching, specified from hatching time as a function of incubation temperature (Lo 1983). Thus, as larvae grow older, the rate at which they appear in the next age group is diminished by the factor given by β.

The above equation (referred to subsequently as the nonlinear model) can be expressed in linear form by taking the natural logarithm of both sides:

$$\ln(P_t) = \ln(P_0) - \beta \ln(t/t_0)\,.$$

Both the nonlinear and the log-linear regression models can be used to estimate parameters P_0 and the IMR coefficient β. The log-linear equation is mainly used in this study to compare β between sites.

Production and mortality of anchovy larvae at Site 1 were estimated from 48 bongo samples (20 using 333 μm mesh nets and 28 using 505 μm mesh nets) and from 49 CalVETs using 150 μm mesh nets. At Site 2, these parameters were estimated from 49 bongo samples using 505 μm mesh nets and from 50 CalVETs using 150 μm mesh nets.

Larval Condition

Starvation incidence was estimated from histological criteria on 141 anchovy larvae from Site 1 and on 119 larvae from Site 2. The larvae were collected with nonquantitative bongo nets towed to 50 m. Although the best preservation procedure for histological samples is to preserve larval fish in Bouin's fixative within 3 minutes after capture, 5–6 minutes were required to obtain representative samples to 50 m. After fixing in Bouin's fluid for 24–48 hours, samples were transferred to 70% ethyl alcohol for storage.

The nutritional state of northern anchovy larvae is usually classified by grading the appearance of tissues of the brain, cartilage, notochord, liver, pancreas, and gut (O'Connell 1976). But because many of these tissues had lysed owing to extended time before preservation, an additional criterion was used in this study. This criterion, the height of midgut mucosal cells, was unaffected by the 5–6 minutes needed to fix the larvae (Theilacker and Watanabe 1989). Heights of midgut mucosal cells were divided into three categories (healthy, intermediate, and starved) according to laboratory results (Theilacker and Watanabe 1989). As northern anchovy develop past 6 mm SL, the midgut folds to increase the absorptive area. The fold makes it difficult to measure cell heights of larger larvae. To apply the durations determined for the laboratory fish to the field samples, the size of the field-collected larvae was adjusted to equal the size of preserved laboratory fish of known feeding history (Theilacker 1980). Details of these manipulations are given in Theilacker and Watanabe (1989).

RESULTS

Environmental Variations Within and Between Drifters and Sites

Surface Drift

Drifters were tracked as shown in Figure 2. Released 10 nmi apart at Site 1, Drifters A and B moved generally eastward, away from Santa Catalina Island, on slightly convergent courses. Mean speeds over their 2.7 days at sea were 17.1 cm/s and 18.7 cm/s (about 15.5 km/dy). Range of speeds measured by drifter displacements over 8 h intervals were 5.6–34.7 cm/s and 6.8–32.9 cm/s.

Released 5 nmi apart at Site 2, Drifters A and B moved in a southeast-trending arc, again on slightly convergent courses. Mean speeds over their 2.5 days at sea were 34.6 cm/s and 37.4 cm/s (about 30 km/d), twice as fast as at Site 1. Speed ranges measured were 15.3 cm/s to 45.4

