RELATION OF MEAN GROWTH RATE TO CONCENTRATION OF PREY-SIZED PARTICLES FOR LARVAE OF PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*)

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ABSTRACT

During February 1996, a combined OPC/MOCNESS was used to sample Pacific hake larvae (*Merluccius productus*) at twelve stations within or just offshore of the Southern California Bight. The OPC/MOCNESS simultaneously measured the horizontal and vertical distribution of hake larvae, the fine-scale distribution of prey-sized particles, and the temperature and salinity of the water column. In order to examine the relation between growth and particle concentration, I measured the size-at-age for 60 larvae from 6 stratified samples collected at five different stations. Within the strata examined, the average particle concentrations ranged from 6.36 to 1.44 prey-sized particles L^{-1}, and the average temperatures ranged from 10.5°C to 12.4°C. Estimates of the average growth rate of larval hake contained within these samples ranged from 0.135 to 0.279 mm d^{-1}. Within the range of temperatures examined, the average growth rate of larval hake collected in a sample was not related to the average temperature of that sample ($r^2 = 2e^{-6}$, $p = 0.998$). In contrast, there was a significant, positive relation between the average growth rate of larval hake within a stratum and the average concentration of prey-sized particles in that stratum ($r^2 = 0.795$, $p < 0.02$).

INTRODUCTION

For many decades, scientists have examined the stock-recruitment dynamics of fish populations. In particular, they have searched for the underlying cause of the recruitment variability that often occurs independent of fluctuations in adult biomass. The Pacific hake (*Merluccius productus*) is one species in which such variability occurs. While the per capita recruitment rate of Pacific hake may vary 100-fold interannually (Methot and Dorn 1995; Smith 1995), these fluctuations are not obviously related to the spawning biomass, or to the number of eggs present in the sampling region (Hollowed and Bailey 1989; Hollowed 1992; Methot and Dorn 1995). Recruitment of Pacific hake is determined at a relatively young age. Bailey et al. (1986) report that the abundance of age-0 hake collected in southern California midwater trawl surveys is strongly related to the magnitude of the year class at recruitment. Furthermore, Hollowed and Bailey (1989) demonstrated that measuring the abundance of hake larvae 11.50 to 15.75 mm long made it possible to predict the relative strength of the year class at age three. Thus processes that influence the survival of Pacific hake larvae determine, in part, the relative magnitude of recruitment to the adult population.

Many factors influence the survival of fish larvae, including genetic defect, disease (Sindermann 1970; Sissenwine 1984); predation (Hunter 1981; Houde 1987; Bailey and Houde 1989); adverse transport (Hjort 1914; Parrish et al. 1981); growth rate (Ware 1975; Shepherd and Cushing 1980); and starvation (Hjort 1914; Cushing 1975; Lasker 1975, 1978, 1981). Thus it is often difficult to determine the magnitude of any one source of mortality. Pacific hake larvae, however, possess a unique suite of characteristics that may modify their likely sources of mortality.

Hake larvae are generally distributed from 50 to 100 meters, well below the turbulent wind-mixed layer, and they are occasionally found as deep as 200 meters (Ahlstrom 1959). This subsurface habitat may protect them from Ekman drift and wind-driven transport (Smith 1995), factors that can increase mortality if larvae are advected from areas where temperature and prey concentrations are favorable for growth (Bailey 1981; Parrish et al. 1981). However, this subsurface habitat is also below the zooplankton biomass maxima located within the euphotic zone.

The diet of larval hake consists primarily of copepod nauplii, copepodites, and adult copepods (Sumida and Moser 1980). It has been estimated that first-feeding Pacific hake larvae must ingest 0.13 calories per day to balance the cost of metabolism and growth (Bailey 1982). Bailey predicts that this ration could be obtained by consuming 25 copepod nauplii, 15 small copepodites (or small adult copepods), or 1 large adult *Calanus* each day. Considering the limited mobility, small daily ambit, and poor ability of first-feeding larvae to capture prey, it is evident that the growth and survival of first-feeding hake larvae may be limited by the low prey concentrations often found at depth in the California Current region.

