VERTICAL DISTRIBUTIONS OF ZOOPLANKTON AND LARVAE OF THE PACIFIC HAKE (WHITING), *MERLUCCIUS PRODUCTUS*, IN THE CALIFORNIA CURRENT SYSTEM

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ABSTRACT

As part of an investigation of the vertical distributions of larval hake and potential food in March 1995, we used a pump to sample microzooplankton larger than 73 μm and an optical plankton counter (OPC) for zooplankton 250 μm or larger, at depths to 250 or 300 m at eight stations where larvae were found, and one other station. We also intercalibrated the two techniques for sampling potential food. Copepod nauplii and copepodids dominated the microzooplanktonic biomass. The greatest fraction of larval hake was found in the 50–75-m layer, together with the greatest fraction of the potential food (by either mensural technique) deeper than 50 m. The depth distributions of larvae and OPC-estimated zooplankton were positively correlated from 50 to 300 m, but this relation was not significant between the larvae and potential microzooplanktonic food caught by pumping. Because of a great abundance and relatively shallow distribution of larvae at one particularly rich station, however, there was an overall correlation between the abundance of larvae in a particular sample and the biomass of their food.

INTRODUCTION

The small-scale distribution of larval fish relative to their food supply has frequently been examined in attempts to determine whether availability of food during early life affects the success of eventual recruitment to the adult population. Larval Pacific hake (whiting), *Merluccius productus*, are particularly interesting in this regard, since they occur deeper in the water column than the larvae of most other commercially important species (Ahlstrom 1969), and therefore presumably experience quantitatively different environmental factors, including significantly lower concentrations of food, than do larvae living nearer the surface at the same locations.

Microzooplankton (heterotrophs a few tens to a few hundreds of μm in size, including proto- and metazoans) is awkward to sample—often too rare to enumerate precisely when sampled with water bottles, and too small to be retained in towed nets of commonly used mesh sizes. Yet one of the components (copepod nauplii) is perhaps the most important type of food for larval fish. One of the few investigations of the vertical distribution of microzooplankton in the California Current system off southern California was conducted by Beers and Stewart (1969), who obtained samples of total seston, total chlorophyll, and organisms passing through a 202-μm mesh from six depth intervals between the surface and 200 m at three offshore stations. Most relevant for comparison to the present work are data concerning microzooplankton retained on a 103-μm mesh. Copepod nauplii and copepodites dominated this size category, and were more abundant above 50 m than below this depth. Radiolarians also contributed significantly to the total abundance of microzooplankton below 50 m, which was $\leq 5 \cdot L^{-1}$. We used similar methods and addressed many of the same questions, but did not attempt as complete an assessment of taxa or of trophic or size categories.

We also used an optical plankton counter (OPC) to categorize by size and to assess the vertical distributions of somewhat larger zooplankton, on which the larvae increasingly depend as they grow. Because the OPC was attached directly to the opening/closing net used to determine the vertical distribution of larval hake, it provided a direct measure of the concentration of various food-sized particles in the depth strata where larvae were (or were not) caught, together with estimates of variability at smaller scales within strata.

METHODS

Sampling the Larval Hake

Our study was conducted during a March 1995 research cruise organized by the Coastal Fisheries Resources Division, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, on the RV *David Starr Jordan* (Lo 1997). We sampled a subset of the stations at which vertical distributions of larval hake were determined; this subset represented a variety of distributions and abundances (table 1).

The larval hake (along with other macrozooplankton) were sampled by a multiple opening/closing net and environmental sensing system (MOCNESS; Wiebe et al. 1976). This system was routinely deployed to 300 m, and nine depth strata were sampled between that depth and the surface—nominally strata 50 m thick below 150 m, and 25 m thick above that depth.

TABLE 1
Locations, Dates, Local Times of Samples, and Abundance of Larval Hake

Station	Lat., long.	Date (March 1995)	Time MOCNESS and OPC started	Time pump started	Larval hake/m^2	Median depth stratum (m)*
80.0, 85.0	33°18.9'N 122°52.9'W	12	1017	1230	0	x
80.0, 60.0	34°09.0'N 121°09.0'W	13	0608	0800	17.5	50–75
80.7, 58.8	34°03.8'N 120°58.6'W	13	1346	1530	10.5	75–100
79.3, 58.7	34°19.0'N 121°08.8'W	14	0511	0700	18.2	50–75
66.7, 80.0	35°47.2'N 124°11.7'W	17	1212	1400	7.1	125–150
67.4, 78.8	35°42.2'N 124°01.2'W	17	1833	2030	4.1	100–125
66.0, 78.7	35°57.2'N 124°11.7'W	18	1119	1230	2.4	75–100
74.3, 68.8	34°50.9'N 122°27.4'W	20	0736	0930	43.7	50–75
75.7, 66.3	34°40.9'N 122°06.5'W	20–21	2204	0030	9.8	50–100

*Stratum fished by the MOCNESS where 50% of the larval hake occurred in that stratum or shallower, and 50% in that stratum or deeper.

Sampling by Pump

Samples for microzooplankton were taken by lowering the intake of a 3.8-cm-diameter hose attached to a weighted hydrographic wire to 240 m and then pumping water from each successively shallower depth through an on-deck centrifugal pump into a collecting tub (after allowing the hose to flush with water from each new depth). From the tub, the water passed through a flowmeter and into a 73-μm-mesh net (figure 1 in Star and Mullin 1981; Miller and Judkins 1981). Each net-concentrated sample was preserved in 5% formalin-seawater. A subsample of the flow from the tub was diverted into a bucket in which temperature was measured. Depths were generally chosen to correspond to depths fished by the MOCNESS, with some finer detail near the surface, but we took no samples of microzooplankton in the 250–300-m or 100–125-m strata sampled by the MOCNESS.