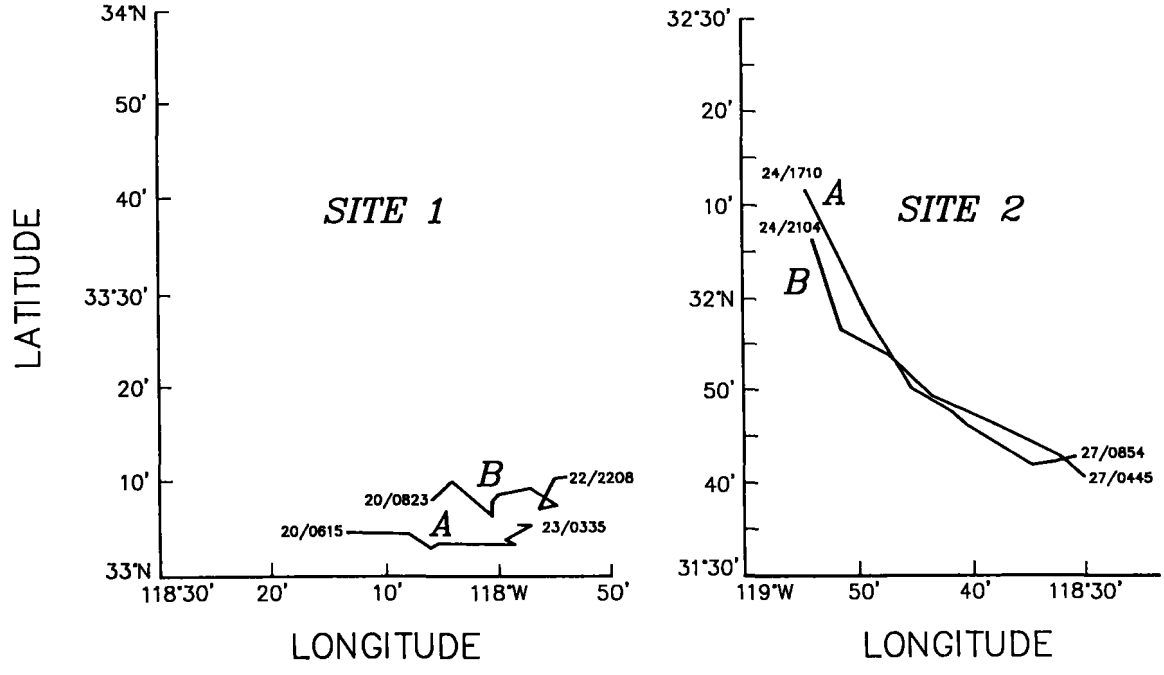
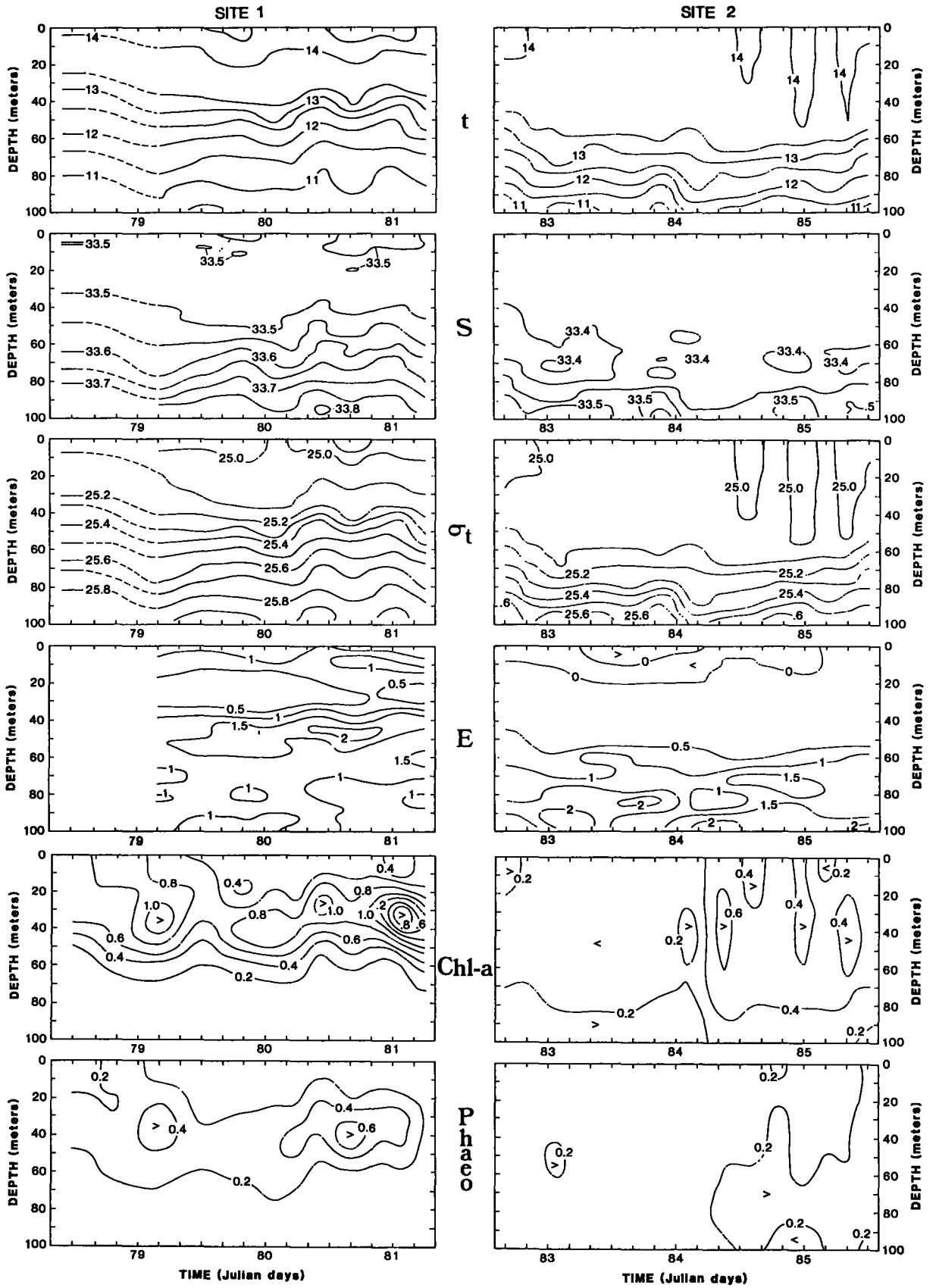


FIGURE 2.—Drifter trajectories along *Sites 1* and *2*.


SITE 1
SITE 2
t
S
σt
E
Chl-a
Phaeo
DEPTH (meters)
TIME (Julian days)

cm/s and 18.8 cm/s to 48.2 cm/s. Drift direction at Site 2, predominantly longshore, indicated that Site 2 larvae had been spawned offshore rather than drifting out from an onshore spawning area.