The objective of this study was to determine whether prey concentration limits the abundance and growth rate of Pacific hake larvae. Two questions were examined. (1) Was the concentration of larval hake within a stratum related to the average concentration of prey-sized

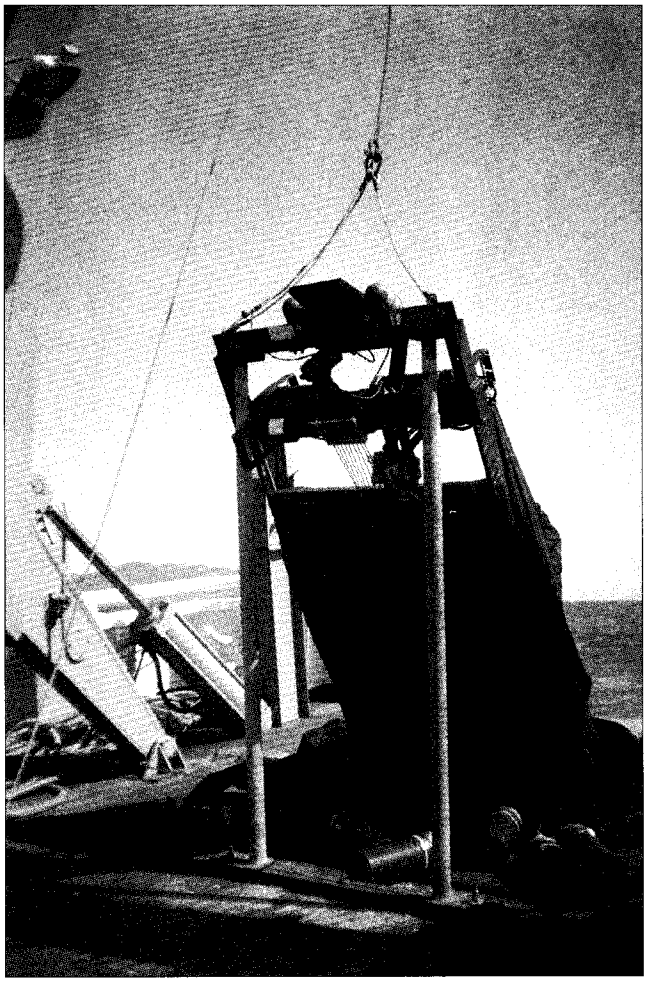

Figure 1. The OPC/MOCNESS. The optical particle counter can be seen atop the MOCNESS frame.

particles in that stratum? (2) Did hake larvae have higher average growth rates where the ambient concentration of prey-sized particles was elevated? Although the objective of this study is not novel, the approach is unique. The OPC/MOCNESS enables simultaneous measurements of both predator and prey. These data provide unique insight into the relation between prey concentration and the abundance and growth rate of Pacific hake larvae.

METHODS

Sampling with the OPC/MOCNESS

The horizontal and vertical distribution of Pacific hake larvae and the fine-scale distribution of particles were measured simultaneously with a combined opening/closing net and environmental sensing system (MOCNESS; Wiebe et al. 1976) and optical plankton counter (OPC; Herman 1988, 1992; figure 1). Pacific hake larvae were collected with a 1-m^2 MOCNESS with ten 333-μm-mesh nets. The MOCNESS was deployed to a depth of 225 m, and sampled nine 25-m strata from 225 m to the surface. In addition, one net was open throughout the downcast. This net provided an integrated sample that was not examined.

Particles were counted with a Focal Technologies OPC attached directly to the MOCNESS frame. The OPC uses an array of light-emitting diodes to count particles. The light travels through a cylindrical lens and is focused into a parallel beam extending across the sampling tunnel, at the end of which it passes through a second lens and is refocused onto a photodiode receiver. The amount of light reaching the photodiode receiver is converted to a corresponding voltage. As a particle passes through the sampling tunnel, it attenuates the light beam by an amount proportional to the cross-sectional area of the particle and its transparency. In turn, the amount of light that reaches the photodiode receiver is reduced, as is the corresponding voltage. Each time the voltage is reduced, a particle is counted. The analog decrease in voltage is converted to a digital size for the particle (Herman 1988, 1992). By means of a standard calculation that assumes that all particles are spherical, the digital size can then be converted to an equivalent spherical diameter (ESD).

The OPC can be used to identify and estimate the abundance of specific taxa (Herman et al. 1993; Osgood and Checkley, in press). However, this is practical only when the species composition is limited to a few members with distinct optical attributes, or when most of the biomass is accounted for by a single species. Such was not the case during this study, so it was necessary to estimate the size range of particles that could be prey for larval hake.