Some caution is necessary in interpreting the results. The issues are actual depth of sampling, sampling efficiency, and synchronism. The temperature of the deepest samples was usually higher than the temperature measured at comparable depths by the MOCNESS, even when the hose was vertical. Although this probably resulted from heating as the samples passed through warmer surface waters, plus perhaps some frictional heating in the hose, it is possible that some water leaked into the hose from shallower depths.

We did not assess avoidance by zooplankters, nor rigorously compare the catches to those of some other, more conventional device such as a net, though a comparison with samples collected by water bottle satisfied us that nauplii and small copepodites were not destroyed by the pump. But because the hose was shortened to 100 m when that depth was reached, the flow rate increased significantly, and thus it is possible that avoidance was less important above 100 m than in the deeper samples. We tested this possibility by comparing six catches taken from 100 m with 240 m of hose (flow rate 49 L·min^{-1}) with five preceding and five following catches from the same depth but with only 100 m of hose (flow rate 79 L·min^{-1}).

For each enumerated category, there was no significant difference between median abundance in samples taken at the slower flow rate (longer hose) or the faster flow rate ($p > 0.10$ of no difference by rank sum test in all cases). Hence, efficiency of capture, though unknown, did not change significantly when the hose was shortened. Horizontal patchiness of all enumerated categories of organisms is shown by the coefficients of dispersion (variance/mean), which ranged from 9 for the least abundant category to about 60 for the most abundant.

It is also worth noting that the vertical profiles obtained by pump followed the MOCNESS tow (table 1), and took up to three hours to complete. The ship's motion caused some vertical and horizontal integration during sampling. In spite of time lag and drift, we assume that each depth sampled by pump was assignable to the

stratum sampled by the MOCNESS which included that depth (i.e., an assumption that horizontal layering was the dominant form of variability on this scale).

Microzooplankters in each sample were enumerated and measured under a dissecting microscope by one of two people; the counters were unaware of the sample's identity, and counted the samples in haphazard order. They assigned organisms to one of the following categories of maximum width: eggs; protozoans (mainly dinoflagellates and radiolarians); copepod nauplii <160 μm and ≥160 μm; copepodites <160 μm, 160–400 μm, and >400 μm; and other metazoans <160 μm, 160–400 μm, and >400 μm. The categorization was based on width of the mouth and maximum width of food items found in the guts of larval hake of various lengths (Sumida and Moser 1980). The mouth of a 33-mm larva is approximately 400 μm wide, although prey that large were actually found only in guts of larvae >40 mm long, and probably do not become a frequent part of the diet until a larva reaches 100 mm. Of larvae shorter than 40 mm with prey in their guts, approximately half contained prey at least 160 μm wide (but smaller than 400 μm).

To calculate the biomass of particular kinds of food as sampled by the pump, or the sum of all kinds, we assumed (1) that the eggs and protozoans were 100-μm spheres; (2) that the nauplii were cylinders with height equal to twice the diameter, small nauplii were 120 μm in diameter, and large nauplii were 253 μm in diameter; and (3) that copepodids and "other" metazoans were cylinders with heights equal to thrice the diameters, and the respective diameters of small, medium, and large animals were 120, 253, and 450 μm.

Sampling by Optical Plankton Counter

Because the MOCNESS required a conducting cable for towing, we were able to record data from an optical plankton counter (OPC) mounted directly on the top of the MOCNESS frame while the MOCNESS was being fished. This also allowed us to use the rate of travel of the MOCNESS through the water, monitored by an electronic flowmeter, to estimate the volumetric rate of sampling of the OPC, and to monitor the depth of sampling.

The OPC provided data categorized only by size of particle (indeed, there is no proof that all the particles counted were individual, living zooplankters), but with much greater vertical resolution than did the pump, and with no horizontal offset from the samples of larval hake. In fact, the vertical resolution of OPC data within the stratum sampled by each MOCNESS net was of little use except to indicate the range of concentrations of potential prey for the larvae caught in that stratum.

The OPC is described by Herman (1988), and has been used fairly often on towed or lowered devices to count zooplankton in situ at sea (e.g., Herman et al. 1991; Osgood and Checkley, in press). The size of particles detected by the OPC is expressed as equivalent spherical diameter (ESD), based on the calibration with spheres. Particles with ESDs 250 to 1,000 μm were counted in our application. The lower size limit is approximately equal, in terms of volume, to the separation between "small" and "large" nauplii and "small" and "medium" copepodites in the pump samples, described above. The upper size limit of the OPC is equivalent to a copepodid of 600-μm maximal width. Thus the particles detected by the OPC and the organisms counted microscopically from pumped samples overlap in size range.

We merged data from the OPC and MOCNESS sensors into 7.2-sec. time intervals, producing many estimates of the particle concentration experienced by the larval hake collected in a single sample, since a single MOCNESS net fished in a depth stratum considerably longer than this. We sorted the OPC data on sizes of particles into eight categories of ESD, in μm: 250–305, 305–398, 398–497, 497–602, 602–700, 700–803, 803–903, and 903–1,000. From the number of particles (n_i) detected in each size category (i), the mean ESD of that category (ESD_i), and the volume of water (v_t, m^3) sampled by the OPC during each time interval, we estimated the total biomass of particles ($mm^3 \cdot m^{-3}$) as:

$$\text{Biomass} = \Sigma\ 1.33 \cdot \pi \cdot (0.5 \cdot ESD_i)^3 \cdot 10^{-9} \cdot n_i \cdot v_t^{-1}$$

We thus assume that the particles are spherical, and that all particles are suitable as food for some size of larval hake. These estimates of biomass were then averaged for all periods within one stratum sampled by one MOCNESS net.

