Title
A comparison of zooplankton sampling methods in the CalCOFI time series

Authors
Ohman, MD
Smith, PE

Publication Date
1995

Peer reviewed

A COMPARISON OF ZOOPLANKTON SAMPLING METHODS IN THE CALCOFI TIME SERIES

MARK D. OHMAN
Marine Life Research Group 0227
Scripps Institution of Oceanography
University of California, San Diego
La Jolla, California 92093-0227

PAUL E. SMITH
Southwest Fisheries Science Center
National Marine Fisheries Service, NOAA
P.O. Box 271
La Jolla, California 92038

ABSTRACT

We review changes in macrozooplankton sampling methods over the course of the CalCOFI time series (1949–present). After 1951, two major changes occurred: sampling depths were extended from 140 m to 210 m in 1969, and the 1.0-m-diameter bridled ring net was replaced with a 0.71-m-diameter bridleless bongo net in late 1977. We compare how these two changes affected the efficiency of collecting zooplankton biomass. We provide conversion factors between these sampling methods, supplemented by a description of the nonlinear relationship between wet and dry zooplankton biomass in the California Current system.

INTRODUCTION

Increased attention to long-term changes in world climate has renewed the scientific focus on measurement programs for detecting natural variations—and anthropogenic influences—over periods of decades or longer. The CalCOFI (California Cooperative Oceanic Fisheries Investigations) time series is among the very few oceanic measurement programs that permit such time scales of fluctuation to be discerned for biological properties. CalCOFI water-column measurements have illustrated the importance of large-scale interannual variations in the California Current system (Chelton et al. 1982; Roesler and Chelton 1987) and even longer-term, interdecadal variations in upper-ocean properties such as temperature, sea level, and zooplankton biomass (e.g., Roemmich 1992; Roemmich and McGowan 1995a, b). The sedimentary record has revealed natural, cyclical oscillations in pelagic populations of the Pacific sardine and northern anchovy (Baumgartner et al. 1992).

A cardinal concern for detecting and quantifying such long-term changes is the accuracy of sampling and analytical methods and the comparability of different methods that may be employed over time. A hallmark of the CalCOFI measurements is the attention given to calibration of biological, physical, and chemical methods, and the rigor with which different methodologies have been compared. The focus of this paper is on the principal methods used to sample the epipelagic macrozooplankton over the course of the CalCOFI time series. We analyze the efficiency of different sampling techniques for zooplankton biomass, in keeping with the tradition of careful attention to sampling methods.

What we now consider the CalCOFI time series began in 1949, although there were several ichthyoplankton surveys conducted from 1937 to 1941 (Hewitt 1988). Vertically stratified sampling on these early ichthyoplankton surveys showed that sardine eggs and larvae were distributed primarily in the upper 40 m of the water column, with none to be found below 70 m. Thus in the original standard tows that began in March 1949, 100 m of wire were paid out, for a nominal sampling depth of 70 m with a 45° wire angle (table 1). Beginning in 1951, the nets were deployed to depths of 140 m. Although it is not recorded why the depth was doubled at that time, the low diversity and abundance of zooplankton in the upper 70 m in daytime have been mentioned as factors by Edward Brinton and Joseph Reid (pers. comm.). The new depth was set at a nominal 140 m based on 200 m of wire out.

Subsequently there were two major changes in the methods used to sample macrozooplankton (table 1). (1) In 1969 the depth of hauls was increased to 210 m, and the net was changed from 0.55-mm-mesh silk to 0.505-mm-mesh nylon. The increase in sampling depth to 210 m (300 m of wire out) was made to encompass the vertical distribution of Pacific hake larvae. This increase was motivated by the onset of a large fishery on Pacific hake by the Soviet fishing fleet, amidst concerns about possible overfishing. The switch to an interlocking-monofilament nylon mesh was made because of the improved durability, lower cost, and improved filtration efficiency of the nylon mesh nets relative to silk. Although it was also determined that 0.333-mm mesh would retain an important fraction of anchovy eggs, the option to decrease the mesh size was not exercised because sorting fish larvae from the increased phytoplankton in finer mesh nets was much more costly. (2) In 1978 the standard sampling net was changed from a 1.0-m-diameter ring net to a 0.71-m-diameter bridleless bongo net because of the bongo net's improved collection of motile zooplankton (McGowan and Brown 1966). It is these two changes in methods that we wish to compare here. Although comparisons have been published of the catch efficiency of bongo and ring nets for individual eu-

[Manuscript received February 27, 1995.]

