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NOTES

Comparative Standing Stocks of Mesozooplankton and Macrozooplankton in the Southern Sector of the California Current System

The long-term (40-year) time series of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program has characterized low frequency changes in ocean circulation, macrozooplankton biomass, and ichthyoplankton and holozooplankton populations (Reid et al. 1958; Brinton 1981; Chelton et al. 1982; Smith 1985; McGowan 1985; Roesler and Chelton 1987). The Atlas series of the CalCOFI program provides extensive summaries of the hydrography of the California Current system and the large-scale distribution of its planktonic fauna (Atlas Nos. 1–30, Scripps Institution of Oceanography 1963–82). These investigations constitute an excellent foundation for studies ranging from experimental work with individual pelagic species to projections of global climate effects on ocean populations and production.

The primary emphasis of the zooplankton component of the CalCOFI program has been the larger macrozooplankton ($>505 \mu\text{m}$) and the ichthyoplankton. In the present study, we assess the biomass of the mesozooplankton (defined here as the zooplankton fraction passing through a $505 \mu\text{m}$ mesh net but retained in a $202 \mu\text{m}$ mesh net) in comparison with that of the historically sampled macrozooplankton. Efforts to close budgets of material and energy in the California Current system (Roemmich 1989) may require consideration of the contributions of the mesozooplankton to standing stocks and metabolic transformations. Further, given the selective nature of predation by planktivorous fish in this region (Arthur 1976; Koslow 1981), the mesozooplankton may be disproportionately significant as prey items to particular size classes of pelagic predators.

Materials and Methods

Comparisons of mesozooplankton and macrozooplankton standing stock were carried out between September 1986 and May 1987. A vertically retrieved bongo (VERB) net frame was used to take paired zooplankton samples (Fig. 1).

The net incorporated features of the Brown and Honegger (1978) vertical net and the McGowan and Brown (1966) oblique bongo net, with several differences. Unlike the Brown and Honegger net, the net rings did not hinge and presented less surface area. In contrast to the bongo net, the VERB frame did not pivot around a central axis, and the system was designed to filter only during vertical ascent rather than during oblique descent and ascent. The net mouth

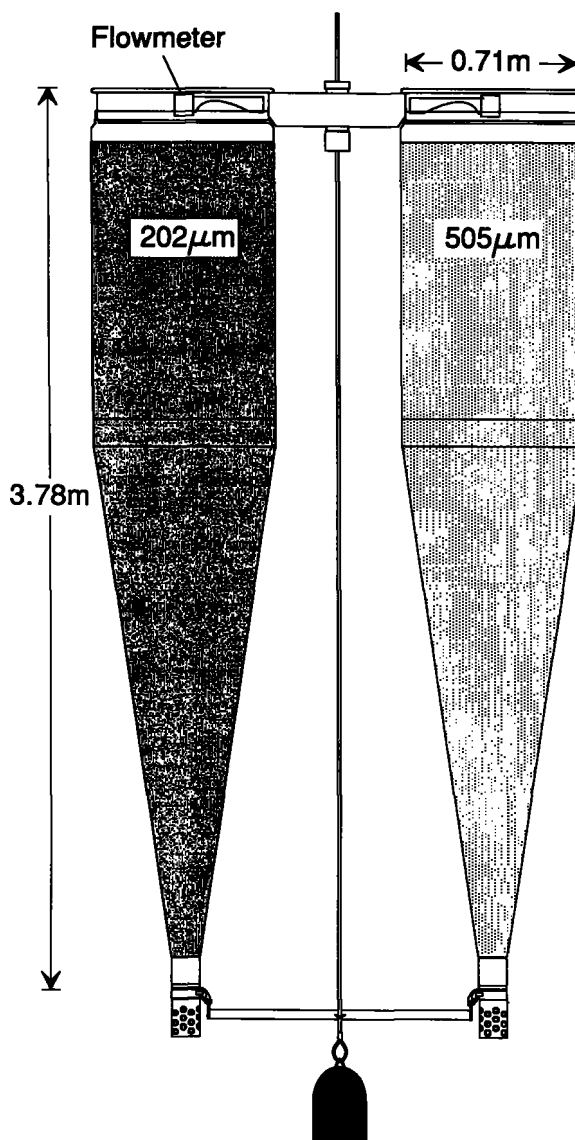


FIGURE 1.—Illustration of VERB frame and nets.

openings were each 71 cm in diameter and the net open area ratio was no less than 5.0 (Tranter and Smith 1968). A 100 kg weight was secured to the end of the hydrowire. TSK flowmeters¹, modified to display flow counts digitally, were mounted inside both net rings. The frame was deployed with one 202 μm Nitex mesh and one 505 μm mesh net, each with rigid cod ends having apertures of the same mesh size.

The VERB frame was lowered at a speed of 40–50 m min^{-1} to 200 m and retrieved at 60 m min^{-1} . Each net filtered approximately 80 m^3 of water, minimizing clogging of the finer mesh net. Rapid deployment and recovery, combined with maneuvering the research vessel, served to minimize deviation of the hydrowire angle from the vertical. Wire angles were recorded at least four times during ascent.