The degree to which drifter displacements paralleled one another at each site (Fig. 2) indicated homogeneous, nondivergent flow of the surface layer and general integrity of each water corpus being investigated. Similar rates of separation of drifter pairs indicated no differences between rates of lateral diffusion between sites.

Vertical Structure

Physical structure of the upper 100 m at both sites exhibited no overall trends for the duration of the study (Fig. 3). Variations of isopleth depths in the pycnocline at Site 1 were greater during the second half of the period, perhaps owing to increased internal wave activity.

A slight warming trend over the course of the studies was indicated by increased surface layer temperatures at both sites. The trend was likely due to local heating of the mixed layer. Heat content of the upper layer increased at Site 2 but no trend was detected at Site 1.

Local diurnal heating was apparent at Site 1 from continuous temperature records at 3 m depth as well as from CTD casts. Higher winds and a thicker mixed layer at Site 2 obscured diurnal temperature variations.

Vertical sections of phytopigments (Fig. 3) gives a less conservative picture of variations. Intensification of the maximum chlorophyll and phaeopigment layers over the course of studies occurred at both sites. In view of the lack of change of temperature, salinity, and density structure, the increase in pigment concentration was likely due to local processes rather than to advective processes. The change thus expressed the net product of primary production and grazing.

Composite T-S diagrams (Fig. 4), constructed from CTD cast data at each site, indicate that the drifters were set into waters of different structure and composition at the two sites. Site 2 water, closer in character to California Current core water (Lynn and Simpson in press), was cooler and less saline than Site 1 water. Site 1 water was likely derived from a mix of California Current core water (from the north, offshore) and coastal countercurrent water (from the south, nearshore), further modified by local warming of the surface layers in transit.

Plankton Quantity and Composition

Within sites, no major differences were apparent in plankton quantity or community composition along drifter paths. Over twice as many plankton organisms were caught by 333 μm mesh nets at Site 1 than at Site 2, and predatory copepods were 5 times more numerous at Site 1 than at Site 2 (Table 1). Plankton diversity was somewhat higher at Site 1 than at Site 2: on average. Site 1 tows yielded 144 invertebrate species, whereas Site 2 tows yielded 130 species. Perhaps the most striking difference in the zooplankton was the high abundance of salps at Site 2. No direct interactions are known between fish larvae and salps.

In terms both of rations and numbers, over twice as much larval anchovy food was caught by 75 μm mesh nets at Site 1 than at Site 2 (Table 1).

Summary

To compare habitats at the two sites, Table 1

[3]Lynn, R. J., and J. Simpson. 1989. The influence of bathymetry upon the flow of the undercurrent off Southern California. Unpubl. manuscr.

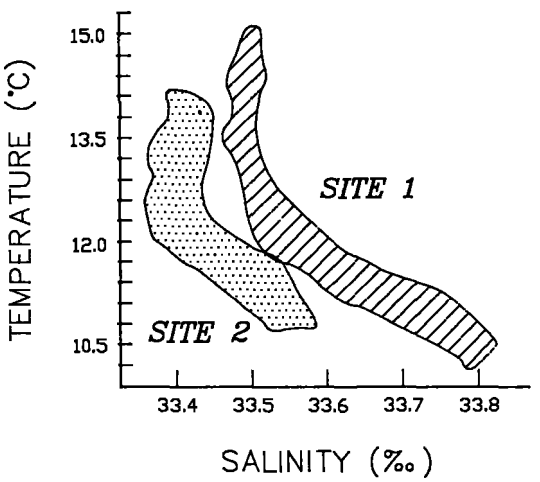


FIGURE 4.—Composite T-S diagrams at *Sites 1* and *2*.

FIGURE 3.—Vertical time sections of temperature (t), salinity (‰), density (σ_t), and stability (E) at Sites 1 and 2. Vertical time sections of chlorophyll-a and phaeopigment at Sites 1 and 2.

TABLE 1.—Comparisons between study sites—means (and standard deviations) of environmental characteristics at Sites 1 and 2. *n* is number of observations. Integrations are to 50 m depth.