Sumida and Moser (1980) state that adult copepods 110 to 600 μm in maximal width make up 73.8% of the gut volume of Pacific hake larvae 3 to 11 mm long. If one assumes that the volume of an adult copepod can be estimated by a cylinder with a height equal to three times its diameter (Mullin and Cass-Calay 1997), a copepod 600 μm wide would have an ESD equal to 1,000 μm. The smallest particle that can be routinely detected by the OPC has an ESD of 250 μm. This value corresponds to a copepod roughly 152 μm in diameter. Therefore I assumed that all particles with an equivalent spherical diameter ranging from 250 to 1,000 μm are "prey-sized particles." In addition, several other assumptions were necessary: (1) that hake larvae and particles are distributed randomly within a stratum; (2) that the amount of food available to the hake larvae within a stratum can be estimated by the average concentration of prey-sized particles within that stratum; and (3) that the distributions of hake larvae and prey persist over a period of days to weeks.

Calculating the Concentration of Prey-Sized Particles

By merging the OPC and MOCNESS data I was able to calculate the concentration of prey-sized particles in each stratum with the equation

$$\frac{N}{l} = \frac{N}{t} \cdot \frac{t}{v \cdot t \cdot A} \cdot 10^{-3}$$

where N is the number of prey-sized particles; l is the volume sampled (l); t is duration of the sampling interval (s); v is the net speed (m/s); and A is the area of the OPC aperture (m^2). The OPC/MOCNESS measurements provided one estimate of particle concentration every 3.6 seconds. Since each MOCNESS net was open for approximately 3 minutes, about 50 concentration estimates were made in each 25-m stratum. The average particle concentration within a stratum is simply the arithmetic mean of these estimates.

Preserving the Samples

In order to allow examination of both the gut content and growth rate of larval hake, it was necessary to split each MOCNESS sample into two equal portions. So the entire MOCNESS sample was rinsed out of the cod end into a 32-ounce jar. The sample was then poured into a containment reservoir. Before the sample settled, a stopcock was opened to shunt the sample into two 32-ounce collecting jars. All plankton was then carefully rinsed out of the splitter and into the two collecting jars. One portion was preserved in a solution of seawater containing 5%–10% formalin saturated with sodium borate. The second portion was strained, then preserved in 80% ethanol. The ethanol was replaced after 24 hours. To prevent dissolution of the calcium carbonate otoliths, the ethanol was buffered with a saturated solution of Sigma 7–9 tris buffer in deionized water. Eight milliliters of the saturated tris solution were added to every liter of 80% ethanol.

Measuring Size-at-Age

Because the hake larvae had been preserved in ethanol for several months, before microscopic examination they were soaked in deionized water for several minutes to restore the tissues to osmotic balance and to minimize shrinkage. I used a dissecting microscope with ocular micrometer to measure standard length. I used a dissecting microscope at 250× magnification, fitted with two polarizing filters, to remove the sagittal otoliths. The otoliths were then mounted on a glass slide, dried, and covered with a drop of liquid coverslip.

I used a digital analysis system at the NMFS/Southwest Fisheries Science Center to count growth increments. The digital analysis system included a compound microscope, a high-performance CCD camera, a high-resolution monitor, a video coordinate digitizer, and a computer to log data. To estimate the age of a larva, I examined several transects at 400× and 630× magnification across the widest part of both sagittal otoliths. The center and the edge of the otolith were digitized during each transect. Additional transects were made until every increment and the focus of the otolith were well resolved. I then used a software package designed to estimate the age and growth rate of larval fish to average the data.

Laboratory experiments have demonstrated that Pacific hake larvae form one growth increment each day (Bailey 1982). The first increment appears a few days after hatching, perhaps as feeding commences (Bailey 1982). Because otolith analysis can be somewhat subjective, otoliths were mounted on slides labeled with a random number. No depth, temperature, prey concentration, or size information was recorded on the slide. In addition, slides were analyzed in random order. Both sagittal otoliths were analyzed to minimize the variability in the age estimate. A single reader made all the measurements.

Estimating the Mean Growth Rate

The mean growth rate of the larvae within a given stratum was estimated as follows. A representative subsample was chosen haphazardly, so that a variety of sizes were examined. The size and age were determined for each fish, and a linear equation was fitted to the data. The slope of the fitted line was assumed to be equal to the mean growth rate. It should be noted that a Gompertz curve is generally fitted to size-at-age data in order to estimate growth rates. But I chose a linear equation to facilitate statistical analysis, and because the growth of Pacific hake larvae is described more accurately by a linear equation during the first 20 days after hatching (Bailey 1982).

