

Use of spherical and spheroidal models to calculate zooplankton biovolume from particle equivalent spherical diameter as measured by an optical plankton counter

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Abstract

Three methods of calculating the biovolume of particles from their shadows as recorded by an optical plankton counter (OPC), based on optical geometry, are presented. In the first method (V_{sphere}), particles are assumed to be opaque spheres. In the other two methods, particles are represented as opaque spheroids, oriented with their major axes either parallel to the flow thus presenting maximum shadow area (V_{max}), or randomly orientated relative to the flow (V_{ran}). The models were tested by comparing with net biovolume, measured from samples of a zooplankton assemblage dominated by *Calanus finmarchicus* collected during a cruise to the northeast Atlantic during 2001. The randomly orientated spheroidal model (V_{ran}) provided the best fit with the net data: on average the ratio of OPC biovolume to net biovolume was 1.02, compared to ratios of 0.84 when calculating OPC biovolume as V_{max} and 1.50 when calculating as V_{sphere} . The V_{ran} and V_{max} methods gave reasonable estimates of net biovolume from OPC measurements without recourse to the use of empirical tuning parameters that are otherwise required. This success was enhanced by the fact that the community chosen for validation purposes was dominated by a single species, *C. finmarchicus*, which could be approximated by spheroids of known dimension. The calibration methods are less likely to be effective when applied to zooplankton communities incorporating a diverse range of organisms.

The Focal Technologies optical plankton counter (OPC) is an instrument that counts and sizes particles by measuring the amount of light blocked by them as they pass through a light beam projected across the instrument's sampling tunnel (Herman 1992). The OPC has been extensively used to describe mesozooplankton distributions at a range of spatial scales and has been mounted onto a variety of sampling platforms (Zhou and Tande 2002). Particle abundance is easily determined by dividing the number of recorded shadows by the volume of water sampled.

Ecologists interested in system dynamics ideally need to quantify zooplankton in terms of biomass to study, for example, trophic interactions (Zhou and Huntley 1997) and energy

flow (Platt and Denman 1978). The first step to estimating biomass from OPC data is to calculate the biovolume of particles, from which conversion factors can be applied to derive biomass (e.g., Wiebe 1988). An empirical calibration derived using spherical beads is provided by the manufacturer, such that for each count, an equivalent spherical diameter (ESD), the diameter of a sphere with projected cross sectional area (CSA) equal to the measured shadow area, is recorded. The relationship between ESD and CSA is simply

$$\text{CSA} = \pi(\text{ESD}/2)^2 \quad (1)$$

The simplest way to estimate biovolume from ESD, or CSA, as measured by the OPC, is to assume a spherical relationship, i.e., volume (V) is $4/3\pi(\text{ESD}/2)^3$ (Heath 1995). Mesozooplankton are, however, typically not spherical in shape, so this approach tends to provide overestimates because the ratio volume:CSA is greater for spheres than other shapes (Sprules et al. 1998; Beaulieu et al. 1999).

Mesozooplankton, particularly certain groups such as copepods, may be conceptually described as spheroids (Herman 1992). To calculate the biovolume of a spheroid from a shadow area recorded by the OPC, it is necessary to know its

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length-to-width ratio (i.e., the ratio of major and minor axes) and its orientation relative to the beam. The calculation of biovolume in this way is not easy, involving complex angular geometry accounting for both the shape and orientation of particles. These difficulties have led some workers to empirically calibrate OPC biovolume to match that measured in net samples. For example, Stockwell and Sprules (1995) and Sprules et al. (1998) used the length-to-width ratio (i.e., ratio of major to minor axes) as an empirical spheroidal calibration factor, which was adjusted until OPC biomass was equal to that measured in net samples collected from North American lakes (the resulting ratios of major to minor axes were 1.33 and 1.6 for the two studies).