	Site 1		Site 2	
	mean (SD)	*n*	mean (SD)	*n*
mixed layer depth (m)	37.6 (5.0)	11	57.7 (6.8)	14
wind speed (m/s)	3.27 (1.54)	15	8.97 (2.36)	14
stability max. ($E \times 10^7$)	4.00 (1.54)	11	3.47 (1.59)	14
depth of stability max. (m)	45.6 (7.8)	11	67.6 (8.7)	14
surface current speed (cm/s)	18.9 (10.2)	16	35.4 (10.4)	16
surface temp. (C)	14.50 (0.41)	50	14.04 (0.14)	50
surface salinity ‰	33.50 (0.011)	11	33.42 (0.044)	14
surface chlorophyll a conc. (μg/L)	0.56 (0.20)	11	0.37 (0.15)	12
surface phaeopigment conc. (μg/L)	0.14 (0.13)	11	0.10 (0.09)	12
integrated chlorophyll a conc. (mg/m^2)	45.3 (9.74)	11	33.8 (12.72)	12
integrated phaeopigment conc. (mg/m^2)	20.3 (4.77)	11	15.9 (7.64)	12
Integrated particle conc., 16–160 μm (no/cm^2)	44012 (44761)	11	66980 (67027)	5
Integrated particle conc., 50–160 μm (no/cm^2)	5854 (9405)	11	2607 (1138)	5
Secchi depth (m)	11.5 (2.0)	9	18.1 (2.7)	8
food conc. >75 μm (no/L)	31.4 (13.9)	26	13.5 (12.0)	24
food conc. >75 μm ($\mu m^3/L$)	19.6 (5.7)	26	8.1 (7.0)	24
zooplankton conc. (no/m^3)	625 (216)	26	236 (160)	24
predatory copepods (no/m^3)	121 (79)	26	24 (32)	24
zooplankton spp. (species/tow)	144	26	130	24
copepod spp. (species/tow)	65	26	60	24

gives means and variations among environmental parameters of energy input and dissipation, responses of the plankton communities, and levels of food supply and predation pressure to which the larvae were exposed. Analyses of variance of environmental characteristics demonstrated much smaller variations between drifters within sites than between sites.

In review, changes over study periods at both sites were local, not advective; we resampled the same water and larval population within sites. Vertical gradients were shoaler and more intense at Site 1. Temperature and salinity relations in the upper 100 m indicate different recent histories of the waters at the two sites. Surface layers at Site 1 were warmer, more saline, less turbulent, less transparent, and contained higher concentrations of larval foods and other

plankton. Plankton community structure was different between sites: most notably, predatory copepods were more abundant at Site 1 and salps were more abundant at Site 2.

Larval Parameter Variations Within and Between Drifters and Sites

Larval Growth Rates:

Ranges of size and age of larvae differed between sites. Site 2 samples included larvae that were larger (and older) than those at Site 1. The average age of larvae was 6.9 and 11.5 days from hatching at Sites 1 and 2, respectively. Larval length averaged 7.8 mm and 9.0 mm at Sites 1 and 2, respectively. Thus the offshore Site 2 was inhabited by older and slightly longer larvae than Site 1. Offshore drift of larvae hatched inshore into the region of Site 2 (Smith 1972) may account for this phenomenon, as may higher predation on older larvae at Site 1. The latter explanation is favored because the observed flow patterns (Fig. 2) do not suggest that larvae were transported offshore from nearshore areas.

To assess the growth of larvae in these two stations, the Laird-Gompertz model was used to fit the length-age data:

$$L_t = L_\infty(L_0/L_\infty)^{\exp[-\alpha t]}$$

where t is time since first feeding at 5 days after hatching, L_0 is larval length at first feeding, and L_∞ is the asymptotic length. The maximum and minimum fish lengths in the sample have strong influence on the length parameter estimates (L_0 and L_∞) and on the growth coefficient (α). The resulting growth coefficients at the two sites (Table 2) are 0.1 for the inshore station and 0.05 for the offshore station. A standard growth coefficient of 0.05 is used by CalCOFI (Methot and Hewitt 1980).

We compared total growth rates of fish younger than 18 days (after hatching) at the two sites, assuming a linear growth rate to be reasonable because of difficulties in comparing differences between nonlinear curves. Larvae at the offshore Site 2 had a larger asymptotic length and a lower growth coefficient than at the inshore site. The null hypothesis, that growth was equal at the two sites, was tested using analysis of covariance. When the test was performed on lengths uncorrected for shrinkage or on lengths corrected for the same shrinkage, the slopes at the two sites were not significantly different but the mean lengths were. (A true difference between mean lengths would indicate that anchovy larvae had hatched at a larger size at Site 1 than at Site 2, or that Site 2 larvae underwent starvation at the first-feeding stage and then recovered.) However, when larval lengths from Site 2 were corrected for greater handling time, then neither the slopes nor the adjusted lengths differed significantly between the two sites (Table 3). In short, corrected data indicate that no difference existed in larval growth between the sites.

Larval Production and Mortality Rates

Larval production at age (larvae <20 days from spawning) was used to model larval mortality. For mortality analysis, age is defined as time since spawning. Larval production was computed as described above in Methods, and larval age was derived from live size using a Gompertz growth curve. Three growth curves were available for computing larval age: the standard growth curve used for routine annual anchovy larval assessment, and two site-specific growth curves constructed from length-age data collected at each of our sites. We elected to use the standard growth curve to convert larval size to age for both sites because no significant difference in total growth rates for larvae <20 days since spawning was detected between two site-specific growth curves, and because the growth coefficients estimated from two sites were also similar to that of the standard growth model (all equal to 0.05) when the maximum and minimum lengths of larvae were set to be 27 mm and 4.1 mm, corresponding to the standard growth curve. Both nonlinear and log-linear regression

TABLE 2.—Parameters of Laird-Gompertz growth curves for northern anchovy larvae at Site 1 and Site 2. L_0 is larval length at first feeding; L_∞ is the asymptotic length; and α is the growth coefficient. Lengths are corrected for differential handling times.