Preliminary VERB net trials were carried out on cruise Verb1 (11–12 September 1986; see Figure 2). VERB deployments were then made

on four CalCOFI cruises, designated 8609 (21–29 September 1986; $N = 28$ stations), 8611 (15–24 November 1986; $N = 26$), 8703 (5–14 March 1987; $N = 27$), and 8705 (3–12 May 1987; $N = 30$). The primary stations sampled were along two lines orthogonal to the coastline (lines 80 and 90); additional stations occupied the nearshore segment of lines 83 and 87 (Fig. 2). Time constraints precluded taking VERB samples at all CalCOFI stations.

Zooplankton samples were preserved in 10% formalin buffered with sodium borate. In the laboratory, the sample obtained with the 202 μm net was washed through a 505 μm mesh nested inside a 75 μm mesh, yielding a fraction between 202 μm and 505 μm (“mesozooplankton”) and one greater than 505 μm (“macrozooplankton”). The sum of these two fractions is referred to as “total” net zooplankton, although it quite clearly omits the microzooplankton that are certain to be of considerable significance (Beers et al. 1980; Fenchel 1988). Biomass of zooplankton samples was determined first by measuring displacement volume (Ahlstrom and Thrailkill 1963), then by

¹Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

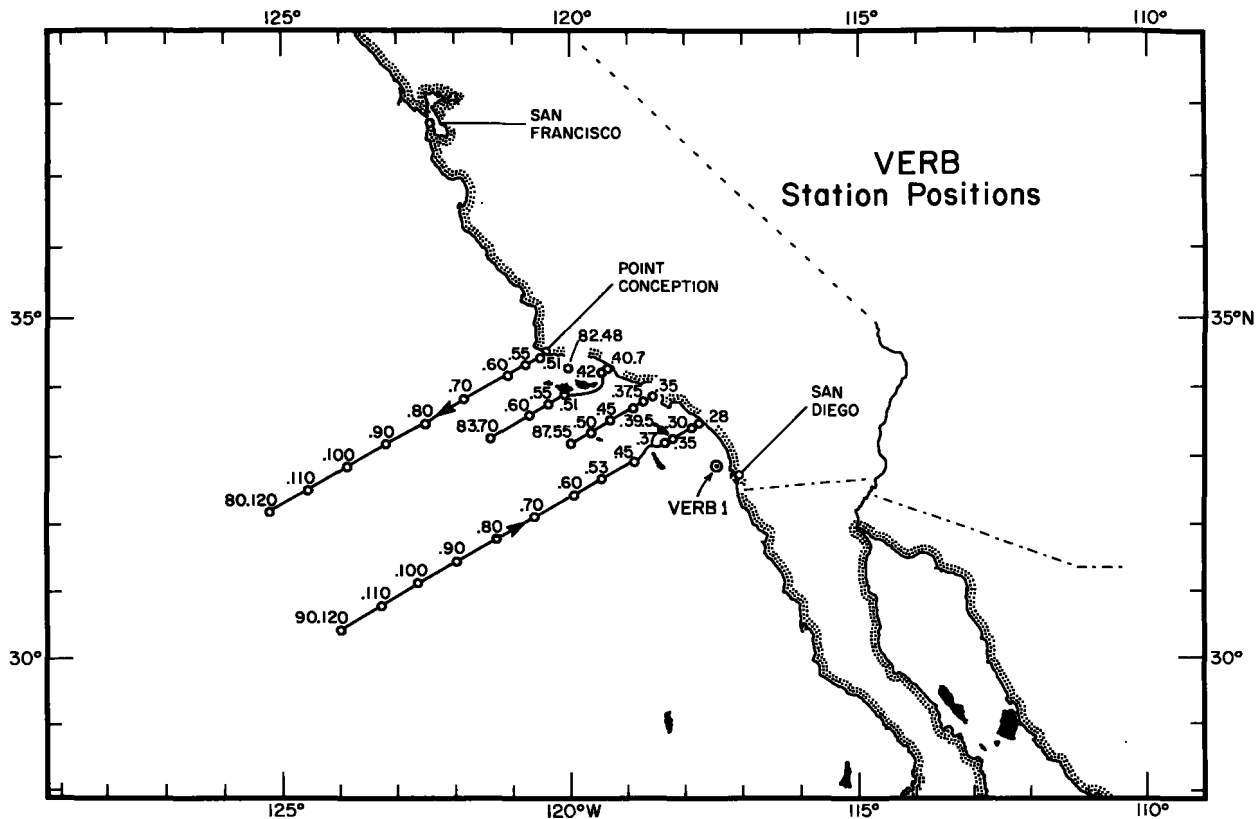


FIGURE 2.—Stations occupied in the southern sector of the California Current. Position of cruise VERB1 is noted, as well as the VERB zooplankton stations sampled on 4 CalCOFI cruises. Note that all indicated stations could not be sampled on every cruise.

measuring ash-free dry mass on a ¼ split of the sample obtained with a Folsom splitter. A split was filtered onto a pre-ashed Whatman GF/C filter, rinsed with a solution of 6% aqueous ammonium formate, and dried at 60°C. After weighing, the sample was ashed in a muffle furnace at 500°C for 4 hours then reweighed to determine ash-free dry mass by difference.