We compared the biomass of optically counted microzooplankton in the 160–400-μm-diameter categories (large nauplii and medium copepodids and other metazoans) with mean biomass in the smallest two size categories (250–398-μm ESD) estimated by the OPC for the same depth stratum (figure 1). Differences in the size categories, or in the calculations of biomass from size, could account for a constant, linear offset from a 1-to-1 relation between the two methods, but the relation is curvilinear. The problem is not due solely to the calculations of biomass from abundances using different geometric approximations, since a plot of abundances of particles counted by the OPC versus abundances of zooplankters caught by the pump was similarly offset from 1-to-1 and curvilinear, and less variance was explained. A reasonable explanation is coincidence in OPC counting at high concentrations of particles: if two or more particles pass through the OPC's sensing zone within the instrument's response time, they will be counted as one larger particle. The curvilinearity, however, is due to a few data points at high concentrations, and other explanations for curvilinearity are plausible.

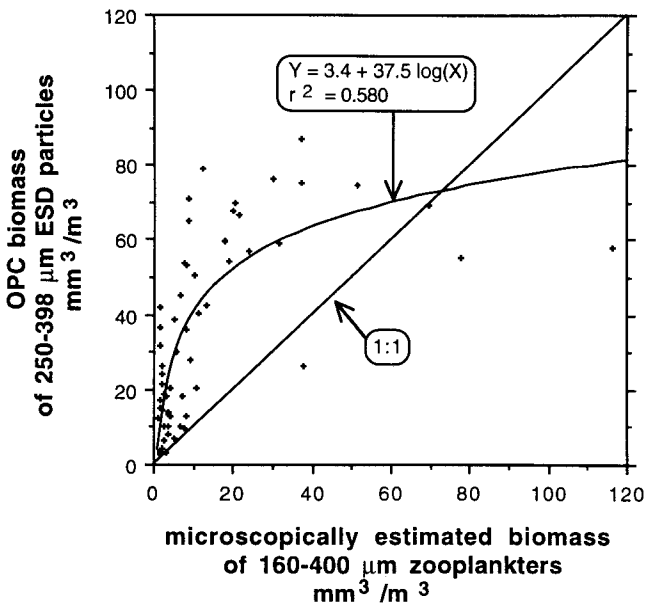

Figure 1. Biomasses of microzooplankton estimated by optical measurements and OPC. For optical measurements, the biomass represents the sum of biomasses of nauplii ≥160 µm, and copepodites and other metazoans 160–400 µm (see Methods). For OPC measurements, the biomasses are for particles 250–398-µm ESD (see Methods).

RESULTS

Pump Samples

As examples for detailed presentation, we selected three stations (table 1): one where larval hake were most abundant and relatively shallow (station 74.3, 68.8; 44 larvae·m^{-2}, median depth 50–75 m, some larvae in the upper 25 m); one where larvae were moderately abundant and relatively deep (station 66.7, 80.0; 7 larvae·m^{-2}, median depth 125–150 m, no larvae above 50 m); and one where the larvae were present but rare, and at an intermediate depth (station 66.0, 78.7; 2 larvae·m^{-2}, median depth 75–100 m). The histograms in figures 2–4 indicate the actual data (abundances of the enumerated categories, per unit volume of seawater at specific depths from which samples were pumped); the connecting lines are linear interpolations. Results are plotted to emphasize the vertical distribution of each individual category. Thus the axes for abundance differ between panels within each figure; analogous panels in different figures may have different axis values; and even within a panel there are usually differences in the volume of water to which the counts of different categories are referenced (except for "other" metazoans, all sizes of which were rare).

Many categories of food were more abundant at station 74.3, 68.8 than at the other two stations (see also figure 5), but there are few other differences clearly related to the occurrences of larval hake (see figure 5 for larval distributions). In particular, the vertical distribution of food at station 66.7, 80.0, where larvae were relatively deep, is not very different from that at station 74.3, 68.8, where the larvae were relatively near the surface, some even in the upper 25 m.

Figure 5 is a composite of data from all stations, showing vertical distributions of total prey biomass, calculated from abundances and geometric approximations of individual volumes, as described in Methods. The biomass of microzooplankton was least at the one station we sampled where no larvae were found (80.0, 85.0), but other differences are not obvious by inspection. Because this is a single station, and farther offshore than most of the