TABLE 1
Standard CalCOFI Nets Used for Sampling Macrozooplankton

Cruises employed	Net mouth diameter (m)	Mesh size	Net type	Nominal depth (m)	Reference
4903–5009	1.0	0.55 mm[a] silk	Ring	70	Ahlstrom 1954
5101–6806	1.0	0.55 mm[a] silk[b]	Ring	140	Ahlstrom 1954; Smith 1971
6901–7712	1.0	0.505 mm nylon	Ring	210	Kramer et al. 1972
7712–present	0.71	0.505 mm nylon	Bongo	210	Smith and Richardson 1977

[a]Mesh opening after shrinkage (small posterior region of 0.25 mm mesh)
[b]Nylon substituted on some cruises in 1956–59 (Smith 1971)

phausiid species (Brinton and Townsend 1981) and for anchovy larvae (Hewitt 1980), there has been no such analysis for zooplankton biomass.

The reader should recall that in addition to the regular macrozooplankton time series, many other types of zooplankton samples have been and continue to be taken on CalCOFI cruises. These include the fine-mesh CalVet or Pairovet samples (Smith et al. 1985) taken in the upper 70 m of the water column on at least the first two of the quarterly cruises each year (the series with 0.150-mm mesh began in 1982). Neuston samples are taken by Manta net (Brown 1979, 0.505-mm mesh) on each cruise; this series began in 1977. Vertically stratified samples have been taken in conjunction with a variety of special studies. The above samples are available at the Planktonic Invertebrates Collection of the Scripps Institution of Oceanography, or the Southwest Fisheries Science Center of the U.S. National Marine Fisheries Service. However, this paper specifically addresses the methods employed in the long-term CalCOFI macrozooplankton sampling program.

METHODS

In all cases samples were taken by oblique hauls, with the hydrowire maintained at approximately 45° angles off the vertical on both descent and ascent. Further sampling details are furnished in Kramer et al. 1972 and the other references listed in table 1. Wet biomass of zooplankton was measured as displacement volume by standardized methods, following removal of animals >5 ml individual displacement volume (Kramer et al. 1972). This measure has the advantage that it is nondestructive and permits the entire sample to be used for other quantitative studies. Conversion from displacement volume to dry biomass is discussed below. Given the pairwise sampling designs, we used the Wilcoxon matched-pairs signed ranks test to test the null hypothesis of no difference between sampling methods.

Ring Net, 140 m vs. 210 m

The first comparison analyzed here is that of the ring net fished to 140 m (1.0-m-diameter, 0.55-mm silk mesh with small posterior region of 0.25-mm silk mesh), as deployed between 1951 and 1968, with a similar ring net of slightly different mesh size and composition (1.0-m-diameter, 0.505-mm nylon mesh throughout) fished to 210 m, as deployed from 1969 through 1977. The data reported here have been presented in tabular form with sampling details (Smith 1974). Briefly, samples were taken in randomized order between 2100 on 28 June and 0300 on 1 July 1968 at CalCOFI station 93.30 (32° 50.5'N, 117° 31.0'W), within 30–60 min. of each other. In one instance, an unusually high value of biomass was collected (838 ml 1000 m^{-3}; nylon mesh net sample at 1020), which was excluded from further analysis.