Standing stocks were expressed per unit volume, using the volume filtered by each net as determined from calibrated flow meters.

Water bottle samples for chlorophyll *a* (Chla) analyses were typically taken at 12–14 depths in the upper 200 m of the water column. Following filtration onto GF/C glass fiber filters, pigments were extracted in refrigerated 90% acetone in the dark and analyzed fluorometrically (Venrick and Hayward 1984). Chla between the surface and 150 m was integrated vertically using the trapezoidal rule. A complete report of chlorophyll data and detailed sampling information may be found in SIO References 87-7 and 87-19 (Scripps Institution of Oceanography 1987a, b).

RESULTS

Several characteristics of the VERB system were analyzed to determine its sampling bias, precision, and estimated filtration efficiency.

Right/Left Bias: A series of replicated vertical hauls was carried out with 202 μm nets mounted on both sides of the VERB frame. This was done over a 2½–3 h interval on 2 occasions. No bias was detected between the ash-free dry mass (AFDM) retained by the left and right nets on either 11 September ($N = 9$ hauls, $P > 0.10$, Wilcoxon Signed Rank test) or on 26 September ($N = 8$ hauls, $P > 0.10$).

Precision: Precision of replicated 202 μm vertical hauls, expressed as the coefficient of variation ($100 \times \text{SD}/\bar{x}$), was determined on 3 occasions, again over 2½–3 hours. Coefficients of variation of AFDM on 3 trials were 18.2% ($N = 18$ samples, 9 hauls), 14.1% ($N = 16$ samples, 8 hauls), and 17.0% ($N = 13$ samples, 13 hauls).

Filtration Efficiency: Filtration efficiency of the 202 μm VERB net was compared against that of the 505 μm VERB net using the respective volumes of water filtered. Filtration efficiency of the 202 μm net averaged $99.4 \pm 1.4\%$ ($\bar{x} \pm 95\%$ C.L., $N = 126$ comparisons) of that of

the 505 μm net, reflecting negligible clogging of the finer mesh net.

Wire Angles: The median wire angle (off the vertical) was 7°. Eighty-six percent of the angles were $\leq 12^\circ$ ($N = 144$). Apart from unusually strong wind conditions when the net could not be deployed, wire angles could generally be maintained at acceptable levels (< 10 – 12°) by maneuvering the vessel.

202 μm vs. 505 μm Nets: Retention characteristics of the 2 nets were compared from the $> 505 \mu\text{m}$ fraction displacement volume. The median ratio of the $> 505 \mu\text{m}$ displacement volume from the fine:coarse mesh nets was 1.17 (nonparametric 95% C.L.: 1.09–1.24, $N = 123$). The departure from a ratio of 1.00 probably reflects a difference between retention characteristics of the 505 μm plankton mesh in the field and in the laboratory. Larger organisms apparently show less escapement through 505 μm mesh under low pressure differential in the laboratory, compared with the high pressure differential across the mesh of a net under tow. To avoid introducing a systematic bias, further analyses are therefore restricted to the 2 fractions ($< 505 \mu\text{m}$, $> 505 \mu\text{m}$) collected by the 202 μm net.

Ash Content: The ash content of the 2 size fractions did not differ significantly ($P > 0.05$). Ash content as a percentage of total dry mass averaged $16.0\% \pm 0.9\%$ ($\bar{x} \pm 95\%$ C.L., $N = 160$) for the fraction $< 505 \mu\text{m}$ and $14.6\% \pm 0.7\%$ for the fraction $> 505 \mu\text{m}$.

Standing Stocks: The relation between displacement volume and AFDM appeared relatively linear when expressed on a log-log scale (Fig. 3A). However, closer inspection revealed that the slope of this relation differed for the 2 size fractions ($P < 0.001$, Analysis of Covariance). Hence a joint regression line was inappropriate. When replotted separately on linear axes, the difference in these relations was more apparent (Fig. 3B, C). A rectilinear function provided an adequate least squares fit for the fraction $< 505 \mu\text{m}$ (Table 1). However, the relation was non-linear for the fraction $> 505 \mu\text{m}$. Use of a curvilinear function (Table 1) decreased the residual sum of squares and removed the serial correlation of residuals that was apparent in a straight line fit ($P < 0.05$). For the fraction $> 505 \mu\text{m}$, a linear relation was a particularly poor