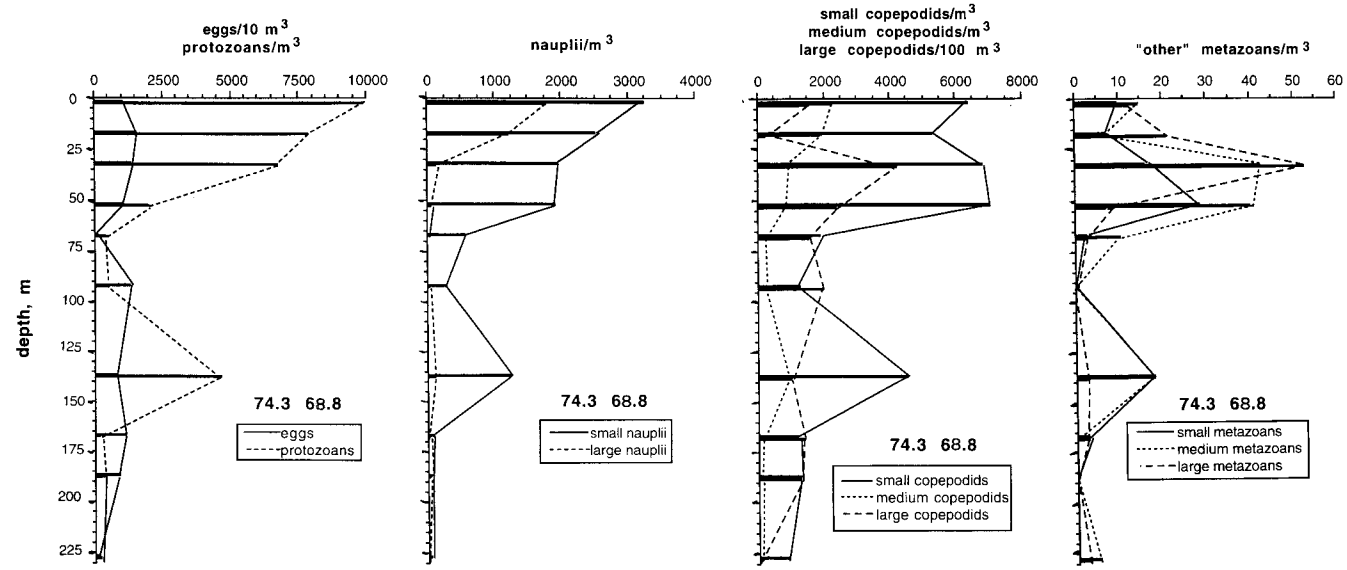

Figure 2. Vertical distributions of categories of microzooplanktonic food at station 74.3, 68.8 (see table 1 for location), where larval hake were abundant and relatively shallow (median depth 50–75 m). Note that volume basis for abundance differs between categories.

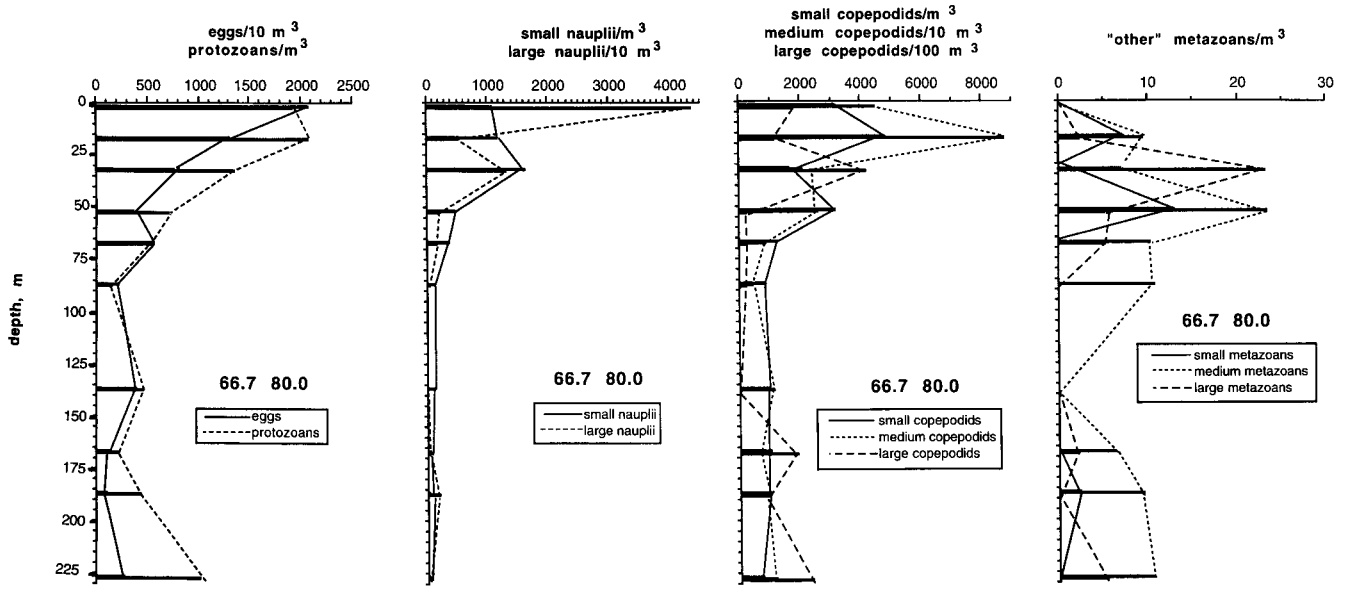

Figure 3. Vertical distributions of categories of microzooplanktonic food at station 66.7, 80.0 (see table 1), where larval hake were moderately abundant and deep (median depth 125–150 m).