Parameter	Site 1	Site 2	CalCOFI
L_∞ (mm)	14.7 (0.6)	20.5 (1.8)	27
L_0 (mm)	4.9 (0.1)	5.2 (0.2)	4.1
α	0.10 (0.01)	0.05 (0.01)	0.05
n	234	141	—
With L_∞ (mm) fixed at 27 mm and L_0 (mm) fixed at 4.1 mm,			
α	0.05 (0.001)	0.05 (0.01)	

TABLE 3.—Comparison of growth rates of northern anchovy larvae between Site 1 and Site 2 for post-yolk-sac larvae less than 18 days old, using analysis of covariance.

Linear regression of growth. L is length, t is time since hatching, and n = total number of larvae sampled.

Site 1	$L_t = 7.33 + 0.46\,(t - 9.99)$	$n = 197$
Site 2	$L_t = 7.82 + 0.46\,(t - 11.54)$	$n = 79$

Analysis of covariance between sites

Source of variation	df	Sum of squares	Mean squares	F	Prob. (tail)
Equality of adjusted means	1	2.57	2.57	3.23	0.07
Zero slopes					
All covariates	1	709.76	709.76	892.98	0.00
error	273	216.99	0.79		
Equality of slopes all covariates and all groups	1	0.02	0.02	0.02	0.89
error	272	216.97	0.80		

were used to estimate the larval production at hatching (P_0) and mortality coefficient (β).

Mortality Estimates

Data in three arrays were used to estimate mortality: bongo larvae alone, bongo larvae plus 2.5–4.0 mm larvae from CalVETs, and bongo larvae plus 3.0–4.0 mm larvae from CalVETs (Tables 4, 5). The nonlinear regression gave estimates of β ranging from 1.15 to 2.18 (equivalent to IMR of 0.115–0.218 for larvae of age 10 days) for Site 1 and 1.06–3.03 for Site 2. The lower values of β were caused by low numbers of 2.5 mm larvae in CalVET samples. The log-linear regression produced more consistent estimates of β than those from nonlinear regression: Site 1 values ranged from 3.32 to 3.94 and Site 2 values ranged from 2.87 to 3.47. Estimates of P_0 at hatching age ranged at Site 1 from 12.03 to 28.38, and for Site 2 from 1.37 to 4.23. For all data arrays, site differences in larval production rates were apparent (Tables 4, 5), but site differences in mortality rates were not (Table 6).

Comparison of Larval Production and Mortality Coefficients Between Sites

Larval samples from bongo tows were used to compare the mortality between sites. Analysis of covariance was performed on the logarithmic transformation of age and larval production. The results of the analysis indicated that the site difference between mortality coefficients was not statistically detectable whereas site difference between larval production rates was (Table 6).

We also compared the larval production and mortality at the two sites (Table 5) with those over the northern anchovy spawning domain as sampled by the CalCOFI 8502 survey ($P_0 = 4.81$ with SE = 0.30, and $\beta = 2.21$ with SE = 0.11 for 37 positive CalVET tows out of 45). Larval production at Site 1 was much higher than the average over the CalCOFI 8502 survey region, but production at Site 2 and larval mortality at both sites were similar to the survey region averages.

Figure 5 shows the larval production-at-age curves at the two sites and, for comparison, larval production curves for anchovy spawning domains as sampled on CalCOFI Cruise 8502, just prior to our site-intensive program. Site 1 displayed high production of all larval ages, which was higher than its subdomain (CalCOFI Region 7), whereas Site 2 production was somewhat above that of its subdomain (CalCOFI Region 8) and somewhat below that of the entire spawning domain as sampled ("all regions").

Starvation Incidence

Midgut cell height is the histological criterion of larval feeding history. The range of cell height and the cell height change with larval size were similar at both sites (Fig. 6). The similarity

TABLE 4.—Northern anchovy larval production per unit area per day at age at Sites 1 and 2 from bongo and CalVET nets, based upon "regular" growth. *n* is total number of tows, pos. *n* is number of tows with larvae.

	Site 1		Site 2	
Capture size (mm)	Average age (d)	Production no./0.05 m^2/d	Average age (d)	Production no./0.05 m^2/d
Bongo net				
2.5	4.72	10.67	5.29	0.95
3.75	8.30	5.57	9.20	0.19
4.75	11.04	0.54	11.91	0.074
5.75	13.44	0.16	14.38	0.033
6.75	15.64	0.096	16.69	0.024
7.75	17.78	0.085	18.86	0.022
8.75	19.84	0.095	21.06	0.016
n(pos.*n*)	48 (48)		49 (46)	
CalVET net				
2.5	3.60	6.44	3.81	0.674
3.0	5.09	7.81	5.37	1.221
3.5	7.16	7.65	7.56	1.503
4.0	8.90	3.19	9.27	0.445
4.5	10.10	0.27	10.50	0.098
5.0	11.41	0.44	—	—
5.5	12.86	0.04	—	—
6.0	13.38	0.04	—	—
6.5	14.78	0.02	—	—
n(pos.*n*)	49(49)		50(40)	
temperature	14.25C		14.05C	
hatching age	3.05d		3.23d	

[1]Production computed from total number of tows(n).