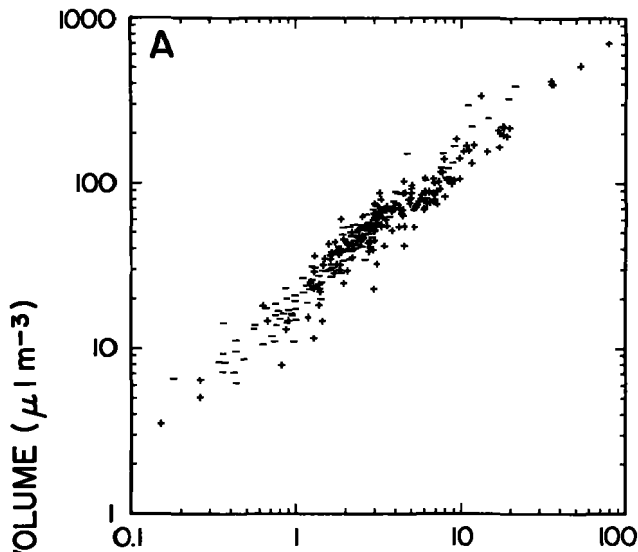
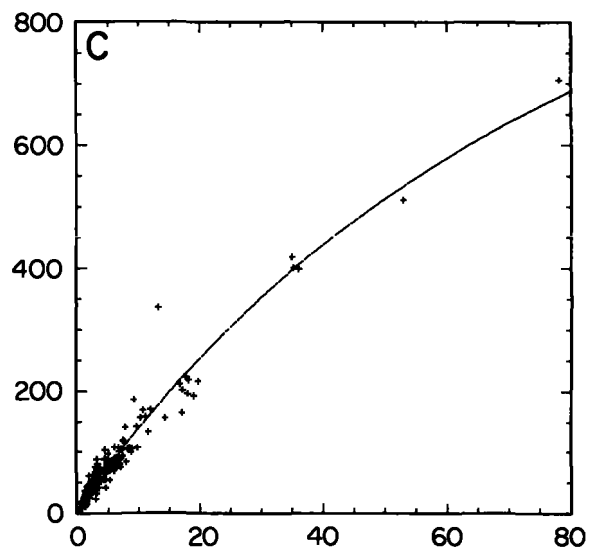
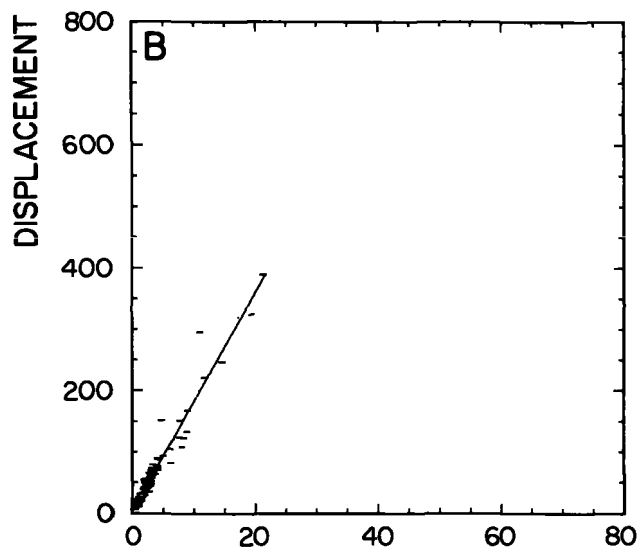


FIGURE 3.—Relationship between displacement volume and ash-free dry mass determined from the same samples, on 5 cruises ($N = 160$). A, Both size fractions ($<505 \mu\text{m} = \text{---}$, $>505 \mu\text{m} = \text{+}$) plotted on a \log_{10} - \log_{10} scale. B, $<505 \mu\text{m}$ on a linear scale. C, $>505 \mu\text{m}$ on a linear scale. Regression equations are reported in Table 1.



ASH-FREE DRY MASS (mg m^{-3})

descriptor at low AFDM values. The F -statistic was inappropriate for testing the goodness-of-fit of a nonlinear curve (Draper and Smith 1981), but the F -ratio reported in Table 1 provided a relative indicator of the adequacy of the regression equation. The fitted curve in Figure 3C was merely an empirical fit that was not meant to imply any theoretical relation. Because of this nonlinearity, perhaps caused by the compressibility of larger organisms at high biomass levels, AFDM was used for subsequent comparisons.

Since both displacement volume and AFDM have natural variability, a functional regression (Laws and Archie 1981) would be a more appropriate statistical model to apply to the data in

Figure 3. However, the need for a nonlinear relationship for the $>505 \mu\text{m}$ fraction complicates the use of a functional regression model. For consistency, the fit for both size fractions is therefore based on predictive regressions with the attendant possibility of introducing biased estimators (Sokal and Rohlf 1981). Users of functional regressions should note that the equation for estimating the confidence interval of the regression slope reported in Jensen (1986; equation 14) is in error.

A comparison of mesozooplankton and macrozooplankton standing stocks for four pooled CalCOFI cruises is illustrated in Figure 4. The median contribution of the mesozooplankton to

TABLE 1—Regression relationships between displacement volume (DV; $\mu\text{L m}^{-3}$) and ash-free dry mass (AFDM; mg m^{-3}). *F*-ratio designates the ratio of regression mean square: residuals mean square. Regression *P*-value indicates the significance of a linear regression, and the residuals *P*-value indicates the significance of the first order serial correlation of regression residuals. *N* = 160 for both size fractions.