RESULTS

Horizontal and Vertical Distribution of Hake Larvae

Samples were taken at twelve stations during February 3–14, 1996, in the region from 32° to 34°N and 118° to 121°W (figure 2). Station locations and times of occupation are summarized in table 1. The average volume of water filtered by the MOCNESS in each stratum was 154.1 ± 4.2 m^3 (mean ±SE). Although Pacific hake larvae were found at all stations, their abundance at a given station varied from 4 to more than 1,100 larvae per collection (table 1). The larvae were most common from a depth of 25 to 100 meters, and the center of the vertical distribution was approximately 50 meters (figure 3).

Temperature profiles were measured with a CTD attached to the MOCNESS frame. These data were used to estimate the depth of the mixed layer. At eleven of

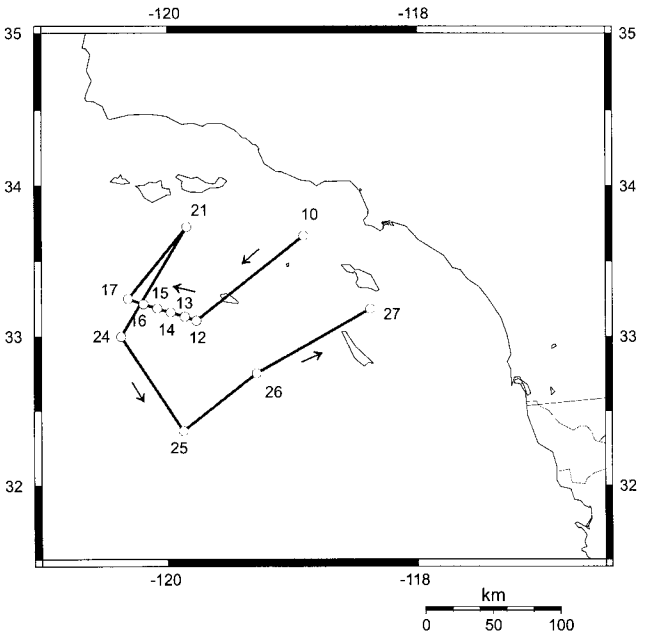

Figure 2. The OPC/MOCNESS cast locations. Twelve stations were occupied (station numbers 10–27) from February 3 to 14, 1996.

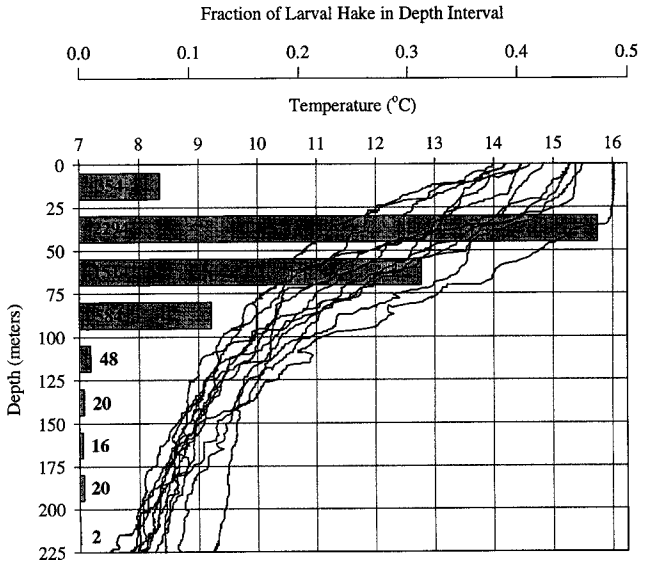

Figure 3. Vertical distribution of all Pacific hake larvae collected during this investigation. The boldface number is the total number of hake larvae found in a given depth interval. Superimposed is the temperature profile at each of the twelve stations.

twelve stations the mixed layer was less than 25 meters deep. At station 24 it was approximately 33 meters deep. Hake larvae were rare in the mixed layer, accounting for less than 7.3% of the larvae collected. More than 90.5% of the hake larvae collected were found in the stratified waters of the thermocline (figure 3).

Larval Abundance as a Function of Particle Concentration

For the following analyses, I examined 97 of the 106 strata sampled. Because the MOCNESS was accidentally reset during deployment, the software for merging the OPC/MOCNESS data malfunctioned. Thus it was impossible to calculate the concentration of particles at station 26. Therefore the nine strata sampled at that station could not be included.