TABLE 5.—Estimated northern anchovy larval production at hatching (P_0) and mortality coefficient (β) from nonlinear and log-linear regression for Sites 1 and 2 using various data sets and "regular" growth parameter estimates.

	Site 1			Site 2		
Data sets	P_0 (SE)	β (SE)	MSE	P_0 (SE)	β (SE)	MSE
Nonlinear bongo only	28.38 (7.70)	2.18 (0.47)	1.78	4.23 (0.15)	3.03 (0.07)	0.0008
CalVET (2.5–4.0 mm) and bongo	12.03 (2.98)	1.15 (0.38)	6.01	1.37 (0.51)	1.06 (0.52)	0.1816
CalVET (3.0–4.0 mm) and bongo	23.79 (5.86)	1.85 (0.38)	2.47	2.99 (1.40)	1.80 (0.68)	0.1238
Log-linear bongo only	4.49 (0.77)	3.9 (0.54)	0.43	1.41 (0.22)	3.05 (0.15)	0.03
CalVET (2.5–4.0 mm) and bongo	3.79 (0.59)	3.32 (0.48)	0.74	1.36 (0.52)	2.87 (0.42)	0.57
CalVET (3.0–4.0 mm) and bongo	4.67 (0.58)	3.94 (0.45)	0.46	2.22 (0.49)	3.47 (0.38)	0.31

suggests that both larval populations had experienced comparable feeding conditions.

Although average daily mortality rates due to starvation of first-feeding anchovy larvae were higher at Site 1, 24%/d, than at Site 2, 12%/d (Table 7), the difference between sites was not statistically significant ($\chi^2 = 2.26$; $P > 0.15$). Incidence of starvation was low or nil after the first-feeding stage at both sites.

TABLE 6.—Comparison of mortality coefficients (β) of northern anchovy larvae (<20 days) between Site 1 and Site 2, using analysis of covariance. P_t is the larval production at age t; t is age (d) from fertilization. The values 3.05 and 3.23 are ages at hatching.

Log-linear regressions of mortality are

Site 1 $\ln(P_t) = 4.49 - 3.90\ [(\ln(t/3.05))]$

Site 2 $\ln(P_t) = 1.4 - 3.05\ [(\ln(t/3.23))]$

Analysis of covariance between sites

Source of variation	df	Sum of squares	Mean square	F	Prob. (tail)
Equality of adjusted means	1	13.26	13.26	50.90	0.00
Zero slopes					
All covariates	1	35.12	35.12	134.80	0.00
error	11	2.87	0.26		
Equality of slopes all covariates and all groups	1	0.52	0.52	2.24	0.17
error	10	2.34	0.23		

DISCUSSION

We had expected to find higher rates of larval northern anchovy growth and survival in the inshore than in the offshore environment. Bias or low precision cannot explain the similarity of growth and mortality coefficients between sites. The larval anchovy parameters might have been biased had we sampled larval populations imported from other sources by advection or diffusion over the course of the measurement periods, but our time series of environmental characteristics display no shifts to indicate short-term change of properties or of populations at the drifters. Similarly, lack of precision cannot be invoked: the number of tows and larvae were sufficient to distinguish mortality coefficients (β) differing by 0.5 with an 86% probability (Lo et al. 1989). We must accept that the mortality coefficients were and that many more similar tows would be necessary to distinguish between them.