Ring Net vs. Bongo Net

This second analysis compares the characteristics of the 1.0-m (bridled) ring net (as deployed from 1969 through 1977) with a bridleless bongo net (as deployed from 1978 to the present; cf. McGowan and Brown 1966, but note that the bongo net is fished continuously open in CalCOFI sampling). The bongo nets used in this particular analysis had a mouth diameter of 0.60 m, though the standard CalCOFI bongo frame has a mouth diameter of 0.71 m. Both types of nets were of 0.505-mm-mesh nylon, and both were fished to 210 m, bottom depth permitting. Brinton and Townsend (1981) compared the catch efficiency of these two net designs for 12 species of euphausiids, each analyzed by length class. Their paper illustrates the two nets (note that the mesh size they reported should be corrected to 0.505 mm) and the sampling locations for the samples analyzed here. The data comparing total zooplankton biomass have not been previously published.

In this comparison, groups of samples were taken at three locations representing northerly, middle, and southerly sectors of the California Current system, on CalCOFI cruises 7501 and 7507. Net deployments were made while following a drogue. The stations occupied on cruise 7501 were 73.60 (12–13 Feb. 1975), 103.60 (21–22 Jan. 1975), and 137.50 (4–5 Feb. 1975); day samples were taken between 1000 and 1530 PST, night samples between 2000 and 0300. The stations on cruise 7507 were 70.60 (15–16 July 1975), 103.65 (28–29 June 1975), and 133.46 (12–13 July 1975); day samples were taken

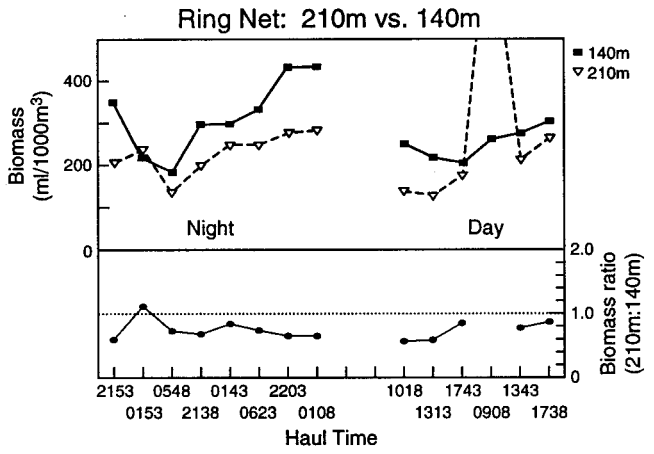

Figure 1. Comparison of zooplankton biomass collected by a 1.0-m-diameter ring net fished to either 140 m or 210 m. *Upper panel* indicates biomass; *lower panel* indicates the 210:140 biomass ratio; *dotted line* indicates a 1:1 ratio. One anomalously high daytime value was excluded from statistical analysis (data from Smith 1974).

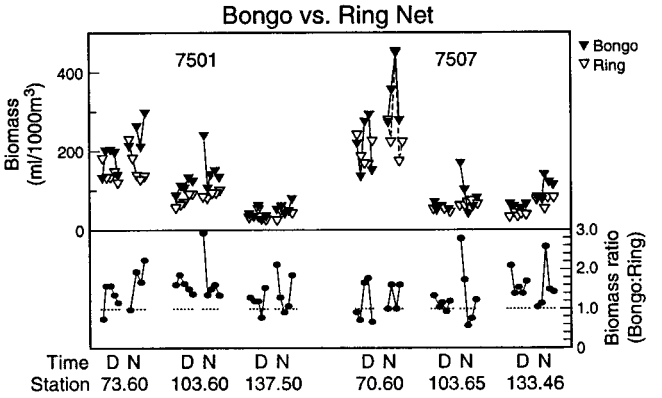

Figure 2. Comparison of zooplankton biomass collected by a 0.60-m-diameter bongo net with a 1.0-m ring net, both fished to 210 m. Comparisons were made on two cruises (CalCOFI 7501 and 7507), at three stations each, both day (*D*) and night (*N*). *Upper panel* illustrates biomass; *lower panel* indicates the 0.60-m bongo:ring net biomass ratio; *dotted line* indicates a 1:1 ratio.

between 1000 and 1615, night samples between 2200 and 0300. Samples were taken in groups of ten at each station, alternating regularly between bongo and ring net. Sample pairs were taken within 30–40 minutes.