TABLE 1
OPC/MOCNESS Station Locations, Dates, Times of Casts, and Total Numbers of Hake Larvae Collected in the Nine Stratified MOCNESS Nets

Station	Latitude	Longitude	Date	Time (PST)	Hake
10	33°40'.4N	118°59'.5W	2-8-96	2056	78
12	33°06'.2N	119°46'.0W	2-9-96	1045	394
13	33°07'.8N	119°51'.6W	2-9-96	1544	392
14	33°09'.6N	119°58'.3W	2-9-96	1807	566
15	33°11'.1N	120°04'.8W	2-9-96	2037	862
16	33°12'.9N	120°11'.4W	2-9-96	2310	1,108
17	33°15'.0N	120°18'.7W	2-10-96	0158	524
21	33°43'.9N	119°50'.7W	2-11-96	0054	180
24	32°59'.9N	120°22'.0W	2-12-96	0406	4
25	32°21'.9N	119°52'.3W	2-12-96	1257	72
26	32°45'.1N	119°17'.2W	2-12-96	2012	196
27	33°10'.9N	118°22'.7W	2-13-96	0852	476

To investigate the relation between prey availability and the abundance of feeding-stage hake larvae, I compared the average concentration of prey-sized particles in a sample to the concentration of feeding-stage hake larvae in that sample. To minimize the effect of strata sampled outside the spawning area (which would include no larvae regardless of prey concentration) I excluded all samples that contained zero hake larvae from the statistical analysis. In addition, since none of the 212 hake larvae larger than 3.9 mm SL examined by Sumida and Moser (1980) retained yolk-sac resources, I assumed that all hake larvae larger than 4 mm SL were capable of feeding.

An analysis of variance indicated that there was a significant, positive relation between the concentration of hake larvae larger than 4.0 mm SL in a given sample and the average concentration of prey-sized particles in that sample (n = 47, r^2 = 0.158, p = 0.006; figure 4). Thus, feeding-stage larvae became more abundant as the particle concentration increased.

I used the same procedure to examine the relation between prey concentration and the abundance of larvae smaller than 4.0 mm SL. Unfortunately, small hake larvae are very fragile, and they were not well preserved. Often the mouth and the gut, which may have contained a yolk sac, had been destroyed during collection, leaving only the more sturdy head and notochord. Therefore, one cannot assume that the fish included in this investigation were all yolk-sac-stage larvae. An analysis of variance indicated that the concentration of hake larvae smaller than 4.0 mm SL contained within a sample was

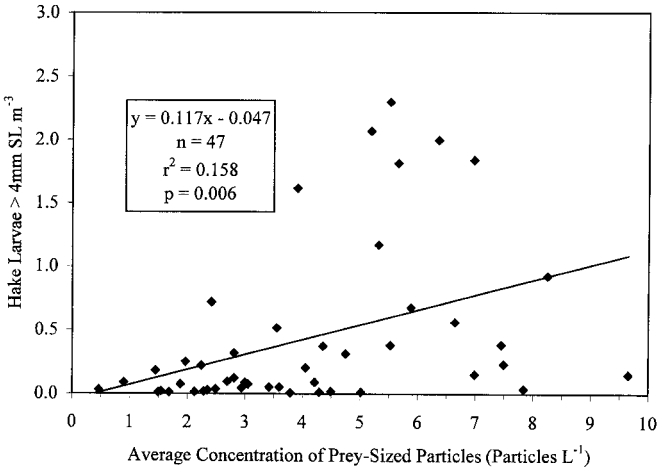

Figure 4. The abundance of larval hake larger than 4.0 mm SL as related to prey concentration. The data are the concentration of Pacific hake larvae larger than 4 mm SL found in a given stratum and the average concentration of prey-sized particles in that stratum. The *solid line* is the linear equation fitted to the data.

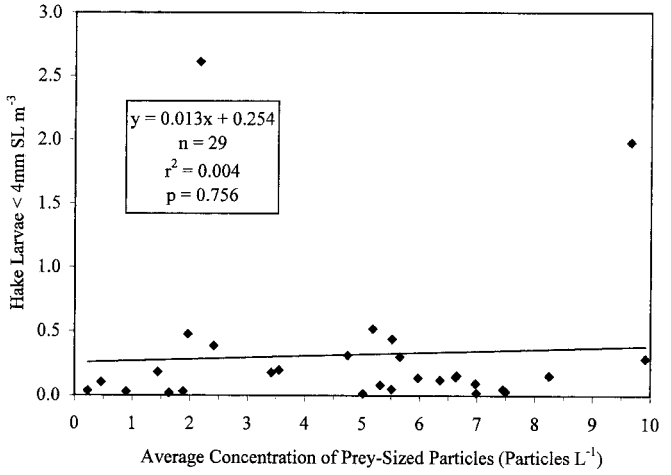

Figure 5. The abundance of larval hake smaller than 4.0 mm SL as related to prey concentration. The data are the concentration of Pacific hake larvae smaller than 4 mm SL found in a given stratum and the average concentration of prey-sized particles in that stratum. The *solid line* is the linear equation fitted to the data.

not related to the average concentration of prey-sized particles in that sample (n = 29, r^2 = 0.004, p = 0.756; figure 5).