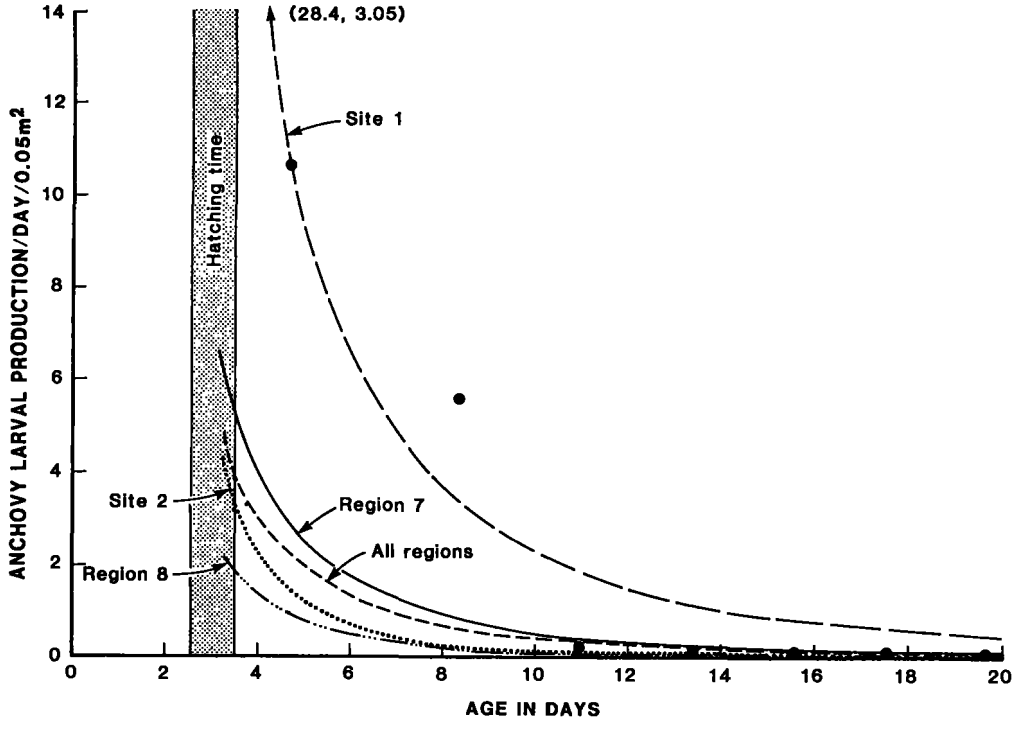


FIGURE 5.—Daily larval production vs. age for northern anchovy and fitted larval mortality curves for Site 1 and Site 2, and for CalCOFI 8502 survey and subregions. Points are for Site 1 only.

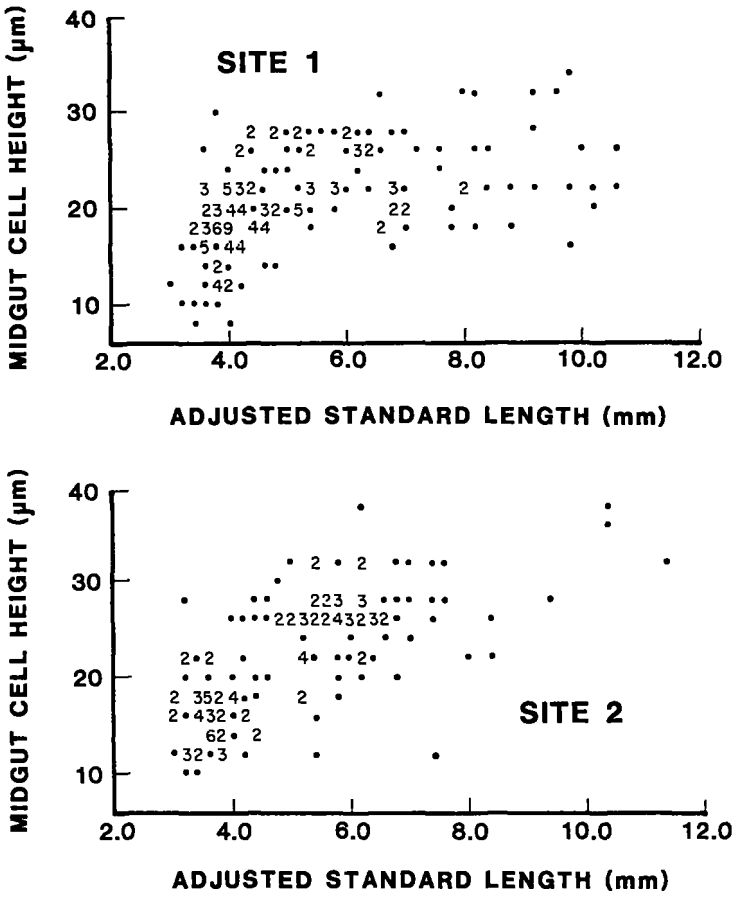


FIGURE 6.—Midgut cell heights of individual northern anchovy larvae collected at Site 1 (inshore) and at Site 2 (offshore).

TABLE 7.—Histological condition of larval northern anchovy at Sites 1 and 2. *n* = number examined; dur = duration; *n*/d = number/day; S = starved; I = intermediate; H = healthy; %/d = % dying/day due to starvation.

	Site 1					Site 2				
	S	I	H	total	%/d	S	I	H	total	%/d
3–4 mm (SL)										
n	9	17	28	54		4	32	21	57	5
dur	2	5	2.5			2	5	2.5		
n/d	4.5	3.4	11.2	19.1	24	2.0	6.4	8.4	16.8	12
4–5 mm (SL)										
n	1	11	48	60		0	5	20	25	
dur	2	3	2.5			3	3	2.5		
n/d	0.3	3.6	19.2	23.1	1	0	1.7	8	9.7	0
5–6 mm (SL)										
n	0	0	27	27	0	0	2	35	37	0
Total number examined				141					119	

Similarity of growth and starvation indices at the two sites indicates that most larvae had encountered sufficient forage to sustain "normal" growth rates, or that the fraction that had not done so were quickly removed from the system, i.e., not represented in our collections. Food abundance estimated from integrative tows may not reflect the actual availability of food to larvae because microplankton prey frequently occur in patches and laminae of very small extent (cf. Owen 1989). Also, larvae may have been sustained on food that passed through the net. Fewer larvae were collected at Site 2 than at Site 1, but starvation incidence was at least as low there as at Site 1. Furthermore, Site 2 larvae were growing as fast as those at Site 1, even though average microplankton concentration at Site 2 was less than half that at Site 1. Despite lower average food concentrations, there were zones at Site 2 that evidently contained enough food to support growth of the larvae.