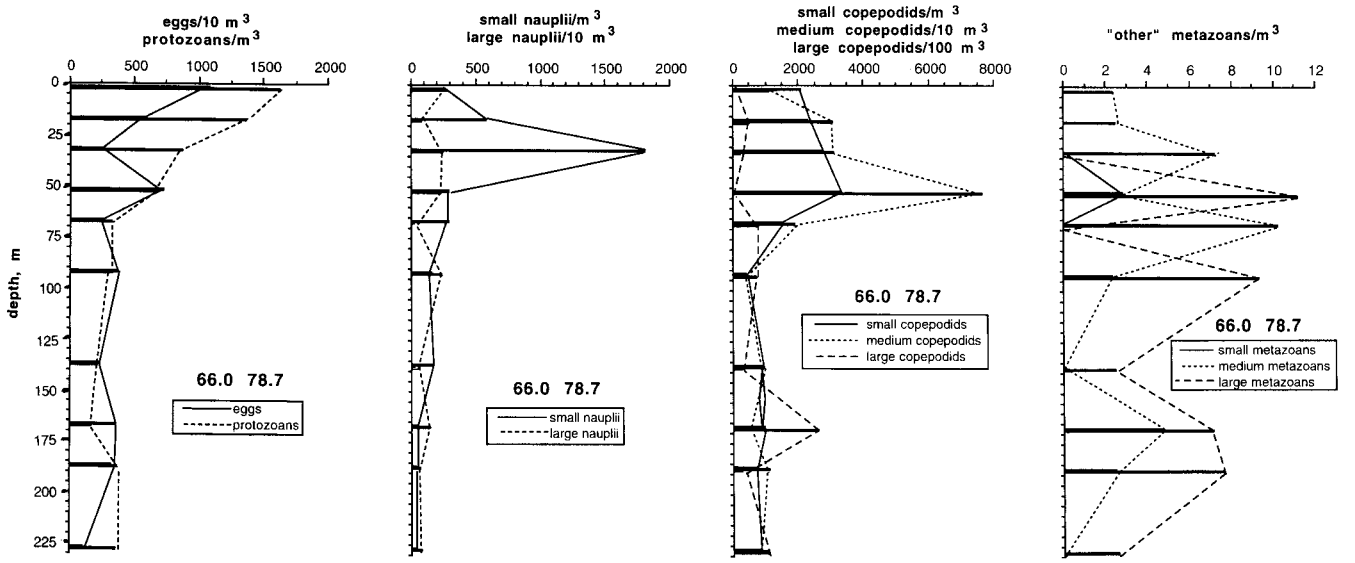

Figure 4. Vertical distributions of categories of microzooplanktonic food at station 66.0, 78.7 (see table 1), where larval hake were present, but rare and centered at an intermediate depth (75–100 m).

stations where larval hake were encountered, it is unrealistic to generalize from it to "hake-less" stations.

Larval hake were found from the 0–25-m stratum to the deepest stratum sampled (250–300 m) at some location within the subset of stations we sampled for microzooplankton (figure 5). Considering only the stations where larval hake were found, there was a significant, positive relation between their abundance and microzooplanktonic biomass (figure 6, left; 7 depths sampled at each of 8 stations). This relation combines the effects of the overall richness of a station, in terms of microzooplankton and larval hake, and the intensity and degree of coincidence of layering of microzooplankton and larvae within stations. We recalculated this relation using only abundances of nauplii and small and medium copepodids as the estimate of available food, but less variance was explained.

There was also a positive relation (figure 6, center) between the integrated abundance of larvae at a station (0–300 m) and the integrated abundance of microzooplankton (0–250 m), as suggested by the comparison (summarized above) of three specific stations. But when we calculated so as to give each station equal weight in the outcome, there was no relation between the fraction