Growth as a Function of Temperature and Prey Concentration

Six stratified samples collected at five different stations were chosen for this analysis. The samples were not randomly selected. Instead, they were chosen to maximize the variation in the average temperature and particle concentration of the samples analyzed. Within the six strata sampled, the average temperature varied from 10.5°C to 12.4°C, and the average particle concentration ranged from 1.44 to 6.36 prey-sized particles L^{-1}.

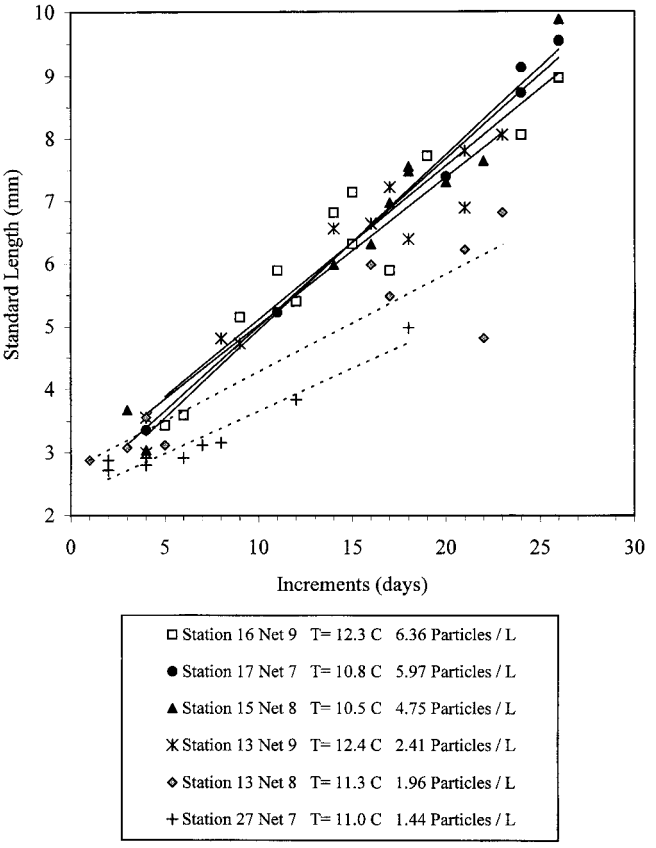

Figure 6. Size-at-age data for all fish analyzed. The various strata sampled are identified with symbols. The average particle concentration and temperature of the strata are given in the key. A linear equation was fitted to the data from each stratum. *Solid regression lines* indicate strata where the average prey concentration exceeded 2.40 prey-sized particles L^{-1}. *Dotted regression lines* indicate strata where the average prey concentration was less than 2.40 prey-sized particles L^{-1}.

The temperature range contained 70.8% of the hake larvae collected; the range of particle concentrations included 81.2% of the hake larvae.

The slope of a linear equation fitted to size-at-age data was used to estimate the average growth rate of the hake larvae within a sample. Although hake larvae do not grow in a strictly linear fashion, in every case the coefficient of determination, r^2, exceeded 0.845. It seems likely, therefore, that the size-at-age of hake larvae smaller than 11.0 mm SL can be adequately approximated by a monotonically increasing linear function, and that the average growth rate can be estimated with the slope of that function.

The average growth rates of hake larvae in the various strata ranged from 0.135 to 0.279 mm d^{-1}. Larvae grew at a rate of 0.235 to 0.279 mm d^{-1} in strata where the average particle concentration was ≥2.40 prey-sized particles L^{-1} (figure 6), but in strata with lesser concentrations the larvae grew more slowly. Below 2.40 prey-sized particles L^{-1}, average growth rates of 0.135 mm d^{-1} and 0.155 mm d^{-1} were measured (figure 6).