An analogous result is given by Butler (1989), which showed that periods of diminished forage production, such as el Niño, have no discernible effect on growth rates of field-caught larvae. But Theilacker and Watanabe (1989) showed by experiment that starvation measurably retards larval growth. This apparent paradox is resolved if, in the sea, larvae that survive to be sampled have found enough food to grow at normal rates even in abnormal periods, whereas larvae that have been deprived to the extent that their growth is adversely affected soon vanish, perhaps by predation owing to their weakened condition rather than by starvation directly.

In contrast with the common view that northern anchovies broadcast sex products indiscriminately with the strategy that some get lucky, we advance the hypotheses that anchovy spawn where their offspring are equally likely to survive, even under widely different environmental conditions, and that these conditions mediate their spawning intensity. This is the central theme of MacCall's (1983) "Basin Model" of habitat selection by the northern anchovy.

The Basin Model postulates that when a population is large, its adults occupy less suitable habitats in which mortality of spawn per capita tends to equal that in more favorable habitats. This occurs because cannibalism of spawn by adults is higher in favored habitats than in peripheral habitats.

We roughly partition sources of overall larval mortality (β_t) into that due to cannibalism (β_c) and that due to other causes (other predation, β_p, and starvation, β_s). Diffusive change, a source of "apparent" mortality, is assumed from physical arguments above to be the same at both sites. Thus,

$$\beta_t = \beta_c + \beta_p + \beta_s .$$

If higher egg concentration denotes higher adult occupation, β_c was greater at Site 1 than at Site 2. Anchovy egg concentration at Site 1 averaged 37/m^3, 15 times the egg concentration at Site 2. This difference is too great to be attributed to differences in batch fecundity of the spawners, which varies by a factor of about two (Hunter et al. 1985).

For larval mortality, β_t, to have been equivalent at the two sites, mortality from other sources ($\beta_p + \beta_s$) is required to have been greater at Site 2 than at Site 1 to the degree of offsetting the difference between sites in parental consumption of spawn (β_c). But neither larval growth rates nor starvation incidence differed between sites, showing that their β_s values were about equal. This being so, cannibalism was offset by other predation rather than by starvation. This requires increased predation (β_p) at Site 2 over that at Site 1.

For comparison of β_p between sites, we formed rough indices of predation pressure, P, from catches by vertical net tow pairs. P is the concentration of the five most numerous predators caught by the 333 μm mesh net, divided by concentration of anchovy eggs and larvae caught in the corresponding 150 μm mesh net. Predator populations in the samples consisted mainly of raptorial copepods and chaetognaths. Mean values of P were 2.8 predators/anchovy at Site 1 (26 tows) and 5.5 predators/anchovy at Site 2 (24 tows). This difference indicates compensatory predation at Site 2. Confirmation of compensatory predation, however, is not possible from this data set because our nets missed larger, faster predators such as euphausiids, and because species-specific and size-specific predation rates are largely unknown.

CONCLUSIONS

Among the several characteristics of the ichthyoplankton investigated at contrasting habitat sites, only one, larval production rate, was clearly different between sites. Growth and

mortality rates were statistically indistinguishable between sites. Mortality due to starvation was about the same at the two sites. Larval production at Site 1 was well above the CalCOFI survey average, but Site 2 production and larval mortality at both sites were similar to those over the entire CalCOFI region.

Habitat characteristics at the two sites differed substantially. Site 1 was relatively eutrophic, as seen by its high concentrations of larval forage, zooplankton, chlorophyll, and phaeopigment. Site 2 was much more energetic, as seen by its greater wind speed, current speed, mixed layer depth, and depth of maximum stability. With the exception of predatory copepod abundance, every measured characteristic of the environment favored larval anchovy well-being more at Site 1 than at Site 2.

Yet the well-being of anchovy larvae was about the same at the two sites. Anchovies spawned under conditions where their larvae could grow and survive at about the same rates, despite the differences noted in the respective environments. Similar larval growth rates and the low incidence of starving larvae indicate adequate forage availability in both habitats. In agreement with MacCall's (1983) Basin Model, rates of larval anchovy mortality at the two sites were not greatly different and the same fraction of the original larval production survived to the schooling stage.

We consider this work to be a pilot effort to stimulate and guide research that we hope will be more experimental in scope and execution. To test our hypotheses, environments that more completely span the "suitable basin" need to be described and occupied long enough to follow characteristics of larval fish cohorts from egg to metamorphosis.

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