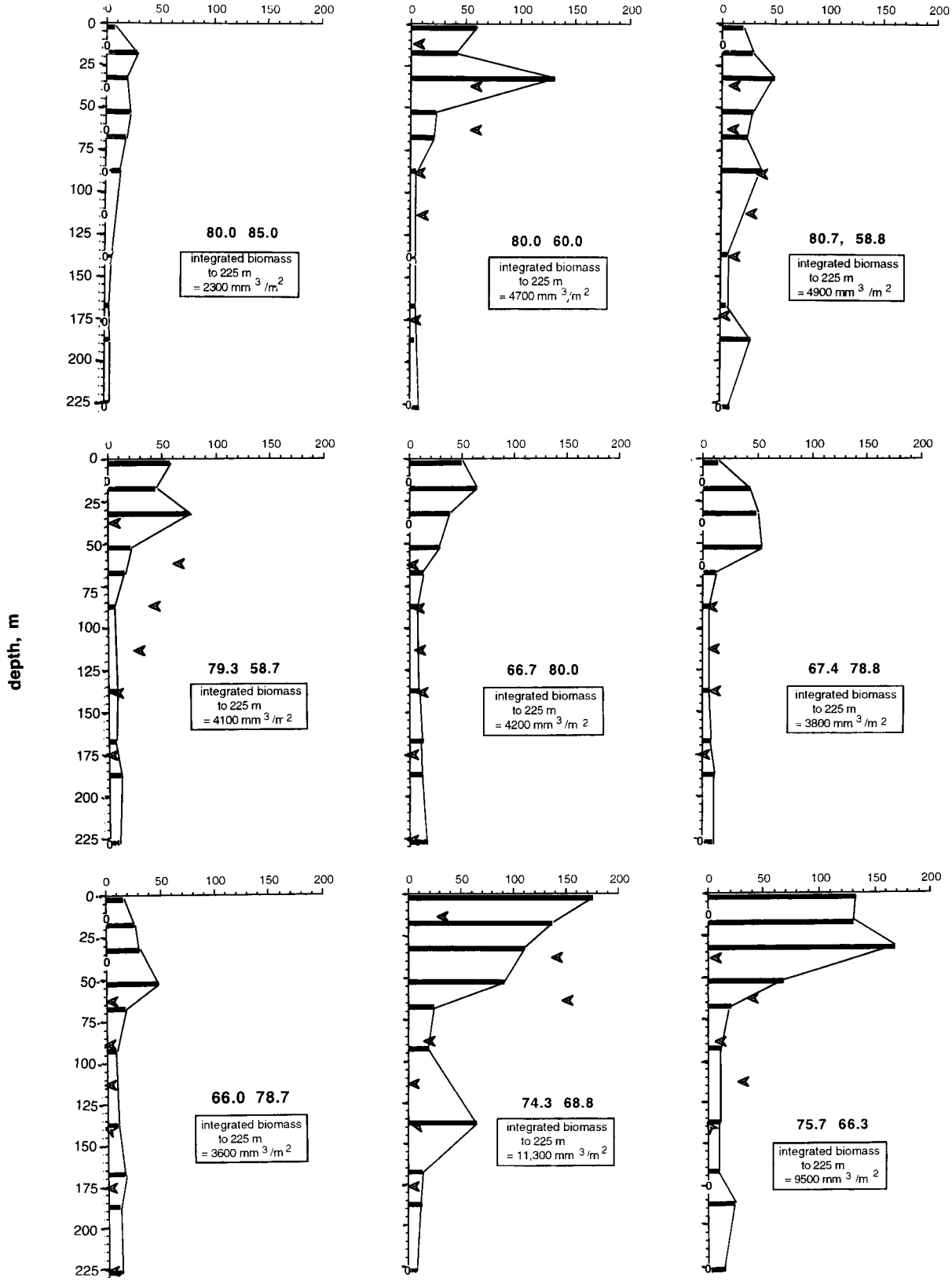

Figure 5. Vertical distributions (at all stations) of total prey biomass sampled by pump ($mm^3 \cdot m^{-3}$, calculated from abundances and geometric approximations of individual volumes, as described in Methods) and of larval hake. *Arrowhead* = larvae present, *0* = larvae absent, larvae·(200 m)$^{-3}$. The placement of the arrowhead indicates the midpoint of each OPC-sampled stratum.

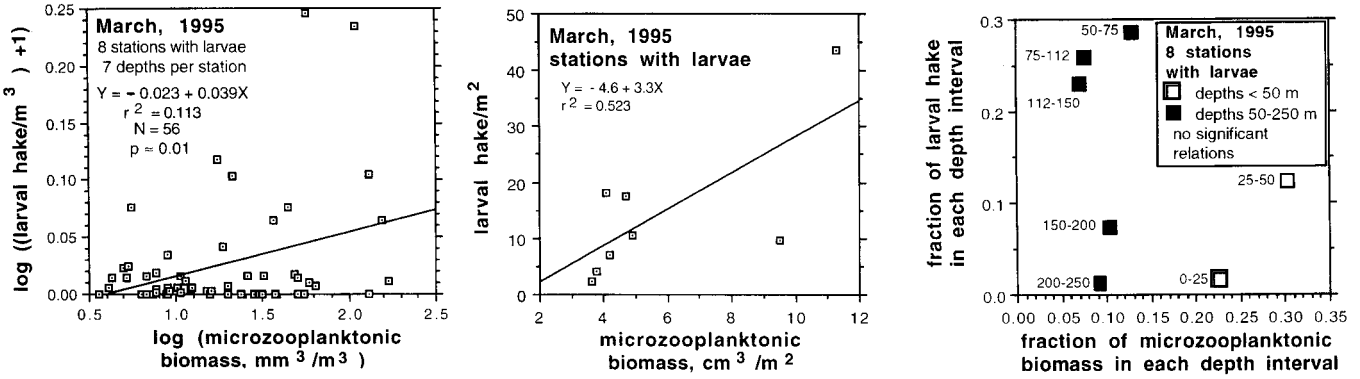

Figure 6. Correlations with pump-sampled microzooplanktonic biomass for stations where larvae were found. *Left*, Log-log correlation of larval hake abundances in specific strata at all stations vs. biomass of microzooplankton in those strata. The regression is significant. *Center*, Abundance of larval hake, integrated 0–300 m, vs. biomass of microzooplankton, integrated 0–250 m. The regression is significant ($p < 0.05$, 2-tailed). *Right*, Fraction of larval hake in each stratum vs. fraction of microzooplanktonic biomass in that stratum. Strata are indicated by numbers adjacent to points, and upper two strata are shown as open squares. The 100–125-m stratum, where larvae were sampled but not microzooplankton, is split between the adjacent strata.

of larvae in a particular stratum and the fraction of the available food that was there (figure 6, right). This was also true when the strata shallower than 50 m (open symbols in figure 6, right) were excluded, even though the 50–75-m stratum contained the greatest fraction of larvae and was richer in potential food than deeper strata.

On conceptual grounds, one would expect larvae to be particularly concentrated in the stratum with the greatest supply of food at those stations where food was scarce overall, and perhaps more broadly distributed where food was plentiful. This concept is not supported by the data. In fact, there is a *positive* correlation (though barely significant) between food available in the water column and the fraction of the column's total larvae that occurred in a single stratum.

OPC Samples

The relations between the vertical and areal distributions of larval hake relative to potential food, estimated as total biomass sensed by the OPC (figure 7) were very similar to those where pump-sampled microzooplankton was taken as the measure of potential food (figure 6). Considering all depths sampled at stations where larvae were found, there was an overall correlation between the abundance of larvae and the zooplanktonic biomass estimated by the OPC (figure 7, left), and a tendency (though a nonsignificant one) for the abundance of larvae in the whole water column to be greater where depth-integrated biomass was greater (figure 7, center). At depths greater than 50 m, the fraction of larvae in a particular stratum was positively correlated with the fraction of biomass found there (figure 7, right). The analogous relation was not significant with respect to pump-sampled microzooplankton (figure 6, right), perhaps because the deepest stratum sampled by the OPC and the MOCNESS (250–300 m) contained the lowest fraction of larval hake and of biomass (figure 7, right), but was not sampled by pump.