Empirical relationships based on tuned parameters are of limited value, being applicable only to the data sets from which they are calibrated. A potentially much more powerful approach to calculating biovolume is to use optical geometry to directly convert shadow areas recorded by the OPC to biovolume, without recourse to additional parameters that must be defined. In this article, we present three such methods of calculating zooplankton biovolume (V) from the cross-sectional area (CSA) recorded by the OPC (i.e., from projected particle shadow areas), based solely on optical geometry. In the first (V_{sphere}), zooplankton are assumed to be spherical in shape. The other two methods assume that zooplankton can be represented by opaque spheroids of uniform shape but variable size. In the first of these (V_{max}), animals are assumed to be oriented perpendicular to the light beam of the OPC, projecting the maximum possible shadow area. In the second, spheroidal calibration (V_{ran}), zooplankton are assumed to be oriented randomly in the flow field. The utility of each method is then tested by comparing OPC biovolume with that measured directly from net data. A *Calanus*-dominated community was sampled to evaluate the calibration method because the OPC has been shown to be a

useful tool in studying this species (Heath et al. 1999; Baumgartner 2003). Data were collected on a cruise to the Iceland-Faroes Ridge in the northeast Atlantic, June 2001.

Materials and procedures

Calculation of biovolume from ESD—Three methods of calculating biovolume from CSA are now presented in turn.

Method 1: V_{sphere} —Animals are assumed to be spherical in shape. Calculation of biovolume is then straightforward because particle orientation need not be considered. Noting that the volume of a sphere is $4/3\pi r^3$, where r is radius, then V_{sphere} is

$$V_{\text{sphere}} = \frac{4}{3} \pi (\text{ESD}/2)^3 = \frac{4}{3} \pi \left(\frac{\text{CSA}}{\pi} \right)^{3/2} \quad (2)$$

Method 2: V_{max} —Zooplankton are now assumed to be opaque spheroids (ellipsoids of revolution) of uniform shape but variable size. The CSA projected by an opaque spheroid in a light beam (Fig. 1) depends on the dimensions of its major and minor axes, a and b respectively (expressed as radii, $V = 4/3\pi b^2 a$), and its orientation relative to the light beam, θ (which is the angle between a plane normal to the major axis and the direction of the beam):

$$\text{CSA} = \pi b(a^2 \cos^2 \theta + b^2 \sin^2 \theta)^{1/2} \quad (3)$$

If the ratio of major to minor axes of a spheroid is w ($= a/b$), then Eq. 3 can be recast as in terms of b :

$$\text{CSA} = \pi b^2 (w^2 \cos^2 \theta + \sin^2 \theta)^{1/2} \quad (4)$$

Particles are assumed to have the same known value of w . The V_{max} calibration assumes that zooplankton are oriented such that their major axes are lined up in parallel to the light field ($\theta = 0^\circ$, i.e., projecting maximum CSA). It is then straightforward to calculate b from the CSA measured by the OPC and w :