The third comparison is also of a 1.0-m (bridled) ring net and a bridleless bongo net, both of 0.505-mm-mesh nylon. But in this comparison, the bongo net had a diameter of 0.71 m, the standard CalCOFI net used since cruise 7712. The data originate from five cruises (CalCOFI 7712, 7801, 7804, 7805, and 7807) with 11–22 pairs of samples from each cruise, usually taken within 30 minutes of each other. The lines sampled ranged from CalCOFI 60 to 130, the stations from 30 to 90. Euphausiid species comparisons, but not total zooplankton biomass, have been reported from some of these samples (Brinton and Townsend 1981). The biomass data are available from the senior author.

RESULTS

Ring Net, 140 m vs. 210 m

Comparisons of the zooplankton biomass per unit volume collected by a ring net fished to 140 m with a net fished to 210 m showed that in 12 out of 13 valid comparisons the biomass density was greater in the shallower samples (Wilcoxon signed rank test, 2-sided, $P < 0.01$; figure 1). This result was previously reported in tabular form by Smith (1974). The ratio of biomass determined by the two methods (210 m:140 m) is 0.731 $\pm$ 0.091 ($\bar{x} \pm 95\%$) and did not differ between day and night ($P > 0.50$, t-test).

Ring Net vs. Bongo Net

The second comparison entailed contrasts between the 0.60-m bongo net and 1.0-m ring net, both sampling between 210 m and the surface (figure 2). There was a significant difference between biomass determined by the two nets (Wilcoxon, $P < 0.0001$), with the bongo collection greater than the 1-m collection in 46/58 comparisons. For further statistical tests the biomass ratio (bongo:ring net) for each pair of samples was $\log_e$-transformed, which resulted in homogeneity of variances (Bartlett's test = 19.29, $P = 0.09$) among the 12 groups of samples (i.e., day and night comparisons at each of six stations). There was no significant difference in bongo:ring net biomass ratio among these 12 groups (1-way ANOVA, $F_{11,46} = 0.998$, $P > 0.40$; see figure 2). Although the sampling design may appear appropriate for a nested analysis of variance, a nested ANOVA cannot be applied because subordinate-level groupings were fixed rather than free to vary randomly (Sokal and Rohlf 1981). There was no significant difference ($P > 0.10$, t-test) between the day (1.320 $\pm$ 0.132, $\bar{x} \pm 95\%$) and night (1.513 $\pm$ 0.228) ratio, resulting in an overall 0.60-m bongo:1.0-m ring net biomass ratio of 1.413 $\pm$ 0.128 ($N = 58$).

The third comparison was similar to the second, but employed the 0.71-m bongo (figure 3). The anomalously high biomass ratios of 4.9 and 9.7 were excluded from statistical analysis because they doubtless reflected patches of zooplankton and destabilized the variances. There was a significant difference between the biomass collected by the two nets (Wilcoxon, $P < 0.0001$), with bongo collections greater than ring net collections in 101 of 138 comparisons. Following $\log_e$ transformation (Bartlett's test = 9.06, $P > 0.40$), 1-way ANOVA detected significant heterogeneity in the ratio of bongo:ring net biomass among trials ($F_{9,70} = 4.882$, $P < 0.0001$), where each of the ten trials is a series of day or night comparisons on a cruise. The trials that differed most consistently from others (by Tukey HSD multiple comparisons, $P < 0.05$) were the day values on cruise 7801 and both