The OPC also provides a dimension not attained by pump sampling in this study (except the assessment of

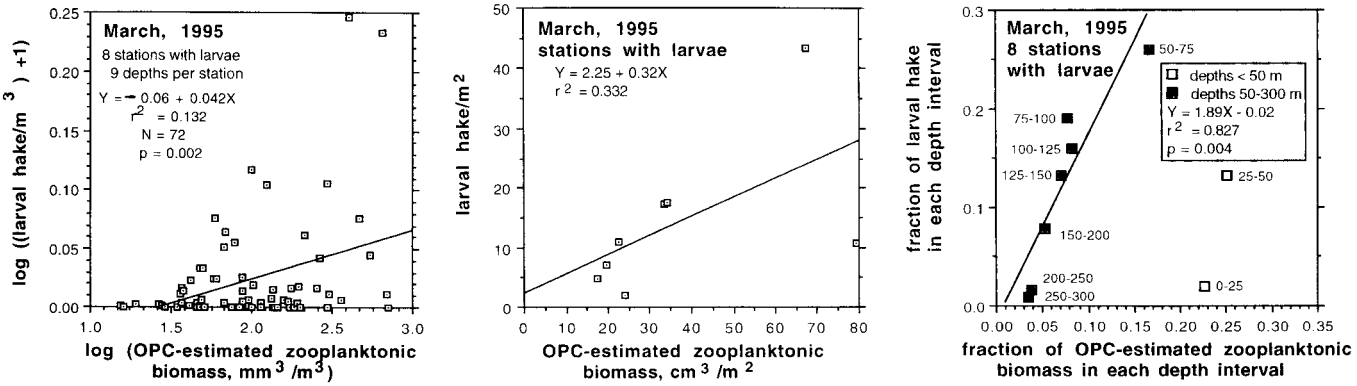

Figure 7. Correlations with zooplanktonic biomass (250–1,000-µm ESD) as estimated by OPC for stations where larvae were found (cf. figure 5). *Left*, Log-log correlation of larval hake abundances in specific strata at all stations vs. biomass of zooplankton in those strata. The regression is significant. *Center*, Abundance of larval hake vs. biomass of zooplankton, both integrated 0–300 m. The regression is not significant. *Right*, Fraction of larval hake in each stratum vs. fraction of zooplanktonic biomass in that stratum. Strata are indicated by numbers adjacent to points, and upper two strata are shown as open squares. When all strata were considered, the relation was not significant, but a significant regression (shown by the diagonal line and equation) was obtained for strata deeper than 50 m.

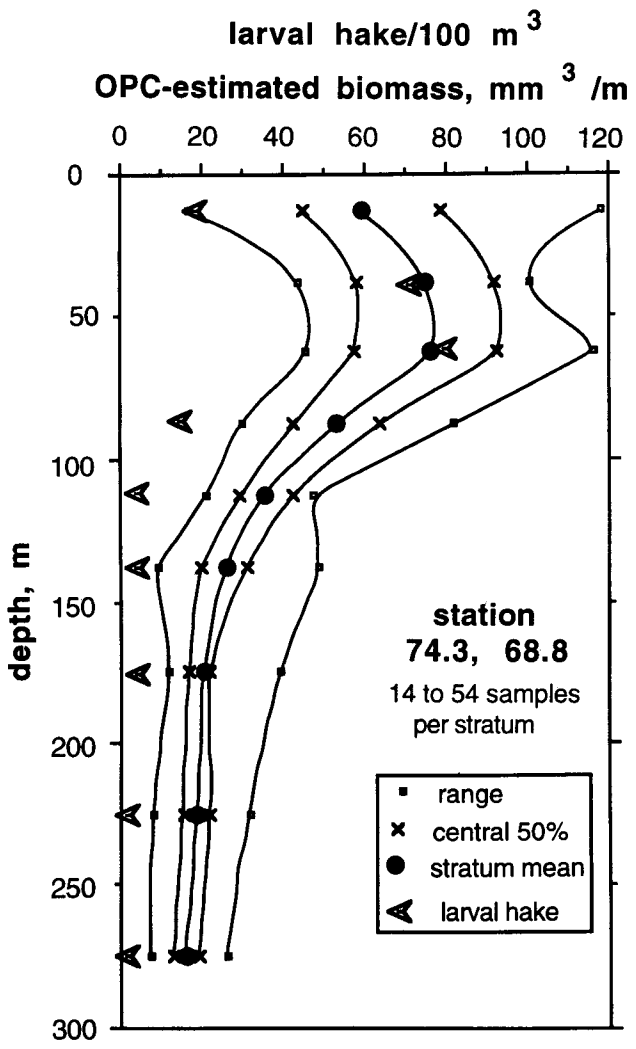

Figure 8. Variability in zooplanktonic food for larval hake at station 74.3, 68.8, based on 14–54 estimates of OPC biomass of particles 250–398-μm ESD per depth stratum sampled for larval hake. Shown for the midpoint depth of each stratum are the mean biomass (*large dot*), the envelope of the central 50% of all estimates (*x*'s), the range of biomasses (*small squares*), and the abundance of larval hake (*arrowhead*).

avoidance as a function of length of hose, reported in Methods): a measure of variation due to patchiness or layering on scales smaller than the depth strata integrated in sampling the larvae, but still potentially relevant to the question of how or where larvae obtain sufficient food to survive. Figure 8 shows an example for station 74.3, 68.8, the richest station with respect to both microzooplankton and larval hake, and where the latter were concentrated in relatively shallow strata. The biomass of zooplankters 250–398 μm in ESD, integrated to 250 m, was 10,500 $mm^3 \cdot m^{-2}$, which can be compared to a biomass of 11,300 $mm^3 \cdot m^{-2}$ of pump-sampled microzooplankton at this station (figure 5). The range of biomasses within any stratum was approximately proportional to the mean biomass there; in fact, the range·(mean)$^{-1}$ ratio varied from 0.75 to 1.5, and had no trend with depth.