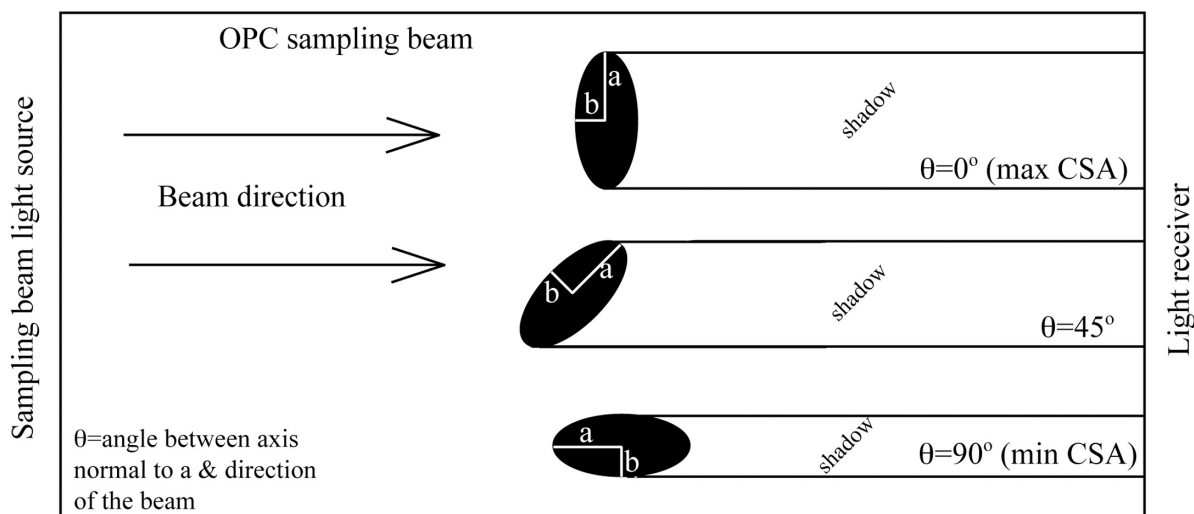


Fig. 1. A schematic two-dimensional representation of the effect of orientation on the CSA projected by an ellipse (cross-section of a spheroid) in a light beam.

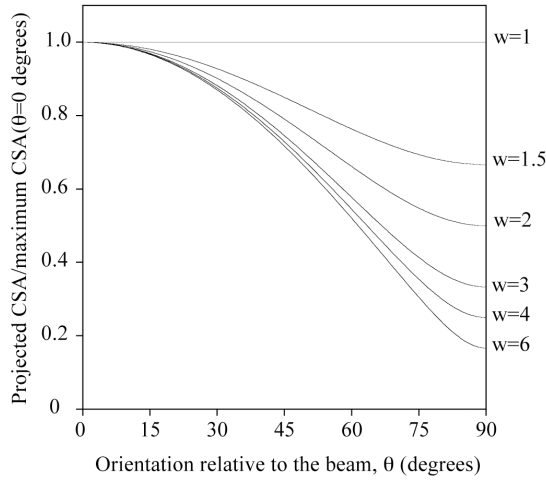


Fig. 2. The cross-sectional area projected by spheroids with different values of w ($w = a/b$) at different orientations, relative to a plane perpendicular to the light beam.

$$b_{\max} = \left(\frac{CSA}{\pi w} \right)^{1/2} \quad (5)$$

The biovolume of n particles recorded by the OPC is given by the sum:

$$V_{\max} = \frac{4}{3} (\pi w)^{-1/2} \sum_{i=1}^n CSA_i^{3/2} \quad (6)$$

Method 3: V_{ran} —This calibration considers that zooplankton are oriented randomly in the flow field. Once again all particles are represented as spheroids with fixed shape w . The effect of θ on the CSA projected by spheroids of different w , normalized to the CSA projected when the maximal shadow is cast ($\theta = 0^\circ$), is shown in Fig. 2. Projected CSA is close (>75%) to the maximum when $\theta < 45^\circ$ for the range of w shown, decreasing markedly for $\theta > 45^\circ$. When particles are randomly oriented, then all angles of rotation in three dimensions occur with the same frequency, but all θ are not equally probable because this angle relates to the specific direction of view of the OPC beam. The mean value of any function $f(\theta)$ is (Kirk 1976)

$$\bar{f}(\theta) = \int_0^{\pi/2} f(\theta) \cos \theta \, d\theta \quad (7)$$

Determining parameter b for any recorded CSA by rearrangement of Eq. 4 is now no longer straightforward because angle θ is not known for any individual OPC measurement. This parameter can however be estimated for a known CSA by using a mean value of $(w^2 \cos^2 \theta + \sin^2 \theta)^{1/2}$ giving

$$b_{\text{ran}} = \left(\frac{CSA}{\pi \int_0^{\pi/2} (w^2 \cos^2 \theta + \sin^2 \theta)^{1/2} \cos \theta \, d\theta} \right)^{1/2} \quad (8)$$