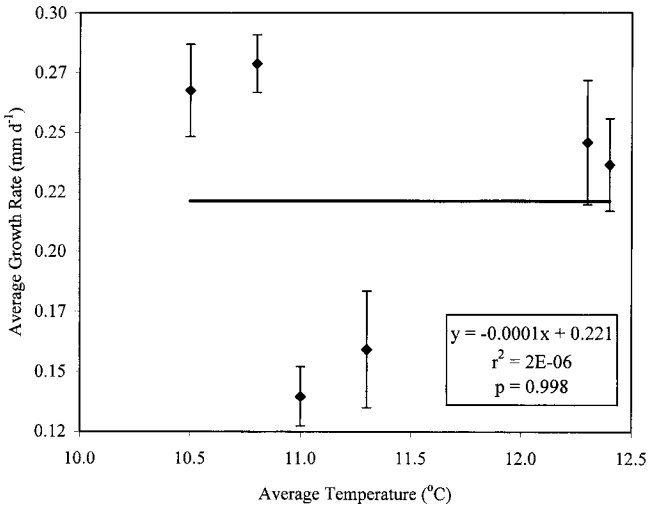

Figure 7. The growth rate of hake larvae as related to temperature. Each data point shows the average growth rate of the larvae within a stratum and the average temperature of that stratum. The standard errors of the growth-rate estimates are shown. The *solid line* is the linear equation fitted to the data.

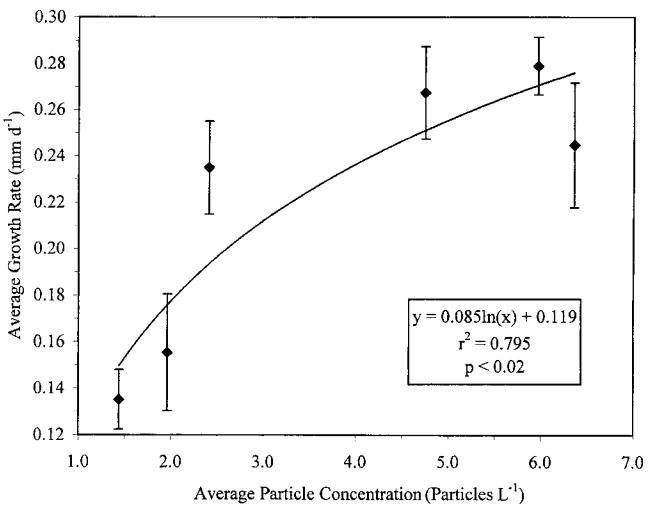

Figure 8. The growth rate of hake larvae as related to prey concentration. Each data point shows the average growth rate of the larvae within a stratum and the average particle concentration of that stratum. The standard errors of the growth-rate estimates are shown. The *solid line* is the logarithmic equation fitted to the data.

To examine the effect of temperature on the growth rate, I compared the average growth rate within each stratum to the average temperature of that stratum. I fitted a linear equation to the data, and tested the significance of the regression with an analysis of variance. The results of this analysis indicated that within the range of temperatures examined, the growth rate of hake larvae was not related to temperature (r^2 = 2E-6, p = 0.998; figure 7).

I used a similar analysis to examine the effect of particle concentration on the larval growth rate. I compared the average growth rate within a stratum to the average particle concentration of that stratum. These data indicated that hake larvae grew faster at elevated particle concentrations, but the relation was not linear. Instead, the results suggested a particle concentration above which the average growth rate did not increase. A logarithmic regression fitted to the data explained a large amount of the variance in the growth rate (r^2 = 0.795; figure 8). To test the significance of the logarithmic regression, I log-transformed the data and fitted a linear regression to the transformed data. An analysis of variance indicated a significant, positive relation between the average growth rate of hake larvae in a stratum and the average prey concentration of that stratum (r^2 = 0.786, $p < 0.02$). Therefore, it appears that particle concentration has a substantial influence on the growth rate of Pacific hake larvae.

DISCUSSION

The purpose of this study was to evaluate how prey concentration influences the abundance and growth rate of Pacific hake larvae. This type of study has been attempted in the past for first-feeding clupeoid fishes that consume much smaller particles including diatoms and dinoflagellates (Lasker 1975, 1978, 1981), and for other gadoid fishes that, like the Pacific hake, consume copepod nauplii and larger zooplankton at first feeding (Buckley and Lough 1987; Canino et al. 1991). Unfortunately, previous attempts to understand the importance of starvation in natural fish populations have been confounded by the inability to simultaneously measure the small-scale distribution of both predator and prey. It has therefore been quite difficult to show that reduced availability of food inhibits the growth of fish larvae in the field. This study demonstrates that the OPC/MOCNESS makes it feasible to simultaneously collect Pacific hake larvae and make in vivo measurements of the abundance and fine-scale distribution of their prey.