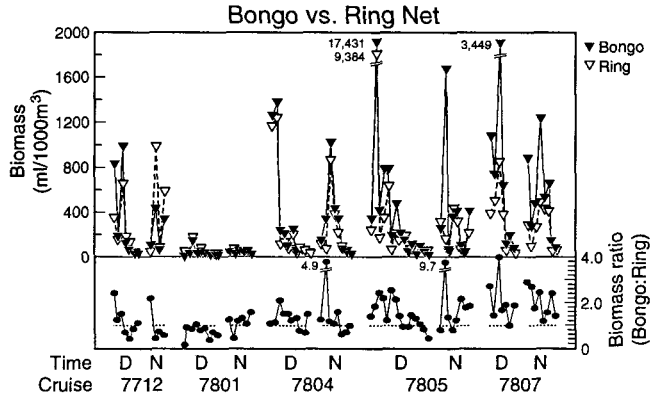

Figure 3. Comparison of zooplankton biomass collected by a 0.71-m-diameter bongo net with a 1.0-m ring net, both fished to 210 m. Comparisons were made on five cruises (CalCOFI 7712, 7801, 7804, 7805, 7807), both day (*D*) and night (*N*). Within a cruise and time of day, stations are ordered from inshore to offshore and then from north to south. *Upper panel* illustrates biomass; *lower panel* indicates the 0.71-m bongo:ring net biomass ratio; *dotted line* indicates a 1:1 ratio. Two anomalously high biomass ratios were excluded from statistical analysis.

day and night values on cruise 7807. In the absence of further information on the specific reasons for these departures on these particular cruises, we pooled ratios to obtain an estimator of the average biomass ratio. For the five cruises 7712 to 7807, the average daytime biomass ratio (1.341 ± 0.214; $\bar{x}$ ± 95%, 0.71-m bongo:1.0-m ring) did not differ ($P > 0.50$, t-test, df = 78) from the night ratio (1.404 ± 0.238). The overall average ratio was 1.366 ± 0.156 (table 2).

The diameter of the bongo net (0.60 m or 0.71 m) had no detectable effect on the biomass ratio with the 1-m ring net ($t_s = 0.44$, $P > 0.50$).

DISCUSSION

These results illustrate that changes in zooplankton sampling methodologies over the course of the CalCOFI time series have resulted in quantifiable differences in zooplankton biomass. This result is not surprising, since the original motivation for introducing these changes was improving the effectiveness of sampling the epipelagic ichthyoplankton and holozooplankton.

Although the analysis of how changes in depth affect sampling would surely benefit from an increased number of samples for comparison, we see no reason to expect that the results obtained in the vicinity of station 93.30 should differ markedly from results in other regions of the California Current system (CCS). By analogy, the bongo:ring net comparison in this geographic region alone was quite comparable to that of the rest of the CCS. If we consider only those bongo:ring net comparisons made in this same region (lines 90 and 93, $N = 13$ comparisons), we obtain a biomass ratio of 1.393 ± 0.462 ($\bar{x}$ ± 95%), which has a broader confidence interval, but similar mean value (1.366 ± 0.156, $N = 80$) to the biomass ratio obtained for the sequence of five cruises in several different geographical locations. Furthermore, the observation of decreasing biomass density (i.e., zooplankton displacement volume per unit volume of water filtered) upon extending sampling to a deeper segment of the water column (from 140 to 210 m) is sensible in terms of the general vertical distribution of zooplankton. The biomass of oceanic zooplankton has long been recognized to show a general decline with depth (e.g., Vinogradov 1970).