Using this method, b_{ran} tends, on average, to overestimate the true value of b when $w > 1$. The ratio of true spheroid volume ($= 4/3\pi b^3 w$) to that calculated using b_{ran} ($= 4/3\pi b_{\text{ran}}^3 w$) is b^3/b_{ran}^3 . It is relatively simple to calculate a correction factor, $R(w)$, for estimating spheroid volume from CSA, which is the ratio b^3/b_{ran}^3 , averaged for randomly oriented particles, for any given w :

$$R(w) = \frac{\left(\int_0^{\pi/2} (w^2 \cos^2 \theta + \sin^2 \theta)^{1/2} \cos \theta \, d\theta \right)^{3/2}}{\int_0^{\pi/2} (w^2 \cos^2 \theta + \sin^2 \theta)^{3/4} \cos \theta \, d\theta} \quad (9)$$

$R(w)$ is one when $w = 1$, and decreases as w increases, but nevertheless remains a minor correction factor ($R[w] > 0.97$ for $w = 6$).

The biovolume of particles passing through the OPC can now be estimated by calculating spheroid volume using b from Eq. 8, multiplying by $R(w)$, and summing over the number of particles encountered ($V_{\text{ran}} = 4/3\pi b_{\text{ran}}^3 w R[w]$):

$$V_{\text{ran}} = \frac{\frac{4}{3} \pi^{-1/2} w \sum_{i=1}^n CSA_i^{3/2}}{\int_0^{\pi/2} (w^2 \cos^2 \theta + \sin^2 \theta)^{3/4} \cos \theta \, d\theta} \quad (10)$$

Assessment

To assess the calibration methods, OPC data were compared with zooplankton samples collected on RRS *Discovery* Cruise 253 during a survey of the waters overlying the Iceland-Faroes Ridge in the northeast Atlantic (63–65°N 8–12°W). The datasets comprised of OPC measurements made from SeaSoar (a towed undulating vehicle; Pollard 1986) and net samples collected with a vertically hauled 500 μm mesh WP-2 net. The net could not be deployed simultaneously with SeaSoar so the datasets presented are not concurrent. Net hauls were made at stations along a transect on the 10 June 2001, and SeaSoar was towed along the same transect at 4 m s^{-1} sampling at the same stations between 13 and 35 h later.

It is important to be sure that equivalent size ranges of zooplankton are being enumerated when comparing the OPC data with that of the net hauls. The mesozooplankton community was dominated by the copepod *Calanus finmarchicus*. OPC data in the size range 1.0 to 1.7 mm ESD were selected for the comparison with net data, corresponding to *C. finmarchicus* stages CIV–CVI, determined by microscopic measurements (converted to ESD according to Beaulieu et al. [1999]). Stages CIV–CVI were efficiently retained by the 500 μm WP-2 net, whereas earlier copepodite stages were not caught.

Abundance comparison—It is important to verify that the zooplankton abundance derived from the OPC was comparable to that sampled by the nets before undertaking a comparison of OPC and net derived biovolumes. The abundance of