DISCUSSION

The purpose of this study was to evaluate the availability of food for larval hake, which are unusual in their deep distribution. In many regions, gadoid larvae use copepod nauplii as their earliest food, and indeed the growth and/or recruitment of larvae is sometimes correlated with the availability of nauplii, on a mesoscale (Buckley and Lough 1987; Canino et al. 1991), seasonally (Haldorson et al. 1989), or interannually (Ellertsen et al. 1990). In most cases, the larvae feed in the uppermost few tens of meters, and the concentrations of nauplii in which they feed can be quite high (e.g., for walleye pollock, up to 144·L^{-1} in Shelikof Strait, Alaska, Incze and Ainaire 1994; 60·L^{-1} in Auke Bay, Alaska, Paul et al. 1991; and 10–20·L^{-1} in the Bering Sea, Dagg et al. 1984). Napp et al. (1996) report 20 nauplii·L^{-1} as minimally necessary for larval pollock, and Ellertsen et al. (1990) suggest a range from 10 to 50 nauplii·L^{-1} for Arcto-Scandian cod.

On the spatial scales of our study (tens of m vertically, tens of km horizontally), prey is much less concentrated in the environment where larval hake must find their first meals. The study of vertical distribution of microzooplankton by Beers and Stewart (1969), summarized above, indicated that prey for larval hake might be considerably less abundant than that for cod or pollock, and the present investigation confirms this. Even if the entire microzooplanktonic biomass below 50 m (≤100 $mm^3 \cdot m^{-3}$; figure 5) were made up of 253-μm-diameter nauplii, the greatest concentration below 50 m was equivalent to <3 nauplii·L^{-1}, and typical concentrations were of the order 1·L^{-1}. The greatest biomass of 250–398-μm ESD particles was 76 $mm^3 \cdot m^{-3}$ (figure 8), which is equivalent to only 4.3 particles·L^{-1} of 325-μm ESD.

The study by Beers and Stewart (1969) was conducted in the correct season (Feb.–Mar.) for comparison with present results, but their stations were either inshore or south of ours. They found concentrations of naupliar and postnaupliar copepods to be 1–5·L^{-1} in samples from >50-m depth caught on 103-μm mesh netting, while the size fraction passing through 103-μm but retained on 35-μm mesh contained up to 30·L^{-1}. For comparison, the abundance of these categories at 55 m at station 74.3, 68.8 (figure 2) was approximately 10·L^{-1} in our 73-μm-mesh samples, and less at greater depths or other stations (e.g., figures 3 and 4). Considering the differences in sampling between the two studies, this is reasonable agreement.

The data from the optical plankton counter are more difficult to compare with published studies because although a great range of sizes was included, the taxonomic composition is unknown. Within the size categories most readily compared, the relation between OPC-sensed particles and optically counted microzooplankton was not

good (figure 1). However, the relations between the larvae and their potential food were similar whether microzooplanktonic biomass or OPC-assessed total zooplanktonic biomass was considered as potential food. This similarity lends some confidence to the conclusions derived from sampling by pump, which was not truly coincident with sampling the larvae and was potentially more sensitive to within-stratum patchiness than was the sampling by OPC.

In addition to the paucity of food for larval hake (relative to other gadoid larvae), there are related trophic implications stemming from their depth. Though the water of the offshore California Current is usually more transparent than the more turbid, near-surface waters inhabited by other gadoid larvae, larval life below 50 m in late winter–early spring means that visual feeding must be possible at rather low intensities of light.

Further, a mechanism that has been invoked to explain high rates of feeding—turbulence-enhanced encounter between a larva and prey (Rothschild and Osborn 1988; Sundby and Fossum 1990; Sundby et al. 1994)—is also likely to be less important for larval hake than for near-surface species because of the decrease in turbulence with depth. Although the volume of water integrated in one of our samples is not unreasonable for the volume searched daily by a large hake larva, copepod nauplii and other prey are known to be patchy on still smaller scales (e.g., Owen 1989). It is therefore possible, at least in principle, that larval hake detect and feed on aggregations of prey on smaller scales than we sampled. Lack of turbulence would encourage the maintenance of such small-scale aggregations (e.g., Davis et al. 1991).

The OPC can sample these small-scale aggregations, though in the example shown in figure 8 there was no indication that patchiness was unusually pronounced (relative to the mean for the stratum) in the strata where larvae were concentrated. To determine the trophic significance of small-scale aggregations, it would be necessary to sample the larval hake, and to determine their feeding, on the various spatial scales of patchiness of food. This would permit tests for positive correlations on a substratum scale. Significant correlations would mean that the mean biomass of potential food in a stratum would underestimate the biomass most relevant to the feeding larvae. Going beyond correlations, one would also have to show that larvae do indeed detect and feed within small-scale aggregations frequently enough to permit observed growth rates.

ACKNOWLEDGMENTS

We thank the participants in this cruise, organized by the Coastal Fisheries Resources Division of the Southwest Fisheries Science Center, NMFS, NOAA, especially Paul Smith, David Griffith (who also provided data on abundances of larval hake), and Ronald Dotson. Ship time for calibrating the pumping system was provided by the University of California. Devendra Lal provided the pumping system, and Brent Gordon counted most of the samples. David Checkley provided the OPC. Two anonymous reviewers improved the manuscript by their careful reading. The research was supported by NOAA grant NA27FE0250; S.L.C-C. was supported by a NOAA Coastal Ocean Program grant to David Checkley as part of the South Atlantic Bight Recruitment Experiment (SABRE) and by a Patricia Roberts Harris Fellowship from the U.S. Department of Education.

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