TABLE 2
Summary Conversion Factors

To convert:		Multiply (A) by:		
			($\bar{x}$ ± 95%)	
From (A)	To (B)	Day	Night	Day-night average
1 m ring 0.550 mm silk 140 m	1 m ring 0.505 mm nylon 210 m	0.719 ± 0.185	0.738 ± 0.135	0.731 ± 0.091
1 m ring 0.505 mm nylon 210 m	0.71 m bongo 0.505 mm nylon 210 m	1.341 ± 0.214	1.404 ± 0.238	1.366 ± 0.156
1 m ring 0.550 mm silk 140 m	0.71 m bongo 0.505 mm nylon 210 m	0.964	1.036	0.998
Displacement volume (μl m^{-3})	Ash-free dry mass (mg m^{-3})	—	—	AFDM = 0.0227 $DV^{1.2333}$
Total dry mass (mg m^{-3})	Ash-free dry mass (mg m^{-3})	—	—	0.854
>505 μm Ash-free dry mass (mg m^{-3})	Total >202 μm Ash-free dry mass (mg m^{-3})	1.538	1.391	1.433

The relations in the last three rows originate from Ohman and Wilkinson 1989.

The improved collection of biomass by the bridleless bongo nets relative to the 1.0-m bridled ring net is probably attributable to reduced net avoidance, although Brinton and Townsend (1981) pointed out that the difference in diameters of the nets to some extent confounds attribution to the presence or absence of a bridle alone. These authors also observed that the relation of catch efficiency of the two net designs varies by species and by developmental stage. For most of the euphausiid species analyzed by Brinton and Townsend, the bongo was a more effective collector of juveniles and adults, while the 1.0-m ring net was a better collector of young larval stages. Because euphausiid biomass is generally dominated by later stages, the bongo was generally a much preferred collector. Hewitt (1980) found that large anchovy larvae avoided the bongo net less than the 1.0-m net.

There is little doubt that the best approach to determining the effects of changes in sampling methods would be a taxon-by-taxon analysis in the manner conducted by Brinton and Townsend and by Hewitt. But this may not always be practicable because of the large number of taxa concerned. Where the integrated epipelagic zooplankton biomass is of interest, approximate corrections can be obtained from the information provided in table 2. The corrections applicable to the two major transitions in sampling methods (i.e., beginning in 1969, line 1; and beginning in 1978, line 2) can be multiplied to give an approximate correction to express the pre-1969 biomass values in terms of the post-1977 methods (table 2, line 3). Remarkably, the product of these two numbers is 0.998 (day-night average), suggesting that the pre-1969 and post-1977 mean biomass values are quite comparable, despite the differences in depths and net styles. However, in the intervening years (1969–1977) a correction is clearly necessary to render these biomass values comparable to those from preceding and following years. To obtain bongo-equivalent values between 1969 and 1977, the 1.0-m ring net values should be multiplied by 1.366 ± 0.156. Roemmich and McGowan (1995b, correcting for an error in Roemmich and McGowan 1995a) did not take into account this change, and therefore their time series needs to be corrected over this nine-year interval. Application of our correction factor to the results of Chelton et al. (1982) and Roesler and Chelton (1987) would slightly increase the long-term mean biomass and thus slightly alter the temporal pattern of anomalies from this mean.

Dry measures of biomass are related in a nonlinear way to wet biomass (Wiebe 1988; Ohman and Wilkinson 1989), and in some circumstances it may be useful to be able to convert between them. Accordingly, in figure 4A the relation between ash-free dry mass and displacement volume is described by a power function, based on 160 comparisons made on four CalCOFI cruises (Ohman and Wilkinson 1989). This regression applies to the macrozooplankton (>505 μm); see Ohman and Wilkinson for the relation applicable to zooplankton collected by 202-μm mesh nets.