This study indicated that Pacific hake larvae became increasingly abundant as the concentration of prey-sized particles increased. This relation could have been caused by several mechanisms. First, hake larvae may emigrate from areas where prey concentration is low, or move into regions where it is high. This mechanism seems unlikely because of the poor mobility of early-stage fish larvae and the large horizontal spatial scales of variability in prey concentration. But vertically, prey concentration varies over much smaller spatial scales (e.g., meters). Therefore this mechanism is feasible if hake larvae migrate vertically. Ahlstrom (1959) and Roberts and Ralston (unpublished data) indicate that there is no significant diel variation in the abundance of Pacific hake larvae captured in net collections. These results suggest that

hake larvae do not undergo diel vertical migration, but they may migrate on longer time scales.

Second, adults may choose to spawn in regions with high prey concentration. This also appears improbable, since the fish spawn at depths of 130 to 500 m (Bailey 1982), whereas larvae are abundant at 50 to 100 m (Ahlstrom 1959). In addition, because spawners do not appear to migrate vertically (Bailey 1982), they are unable to assess the adequacy of the nursery environment. Physical forcing could also cause aggregations of predator and prey. Unfortunately, this issue cannot be addressed with the data presented, but it remains a fascinating topic for future investigation.

This study suggests that elevated mortality caused the reduced abundance of feeding-stage larvae at low particle concentrations. Hake larvae larger than 4.0 mm SL have depleted their yolk-sac resources. Therefore, inadequate prey concentration can increase their mortality directly by increasing the starvation rate, and indirectly by lengthening the stages most vulnerable to predation, as well as by inhibiting the escape response (Ware 1975; Shepherd and Cushing 1980; Folkvord and Hunter 1986). This conclusion is further supported by the fact that there was no relation between the abundance of larvae smaller than 4.0 mm SL and prey concentration. A large portion of these small larvae were in the yolk-sac stage. Since larvae do not require exogenous food until yolk-sac resources are exhausted, there is no obvious mechanism to increase the mortality of yolk-sac larvae found at low prey concentrations.

It is difficult to relate larval growth rates to temperature and prey concentration. Changes in growth rates occur on time scales of days to weeks, whereas the average temperature and prey concentration of a stratum can change much more quickly (hours to days). My results indicate that in strata with high particle concentrations, larvae older than one week were larger than larvae of the same age collected from strata with lower particle concentrations. This trend persisted throughout the first month of life. There are two explanations for this finding: either it occurred by chance, or the ambient conditions where hake larvae are found persist over extended time scales (days to weeks). Since hake larvae are found in the stratified waters of the thermocline where wind-driven mixing is minimal, the latter explanation is reasonable.

This investigation demonstrates that there is a significant, positive relation between the growth rate of Pacific hake larvae and prey concentration. Where prey concentration exceeded 2.40 prey-sized particles L^{-1}, mean growth rates ranged from 0.235 to 0.279 mm d^{-1}. Below this concentration, growth was reduced by as much as 50%, to 0.135 to 0.155 mm d^{-1}. The lower values are consistent with a published average growth rate of 0.160 mm d^{-1} for hake larvae collected off southern California during 1977, 1978, and 1979 (Bailey 1982).

Recruitment of Pacific hake is positively related to a number of processes, including weak offshore transport in early winter (Bailey 1980, 1981; Bailey and Francis 1985; Hollowed and Bailey 1989); warm January sea-surface temperature (Bailey and Francis 1985; Hollowed and Bailey 1989); and increased upwelling in March (Hollowed and Bailey 1989). Bailey and Francis (1985) suggest that strong year classes often develop when water temperatures are warm; when spawning occurs at the northern extent of the potential spawning region, near Point Conception; and when larvae are abundant in the inshore regions. Arthur (1977) examined the distribution of microzooplankton in the California Current system and found that the abundance of microcopepods was 4 to 5 times higher in the inshore regions. In addition, Chelton (1981) reports that zooplankton biomass is generally higher in the northernmost region occupied by Pacific hake larvae and that zooplankton biomass decreases as one moves offshore, or to the south. Therefore, it is reasonable to conclude that the abundance of prey available to early-stage larvae determines, in part, the growth, survival, and eventual recruitment rates of Pacific hake.

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