Size fraction	Equation	<i>F</i> -ratio	Regression <i>P</i> -value	r^2	Residuals <i>P</i> -value
<505 μm	$\text{DV} = 17.86(\text{AFDM}) + 3.86$	2,869.1	<0.001	0.938	>0.10
>505 μm	$\text{DV} = \frac{1594.7(\text{AFDM})}{105.5 + \text{AFDM}}$	2,725.6	—	—	>0.10

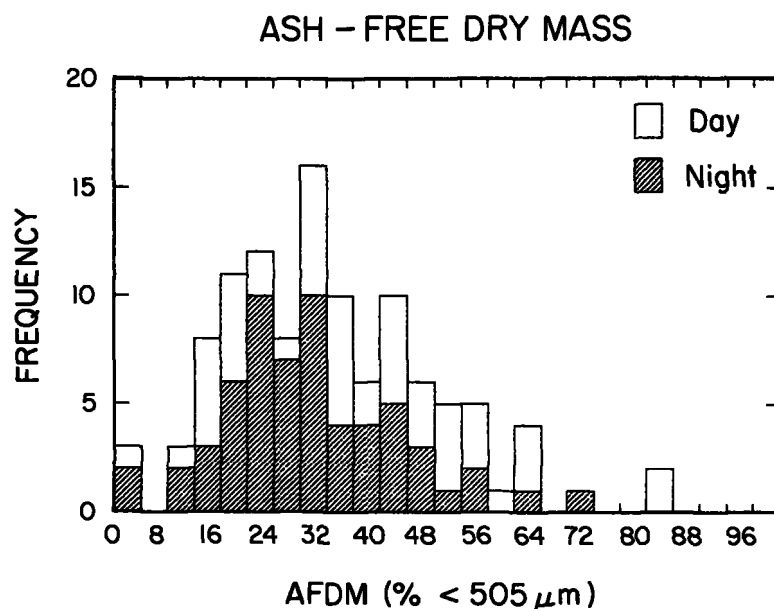


FIGURE 4.—Frequency distribution of the percentage of ash-free dry mass in the fraction <505 μm , from 4 CalCOFI cruises (*N* = 111).

the total standing stock was 30.2%. Partitioned by time of sampling, the day mesozooplankton averaged 35.0% and the night mesozooplankton 28.1% of total standing stock. Day and night medians differed significantly ($P < 0.05$, Mann-Whitney U test). The higher proportion of macrozooplankton (>505 μm) in nighttime samples probably reflects nocturnal vertical migration of larger zooplankton into the upper 200 m of the water column or, perhaps, diurnal net avoidance. At individual stations, the mesozooplankton contribution ranged up to 82% of the total.

Despite considerable variance in the relationship, zooplankton standing stocks were positively correlated with the Chla concentration (Fig. 5). This relation, apparently curvilinear, is illustrated as log AFDM plotted against the log maximum Chla concentration in vertical profile

at each station for the fraction <505 μm (Fig. 5A: $r = 0.73$, $P < 0.001$, Spearman's rank correlation, $N = 110$) and that >505 μm (Fig. 5B: $r = 0.70$, $P < 0.001$, $N = 110$). When plotted against the log chlorophyll integrated to 150 m the correlation coefficients were slightly smaller (<505 μm : $r = 0.71$; >505 μm : $r = 0.64$).

The relative contribution of mesozooplankton to total standing stocks varied independently of Chla concentration. Neither in the day samples ($r_s = -0.117$, $P > 0.10$, $N = 49$) nor in the night samples ($r_s = 0.060$, $P > 0.10$, $N = 61$) was the fraction of standing stock <505 μm associated with Chla (Fig. 6).

Sufficient samples to analyze cross-shore gradients in total standing stock and in the percentage of standing stock contributed by the mesozooplankton were obtained only along lines

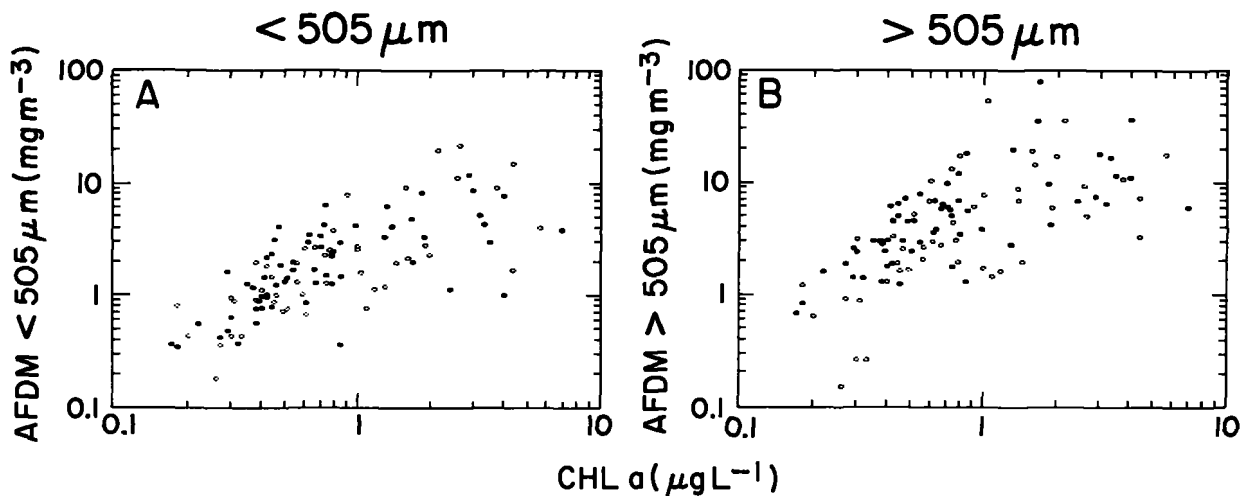


FIGURE 5.—Relationship between ash-free dry mass (AFDM) and maximum Chl α concentration, from 4 CalCOFI cruises. Open circles are day samples, closed circles are night samples. A, AFDM < 505 μm ; B, AFDM > 505 μm .