For comparison with other data, the fit of a model

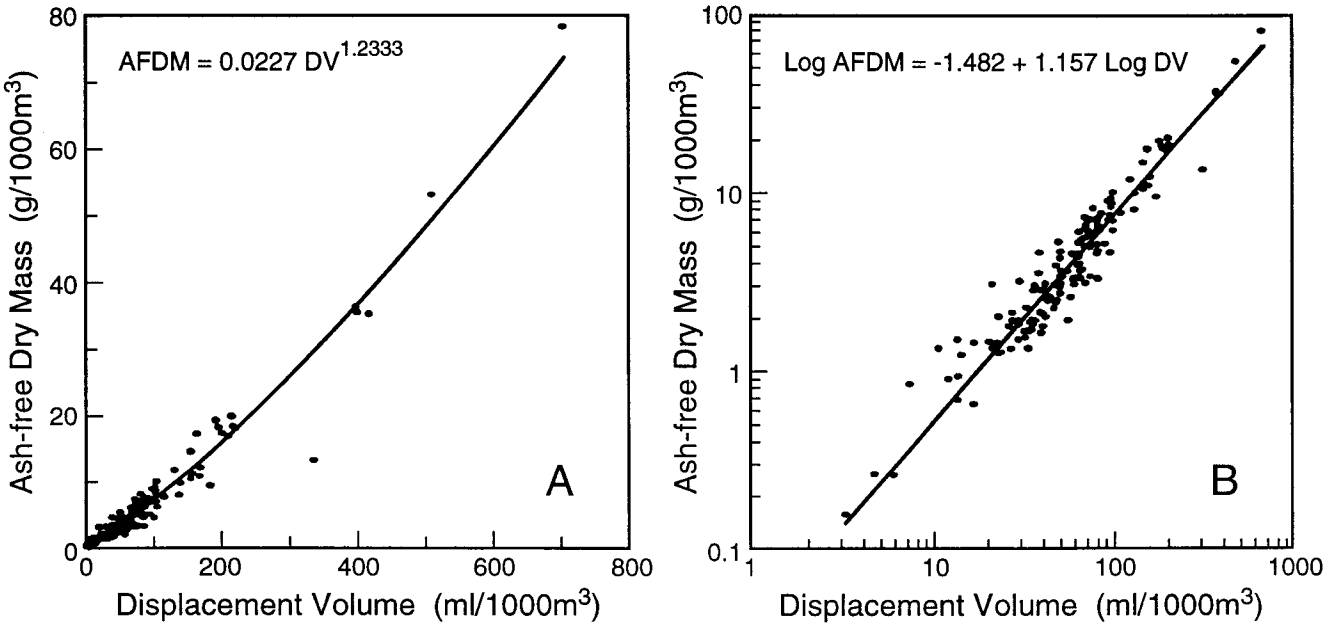

Figure 4. Relation between zooplankton biomass determined as ash-free dry mass and as wet displacement volume, based on samples collected on four CalCOFI cruises (8609, 8611, 8703, 8705; data from Ohman and Wilkinson 1989, >505 μm size fraction, N = 160). *A*, Nonlinear regression fitted by the Simplex method (r^2 = 0.971); *B*, geometric mean functional regression fitted to $\log_{10}$-transformed data (r^2 = 0.917).

II or functional regression to the $\log_{10}$-transformed values is shown in figure 4B, though the nonlinear fit in figure 4A is preferred because of the higher r^2 and lower serial correlation of residuals. The slope of the relation in figure 4B (1.157) is nearly identical to the slope of 1.156 obtained by Wiebe (1988, equation 4) when his equation is rearranged in the same manner as shown here and expressed in common units. The present intercept (−1.482) is lower than that for Wiebe's regression (−1.339), as expected, because we used ash-free dry mass whereas he used total dry mass. Converting the present data to total dry mass (=1.171 × AFDM; table 2, line 5) still produces a slightly lower intercept. The 15% difference between the two regressions may be attributed to the determination of dry mass from frozen samples in Wiebe's (1988) study and from Formalin-preserved samples in this study, or perhaps to a difference in faunistic composition of the two groups of samples. Another useful quantity is the relation between zooplankton biomass collected by the 505-μm net and the total zooplankton biomass greater than 202 μm (table 2, line 6). Although such expressions may be useful as general conversions, the temporal and spatial variability associated with them suggests that caution be exercised in their application.

In conclusion, we have verified that the two major methodological changes associated with the CalCOFI macrozooplankton time series have resulted in significant, but quantifiable, changes in measures of zooplankton biomass. Attention to these changes should facilitate rigorous analysis of long-term variations in zooplankton biomass—and of their underlying causes—in the California Current ecosystem.