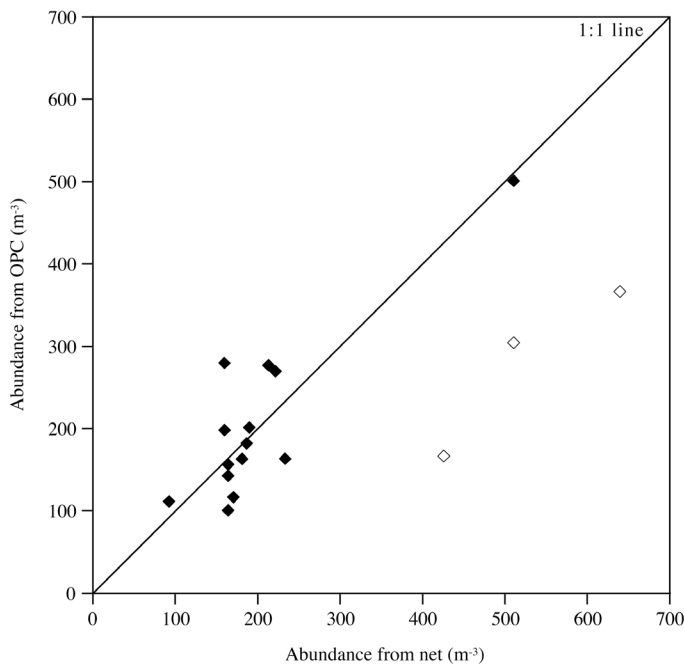


Fig. 3. Zooplankton abundance from the OPC, in the size range 1.0 to 1.7 mm ESD, representing the dominant species *Calanus finmarchicus* stages CIV-CVI, are plotted as a function of zooplankton abundance determined from net samples for the same size range of zooplankton. Data are averaged over the upper 120 m. Open points show stations where net-measured abundance was much larger than OPC-measured abundance, and these data are excluded from the biovolume calibration.

particles detected by the OPC was enumerated as the number of counts per volume of water sampled, averaged with a resolution of 5 km along the transect and between the surface and 120 m, the depth range over which the net was hauled. The volume of water sampled by the OPC was not measured directly and so was determined, instead, as the product of the distance traveled and the sampling tunnel aperture dimensions (10 cm²). Zooplankton abundance in net samples was determined by counting with a microscope, identifying most types to species level, and the dominant species *C. finmarchicus* to copepodite stage. The size of between 120 and 159 randomly selected zooplankters was measured microscopically from each net to determine which species and stages were represented in the 1.0 to 1.7 mm ESD size class. Zooplankton abundance was dominated by *C. finmarchicus* to the extent that it accounted for, on average, 98.4% of the abundance in the 1.0 to 1.7 mm ESD size class.

The average abundance of zooplankton in the 1.0 to 1.7 mm ESD size class in the upper 120 m determined by OPC was in most instances close to a 1:1 line when compared with the net measured abundance at each station (Fig. 3). At three stations the net abundance was twice that measured by the OPC, possibly a result of the OPC and net sampling different zooplankton communities as a result of advection between sampling by the OPC and the net. On the basis of this difference, these

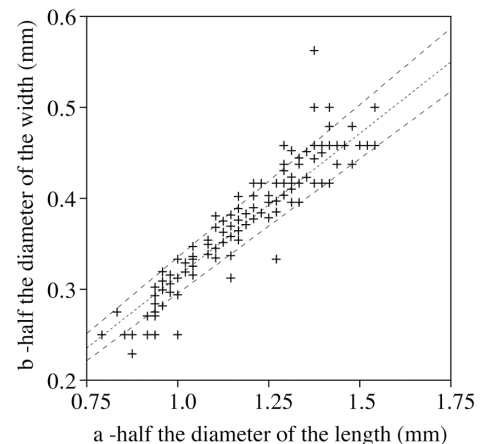


Fig. 4. Length-to-width ratios of zooplankton, mainly *Calanus finmarchicus* CIV-CVI. Lines showing the mean ratio from these data (w) and the mean \pm the standard deviation are also plotted on the graph.

data were not used in the subsequent evaluation of the OPC biovolume calibration methods.

Biovolume comparison—It is now important to ensure, as far as possible, that the measured biovolumes of net samples correspond to OPC data in the 1.0 to 1.7 mm ESD size range. Net biovolume, unlike abundance, may be significantly influenced by the presence of a few large individuals. Determining the biovolume for a size range within a net sample is often a difficult task, but was facilitated in this case because of the dominance of single species, *C. finmarchicus*. To estimate biovolume solely in the 1.0 to 1.7 mm ESD size range, occasional large animals from groups such as medusae, siphonophores, large amphipods, large euphausiids, and chaetognaths were picked out of the samples. Note, however, that these animals constituted only a very small proportion of the samples, which were dominated by *Calanus* (accounting for, on average, 98.4% of all individuals in the size class). Any animals that were similar in size to *Calanus*, but belonging to other taxa, were left in the samples because these are also enumerated by the OPC. The biovolume of each sample was measured as displacement volume by recording the increase in fluid level when each sample was placed in a measuring cylinder (Postel et al. 2000). The volume contributed by interstitial liquid in the samples was minimized by blotting each sample with absorbent laboratory paper.