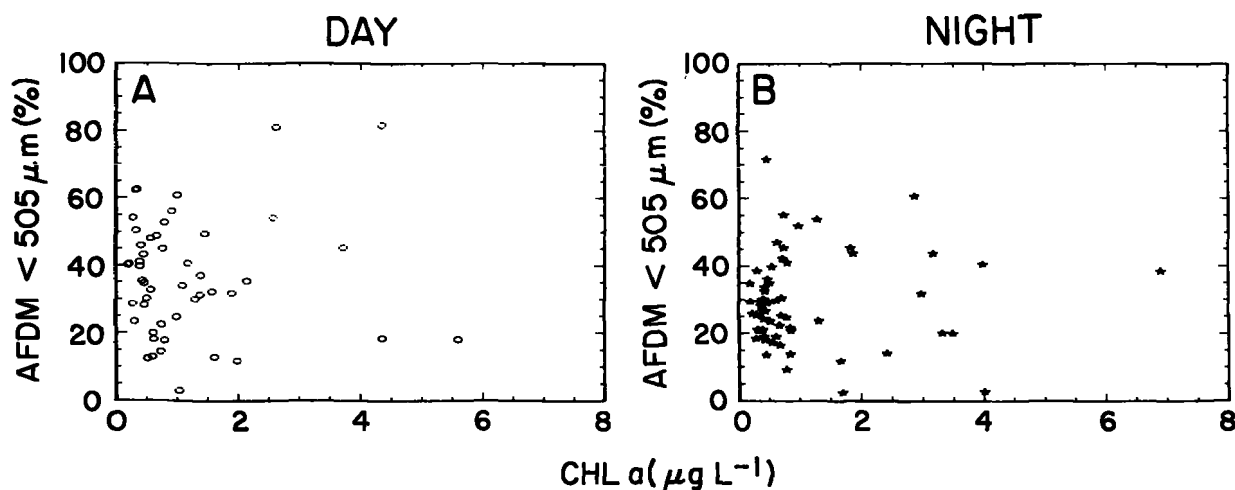


FIGURE 6.—Relationship between the percentage of ash-free dry mass in the fraction < 505 μm and Chl α concentration, from 4 CalCOFI cruises. A, Day samples; B, night samples.

80 and 90. (Even so, the two offshore stations along line 80 were sampled only on cruise 8609.) Samples from lines 83 and 87 are included in Figures 3–6 but were not analyzed for spatial trends. Along both line 80 and line 90 the 4-cruise average of total AFDM decreased in the cross-shore direction (Fig. 7A, B). On individual cruises a secondary maximum of standing stock often occurred offshore along line 80 (e.g., cruises 8609, 8705) and line 90 (e.g., cruises 8609, 8703, 8705).

The percentage of zooplankton standing stock < 505 μm also exhibited some cross-shore trends. On both lines 80 and 90, the median value was highest at the station closest to shore (Fig. 7C, D). On line 80 the median value first

decreased then remained relatively constant in the offshore direction. On line 90 the median value decreased to station 80 then appeared to increase again at the more offshore stations. (This apparent offshore increase at stations 110 and 120 may have been influenced by a higher incidence of daytime samples.) That is, mesozooplankton appeared to make a larger contribution to standing stock at the most inshore stations and possibly at the most offshore stations along line 90.

DISCUSSION

These results demonstrate that, on average, approximately one third of the > 202 μm zoo-