ACKNOWLEDGMENTS

We thank Annie Townsend and Kevin Tinsley for helping to prepare data for analysis, and we express appreciation to the team of CalCOFI technicians for their sustained efforts. This work was supported in part by the Marine Life Research Group of SIO and by NSF OCE90-19639.

LITERATURE CITED

Ahlstrom, E. H. 1954. Distribution and abundance of egg and larval populations of the Pacific sardine. Fish. Bull. 56(93):81–140.

Baumgartner, T. R., A. Soutar, and V. Ferreira-Bartrina. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara Basin, California. Calif. Coop. Oceanic Fish. Invest. Rep. 33:24–40.

Brinton, E., and A. W. Townsend. 1981. A comparison of euphausiid abundances from bongo and 1-M CalCOFI nets. Calif. Coop. Oceanic Fish. Invest. Rep. 22:111–125.

Brown, D. M. 1979. The Manta net: quantitative neuston sampler. Inst. Mar. Res., La Jolla, Calif., Tech. Rep. 64:1–15.

Chelton, D. B., P. A. Bernal, and J. A. McGowan. 1982. Large-scale interannual physical and biological interaction in the California Current. J. Mar. Res. 40:1095–1125.

Hewitt, R. P. 1980. Distributional atlas of fish larvae in the California Current region: northern anchovy, *Engraulis mordax* Girard, 1966 through 1979. Calif. Coop. Oceanic Fish. Invest. Atlas 28:1–101.

———. 1988. Historical review of the oceanographic approach to fishery research. Calif. Coop. Oceanic Fish. Invest. Rep. 29:27–41.

Kramer, D., M. J. Kalin, E. G. Stevens, J. R. Thrailkill, and J. R. Zweifel. 1972. Collecting and processing data on fish eggs and larvae in the California Current region. NOAA Tech. Rep. NMFS CIRC-370:1–38.

McGowan, J. A., and D. M. Brown. 1966. A new opening-closed paired zooplankton net. Univ. Calif. Scripps Inst. Oceanogr. Ref. 66–23, pp. 1–56.

Ohman, M. D., and J. R. Wilkinson. 1989. Comparative standing stocks of mesozooplankton and macrozooplankton in the southern sector of the California Current system. Fish. Bull. 87:967–976.

Roemmich, D. 1992. Ocean warming and sea level rise along the southwest U.S. coast. Science 257:373–375.

Roemmich, D., and J. McGowan. 1995a. Climatic warming and the decline of zooplankton in the California Current. Science 267:1324–1326.

———. 1995b. Sampling zooplankton: correction. Science 268:352–353.

Roesler, C. S., and D. B. Chelton. 1987. Zooplankton variability in the California Current, 1951–1982. Calif. Coop. Oceanic Fish. Invest. Rep. 28:59–96.

Smith, P. E. 1971. Distributional atlas of zooplankton volume in the California Current region, 1951 through 1966. Calif. Coop. Oceanic Fish. Invest. Atlas 13:1–144.

———. 1974. Distribution of zooplankton volumes in the California Current region, 1969. Calif. Coop. Oceanic Fish. Invest. Atlas 20:118–125.

Smith, P. E., and S. L. Richardson. 1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fisheries Tech. Paper 175:1–100.

Smith, P. E., W. Flerx, and R. P. Hewitt. 1985. The CalCOFI vertical egg tow (CalVET) net. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, R. Lasker, ed. NOAA Tech. Rep. NMFS 36:27–32.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. The principles and practice of statistics in biological research. San Francisco: W. H. Freeman, pp. 1–859.

Vinogradov, M. E. 1970. Vertical distribution of the oceanic zooplankton. Israel Program for Scientific Translations, Jerusalem, pp. 1–339.

Wiebe, P. H. 1988. Functional regression equations for zooplankton displacement volume, wet weight, dry weight, and carbon: a correction. Fish. Bull. 86:833–835.