The two spheroidal models (V_{\max} , V_{ran}) require the ratio of major to minor axes (w) to be specified. This ratio was determined empirically by microscopic measurements of the lengths and widths of more than 150 randomly selected zooplankters from net samples (Fig. 4). *C. finmarchicus* completely dominated the 1.0 to 1.7 mm ESD size class, and thus, nearly all the data points are close to the mean value of w of 3.18.

The volume of particles detected by the OPC in the 1.0 to 1.7 mm ESD size range, in the upper 120 m of the water column, was calculated using each of the three calibration methods (for V_{ran} , $R[w] = 0.98$ for $w = 3.18$). These calculated values

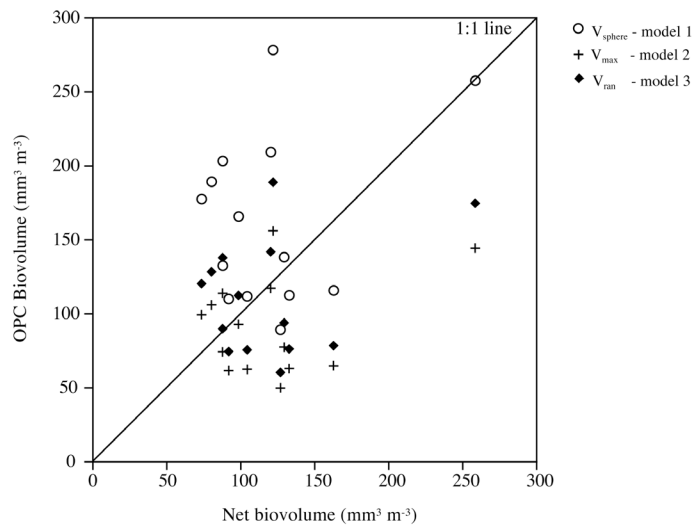


Fig. 5. OPC biovolume in the size range 1.0 to 1.7 mm ESD, determined using the three models: the spherical model (V_{sphere} , Eq. 2), the maximum projected CSA spheroid model (V_{max} , Eq. 6), and the randomly orientated spheroid model (V_{rand} , Eq. 10). OPC biovolume is plotted against net biovolume, determined as the displacement volume for the same size range at each station. Biovolume is averaged over the upper 120 m.

are compared to corresponding net biovolumes for each station (Fig. 5). The biovolume comparison is less closely associated with the 1:1 line as was seen in the abundance comparison. When averaged over all the stations, the randomly orientated spheroidal model (V_{rand}) provided the best fit with the net data: on average the ratio of OPC biovolume to net biovolume was 1.02 ($n = 14$, 95% confidence interval [CI]: 0.72-1.20) compared to ratios of 0.84 ($n = 14$, 95% CI: 0.59-0.99) when calculating OPC biovolume as V_{max} and 1.50 ($n = 14$, 95% CI: 1.05-1.77) when calculating as V_{sphere} .

Discussion

A potentially useful method of calculating particle biovolume from shadow areas recorded by the OPC is to assume that particles are of known shape and use angular geometry. This method does however encounter difficulties, notably that zooplankton come in many shapes and sizes, and account also has to be taken of particle orientation relative to the sampling light beam of the OPC. These difficulties have led, in a number of instances, to OPC biovolume being empirically related to measured net biovolumes (e.g., Stockwell and Sprules 1995; Sprules et al. 1998; Pollard et al. 2002). Calibration methods have been presented here based on the theoretical relationship between the size and shape of zooplankton represented as opaque spheres or spheroids and the shadow areas that would be correspondingly cast and measured by the OPC as these particles pass through a light beam.