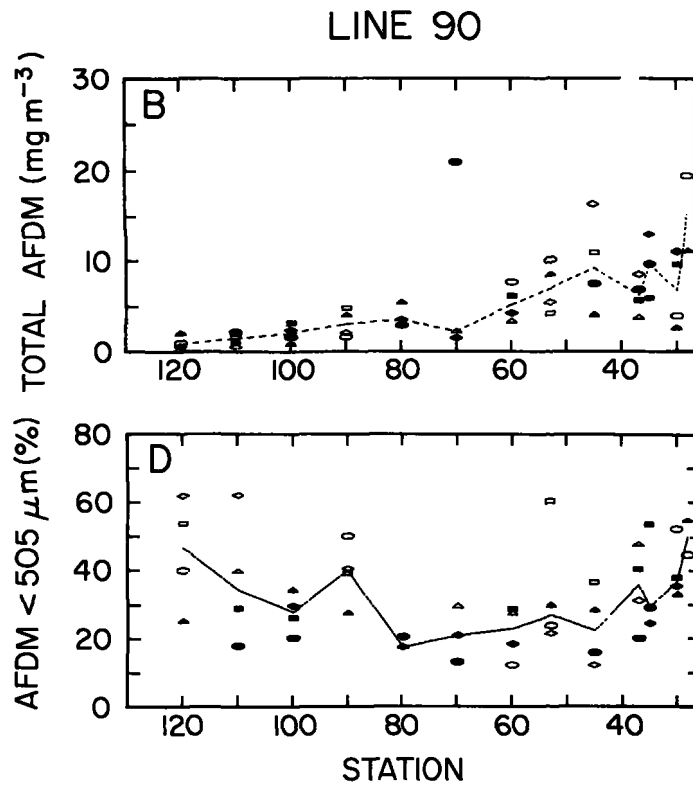
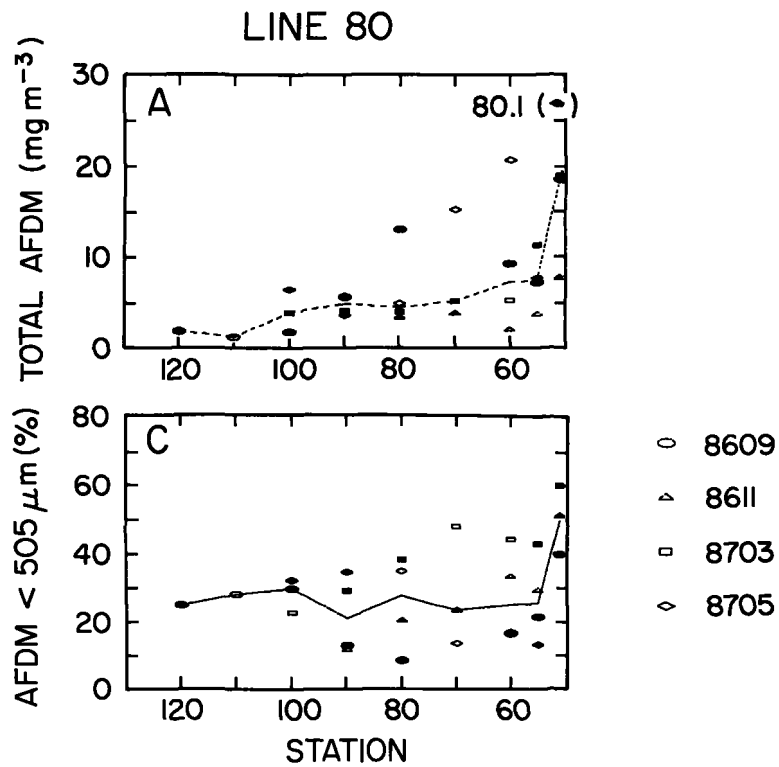


FIGURE 7.—Cross-shore distributions of total ash-free dry mass along (A) line 80 and (B) line 90, and percentage of ash-free dry mass in the fraction $< 505 \mu\text{m}$ along (C) line 80 and (D) line 90. Stations along lines 80 and 90 are aligned vertically. Dashed and solid lines illustrate the median values.

plankton standing stock is in the mesozooplankton fraction in this sector of the California Current system. Considerably higher contributions occur in some regions and on some occasions. It is difficult to estimate the contribution of this standing stock to heterotrophic processes such as grazing, oxidative metabolism, and fecal pellet fluxes without further information on the species composition of the two size fractions. However, because physiological processes depend on body mass (Banse and Mosher 1980), the mesozooplankton would contribute disproportionately to these water column processes.

Consider, for example, *Paracalanus parvus*, a relatively small-bodied copepod representative of the mesozooplankton retained by a 202 μm mesh net, and the larger copepod *Calanus pacificus* and euphausiid *Euphausia pacifica*, the latter two representative of the macrozooplankton captured by a 505 μm mesh net. The maximum daily specific ingestion rate of *P. parvus* females is 1.0–2.2 d^{-1} (varying on a carbon and a nitrogen specific basis, Checkley 1980), while that of *Calanus pacificus* is ca. 0.4 d^{-1} (Frost 1972) and that of adult *Euphausia pacifica* is ca. 0.08 d^{-1} (Ohman 1984). Based on these mass-specific rates, if 30.2% of the zooplankton standing stock were *P. parvus*-like organisms and the remainder were evenly split between *Calanus*-like and *Euphausia*-like organisms, the mesozooplankton could account for 79% of the grazing pressure. The presence of larvaceans and salps would alter this estimate because these gelatinous organisms are relatively large but have higher specific rates of metabolism than most crustacean zooplankton (Alldredge and Madin 1982). Furthermore, the estimate ignores the presence of omnivores and predators and assumes, unrealistically, food-satiated ingestion rates for all taxa. Nevertheless, the mesozooplankton is doubtless a significant contributor to heterotrophic processes.

The increased contribution of the mesozooplankton in the most inshore domain may reflect the presence of early developmental stages of zooplankton species that show relatively high rates of reproduction inshore (Brinton 1976; Checkley 1980; Smith et al. 1986). The possible trend toward a larger contribution of mesozooplankton offshore along line 90 requires corroboration. Much further to the west, in the oligotrophic central North Pacific, 20–40% of the zooplankton standing stock collected with a 183 μm net was <500 μm (Rodriguez and Mullin 1986).