The OPC biovolume calibration methods were evaluated by comparison with net biovolume data collected in the north-east Atlantic during June 2001. Several potential sources of error must be accounted for when undertaking this comparison. Perhaps of greatest importance, sampling by the OPC and the net were not concurrent. Ideally, the net should have been attached to the rear of the OPC to retain all zooplankton that pass through the sampling tunnel, but this was logistically not possible at the time. The OPC sampling traversed the same transect as the nets, but was 13 to 35 h later. In order to be confident that the two measuring devices recorded comparable zooplankton samples, we first microscopically examined the assemblage of particles present and then undertook a comparison of recorded abundances. Obvious possibilities for a discrepancy in OPC and net measurements are if different types of particles are recorded in each case, or if different size ranges of particle are enumerated. Some studies have reported overestimates of abundance as recorded by the OPC when compared to net samples (Heath et al. 1999; Halliday et al. 2001). Such discrepancies are most likely explained by the OPC sensing non-zooplankton particles, e.g., detritus, which can be more numerous than zooplankton (Herman 1992; Heath et al. 1999; Zhang et al. 2000). It should, nevertheless, be noted that some previous studies have found good agreement between OPC counts and net abundance (Herman 1992; Gallienne and Robins 1998). In our study, the zooplankton assemblage was strongly dominated by a single species, *Calanus finmarchicus*, making a comparison between the OPC and net data relatively straightforward.

Stages CIV-CVI were efficiently caught in nets, corresponding to 1.0 to 1.7 mm ESD as measured by the OPC. The average abundance recorded by the OPC was, in most instances, close to a 1:1 line when compared with the net measured abundance at each station. There was no obvious contamination by other types of particles. The size range associated with *Calanus* populations, as detected by the OPC, will vary slightly depending on various factors such as the relative contributions of different stages and degree of transparency (Herman 1992). Our chosen size range of 1.0 to 1.7 mm is smaller than that used by Baumgartner (2003) (1.0 to 2.0 mm) who encountered a dense population dominated by relatively large CV individuals. CIV *Calanus* made up a large fraction in our study. Our range is similar to that of Heath et al. (1999) (0.6-1.7 mm), but their nets also retained the smaller copepodite stages. In our study, only 1% of particles in the size range 1.0 to 2.0 mm ESD were between 1.7 and 2.0 mm ESD (99% were between 1.0 and 1.7 mm).

Of the three methods for calculating OPC biovolume presented here, the spherical model (V_{sphere}) gave the poorest agreement with net data, on average overestimating net biovolume by 50%. On average, spheres cast smaller shadow areas per unit volume than other shapes of particle. An overestimate is therefore to be expected because copepods are clearly not spherical in shape.

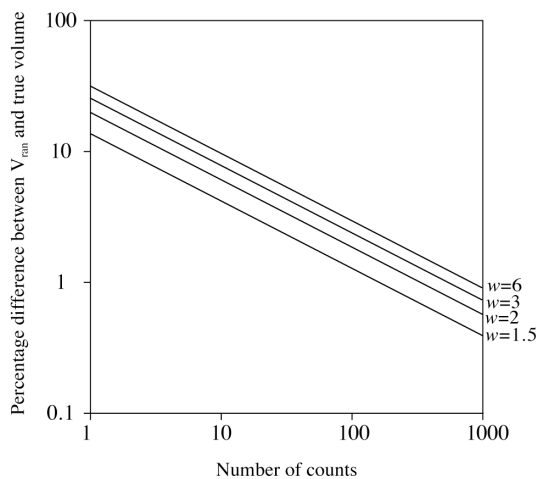


Fig. 6. The error associated with the assumption that each particle has a “mean random orientation” rather than its true orientation in a population of randomly orientated spheroids. The lines show the percentage difference between V_{ran} and true volume plotted as a function of the number of particles sampled with different values of w .

Estimated OPC biovolume more closely corresponds to net biovolume if it is assumed that zooplankton are represented by spheroids rather than spheres. It is then necessary to consider the shape of the spheroids, defined as the ratio of major to minor axes, w , and the orientation of particles relative to the beam. Our calibration methods assumed that all particles have the same shape. This was a reasonable assumption in view of the dominance of the zooplankton assemblage by *Calanus finmarchicus*; a value of 3.18 was microscopically determined for w . Two assumptions were tested regarding particle orientation. In the first (V_{max}), all particles are oriented in parallel to the flow (i.e., perpendicular to the light beam), thus presenting maximum CSA per unit volume. In the second model (V_{ran}), particles are given a random orientation. Of the two models, random orientation produced a better fit with the displacement volume of net samples (ratios of OPC to net biovolume were 1.02 and 0.84 for V_{ran} and V_{max} , respectively). It should be noted however that, if anything, we would expect the estimates of net biovolume by the displacement method to be overestimates because of water retention in the sample. Decreasing the net biovolume estimates would tend to improve the correspondence between V_{max} and the net data, while diminishing the agreement with V_{ran} .

Particles might be expected to be randomly oriented if flow through the OPC sampling tunnel was turbulent. However the flow of water through the OPC sampling tunnel may align the major axis of zooplankton with the flow at SeaSoar towing speeds. Cylindrical particles tend to become lined up in high-speed laminar flows (Bernstein and Shapiro 1994). Behavioral aspects may also play a role. Recent in situ observations by video microscopy have shown that zooplankton can have nonrandom orientations. For example,

Benfield et al. (2000) observed that the majority (75%) of *Calanus finmarchicus* on Georges Bank were orientated within 30° of the vertical. Moderate deviations in orientation away from $\theta = 0^\circ$ cause only small decreases in the projected CSA relative to the maximum; spheroids with $w = 3$ will project more than 90% of their maximum CSA when θ is between 0° and 30° (Fig. 2). Finally, it should be noted that V_{max} was closer to net measured biovolume than V_{ran} in as many as 6 of the 14 stations examined.

The random orientation model may not accurately estimate the true biovolume of particles encountered by the OPC if the number of particles over which the estimate is to be made is small. We investigated the magnitude of this error using a computer program that repeatedly creates samples of imaginary spheroids of random size and orientation. For each sample of any specified size, the CSA that would be recorded by an OPC is calculated, and the resulting biovolume (V_{ran}) compared with the known true volume of the spheroids. The resulting error, averaged over a large number of trials, is shown in Fig. 6. The error in the estimation of biovolume from V_{ran} was greater than 5% when the number of counts per averaging bin is less than 50, but once counts exceed 100 per bin the error was less than 1%. Typically in OPC data averaging there are hundreds of particles in each bin and this error is not significant. However, care must be taken when using V_{ran} when there are few counts per bin, such as in larger size classes where there are fewer particles or where high spatial resolution data are required.

Comments and recommendations

In conclusion, of the three models presented herein for estimating biovolume from OPC measurements, V_{ran} (randomly oriented spheroidal particles) gave the closest match to net data collected in the northeast Atlantic. Nevertheless the V_{max} method (spheroidal particles aligned parallel to the flow) provided a closer match to the net data in 6 out of 14 stations, and so should not be disregarded. We have demonstrated that both the V_{ran} and V_{max} methods can provide reasonable estimates of net biovolume from OPC measurements, without recourse to the use of empirical tuning parameters that are otherwise required. The success of our calibration methods was undoubtedly enhanced by the fact that the community chosen for validation purposes was dominated by a single species, *C. finmarchicus*, which could be approximated by spheroids of known dimension. In a more diverse community, different values of w could be applied for different size ranges of zooplankton. These calibration methods are less likely to be effective when applied to zooplankton communities incorporating a diverse range of organisms.

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