The relation between displacement volume and ash-free dry mass for both size fractions combined is qualitatively similar to that reported in Wiebe et al. (1975, fig. 4a); however, their regression includes several size categories and their dry mass values apparently included ash, so that the two studies are not strictly comparable.

Whether the relative importance of mesozooplankton varies through time, such as during El Niño-Southern Oscillation (ENSO) conditions, is unknown. Smith (1985) documented an appreciable compositional change within the macrozooplankton during the strong ENSO of 1957–59. For example, comparing 1956 and 1958, the average thaliacean (primarily salp, larvacean, doliolid) biomass decreased 27-fold while the total copepod biomass decreased by only $\frac{1}{2}$ during this ENSO (Smith 1985), suggesting differential responses to ENSO events by different members of the pelagic food web.

How such compositional changes within the macrozooplankton might relate to changes in the relative importance of mesozooplankton organisms is not obvious. Since phytoplankton concentrations can decrease markedly during ENSO conditions (Fiedler 1984), the argument could be made that smaller zooplankton, which generally have lower food requirements to sustain growth and reproduction (Huntley and Boyd 1984), might increase in relative abundance. However, the lack of correlation between the fraction of zooplankton <505 μm and Chl *a* suggests that chlorophyll alone is too simple a measure of food availability. Microzooplankton may also be an important prey source. And it should be noted that a model based on energetic considerations makes a contradictory prediction, namely increased body size in oligotrophic regions (Gerritsen and Kou 1985). Additional information beyond food requirements must also be considered, including life history traits and species composition of the constituent zooplankton, as well as mesoscale circulation effects on species distributions (Haury et al. 1986).

The present evidence for the significance of the mesozooplankton in the California Current system is based upon a bulk measure of zooplankton standing stock. Future efforts directed toward understanding the mechanisms of response of planktonic organisms to environmental change should take account of species-specific responses of the mesozooplankton.

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Tuna Larvae Abundance: Comparative Estimates from Concurrent Japanese and Australian Sampling Programs

When estimating the absolute abundance of organisms, the accuracy and bias of sampling methods should be assessed (Andrew and Mapstone 1987). In ichthyoplankton sampling the absolute abundance of organisms will probably never be known; the characteristics of accuracy and bias in different sampling methods can only be inferred by concomitant sampling of the same population. The Fishery Agency of Japan Far Seas Fisheries Research Laboratory (FSFRL) has used a 2 m ring net to sample ichthyoplankton for many years. It has been the principal tool for sampling tuna larvae, particularly southern bluefin tuna, in the eastern Indian Ocean (Yabe et al. 1966; Ueyanagi 1969; Yonemori and Morita 1978; Yukinawa and Miyabe 1984; Yukinawa and Koido 1985). The net routinely samples large volumes of water (approximately 5,000 m³ in a 30-min oblique tow), yet catches of tuna larvae on these surveys are generally low. These low catches may reflect a naturally low abundance of tuna larvae, a contention supported by previous studies (Wade 1951; Strasburg 1960; Klawe 1963;

Richards 1969; Richards and Simmons 1971; Conand and Richards 1982). In this paper we compare catches of tuna larvae by traditional Japanese methods with those developed by CSIRO Division of Fisheries for quantitative surveys. A series of simultaneous tows were made by the CSIRO, FRV *Soela* and the FSFRL, FRV *Shoyo Maru* on the southern bluefin tuna spawning grounds in the east Indian Ocean in January 1987.

Methods

Two identical 2 m ring nets were deployed concurrently by the FSFRL (Fig. 1, Table 1) in surface and oblique tows. For the oblique tow, a predetermined length of warp (approximately 130 m) was rapidly paid out from the stern so that the net reached a depth of 30 m (approximately 4–10 minutes). The warp was then retrieved at a fixed rate until the net reached the surface (approximately 21–26 minutes). The tow profile actually achieved was determined after the tow from traces made by the depth distance recorder. The 20-min surface tow was deployed close to the hull on the starboard side, amidships, with approximately 7/8 of the net below the surface, fishing a depth range of 0–1.75 m.

Two identical 70 cm ring nets were deployed concurrently by CSIRO (Fig. 1, Table 1) in surface and oblique tows. The oblique tow fished from the surface to the thermocline (the thermocline during the experiment was at approximately 32 m) to cover the full known depth range of the tuna larvae (CSIRO, unpubl. data). An operator, guided by real-time depth information from a sensor on the net, produced a V-shaped tow profile, with a descent time of approximately 8 minutes and an ascent of 12 minutes. The surface tow was deployed for 10 minutes, concurrent with the oblique tow, from a boom on the port side amidships, clear of the wake of the vessel. It was towed approximately 0.5 m under the surface, oscillating between about 0 and 2 m due to the roll of the vessel in the 0.5 m swell.

The volume of water filtered for each net was calculated in the following ways. The volumes filtered by both surface and oblique tows with the 70 cm net were calculated from the distance travelled, measured by calibrated flowmeter readings inside the net, and the mouth area of the net. Volumes filtered by oblique tows with the 2 m net were calculated from the distance travelled (determined from the depth distance recorder behind the net) and the mouth area of