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SHORT COMMUNICATION

Estimations of mesozooplankton biomass in a coastal upwelling area off NW Spain

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Abstract. The abundance and several estimators of mesozooplankton biomass (dry weight, ash-free dry weight, displacement volume, carbon and nitrogen) were measured in a coastal upwelling area off La Coruña (NW Spain) at monthly intervals between 1990 and 1995. Holoplanktonic copepods dominated in most of the samples, but meroplankton were also important near the coast, especially during late spring and through summer. Gelatinous organisms (medusae, siphonophores and larvaceans) reached significant abundances (~10%) in shelf waters by late summer, but also near the coast in spring. Log-linear equations were computed between dry weight, displacement volume and the other biomass estimators, to allow for interconversion among different measurements. To prevent the influence of meroplankton and gelatinous zooplankton in the estimations of biomass, the equations were adjusted using only samples in which the abundance of each of these groups was <10% of total individuals. Our equations produced carbon and ash-free dry weight estimates that are comparable to those obtained with the ratios given in other studies in the region. However, the estimations of mesozooplankton carbon from displacement volume using the adjusted equation with our data are lower than those reported previously for the area, which were computed using equations adjusted with data from a different ecosystem. The use of interconversion factors taken from the literature is discussed, along with the implications of the estimations of mesozooplankton biomass in the computations of the flux of carbon through the ecosystem.

The study of zooplankton biomass in upwelling environments has received substantial attention in many regions because of the central role of these organisms within the trophic food web. Most zooplankton species, and especially herbivorous copepods, are able to track the environmental variability and take advantage of the fertilization caused by the upwelling and the subsequent increase in primary productivity (e.g. Verheye *et al.*, 1992). In addition, copepods are one of the most important food resources of the early stages of clupeoid fish (James, 1987; Varela *et al.*, 1990), which form large populations in upwelling areas. Zooplankton biomass may either be measured directly as the weight of fresh or dry matter, or, more commonly, estimated indirectly from other measurements.

One of the most frequently used indirect methods employs the displacement volume of a formalin-preserved sample which is placed in a graduated cylinder (Cushing *et al.*, 1958; Le Borgne, 1975; Wiebe *et al.*, 1975; Roman *et al.*, 1985; Wiebe, 1988). This method requires the calibration of the displacement volume values against directly measured biomass values, generally as carbon weight. There is a substantial variation in the calibration parameters from one study to another, and the application of a certain set of parameters determined for one region to another may cause large errors. As an example, Valdés *et al.* (1990) and Tenore *et al.* (1995) computed zooplankton carbon in the Galician upwelling (NW Spain) using the equation of Roman *et al.* (1985), which was originally adjusted

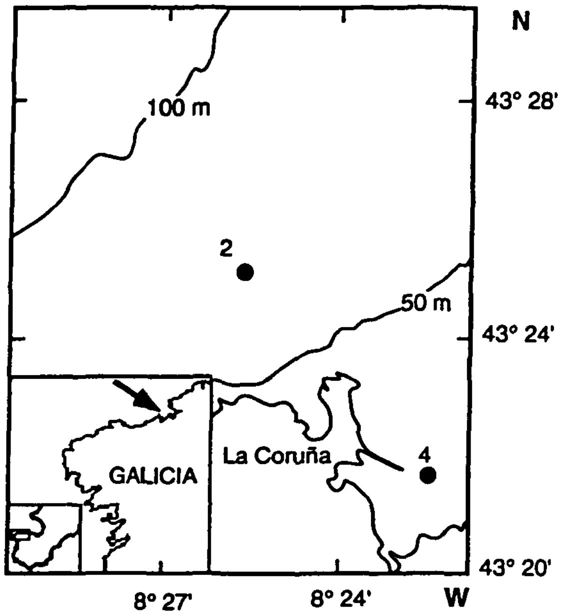

Fig. 1. Location of studied stations.

for samples in an oligotrophic area in the Gulf Stream. Bode and Varela (1994), using parallel measurements of displacement volume and dry weight of zooplankton off La Coruña (NW Spain) provided by Valdés *et al.* (1991), concluded that the use of the equation of Roman *et al.* (1985) would have caused an overestimation of zooplankton carbon in this region. In this paper, we present a set of equations for interconversion among different zooplankton biomass estimates in the Galician shelf waters computed using a large number of observations.

Zooplankton samples were collected at approximately monthly intervals from January 1990 to December 1995 at two stations near the coast of La Coruña (Galicia, NW Spain). Station 2 (70 m depth) was typical of mid-shelf waters in this area (Valdés *et al.*, 1991; Casas *et al.*, 1997), while station 4 (20 m depth) was close to the coast and under the direct influence of the Bay of La Coruña (Figure 1). The stations were sampled during daylight. Zooplankton were collected using double-oblique tows from the surface to 5–10 m from the bottom with Juday–Bogorov nets equipped with flow and depth meters. The size of the mesh was 250 μm, and in the following the term mesozooplankton will be used to name the material and specimens collected. Several aliquots were taken from each sample to determine mesozooplankton abundance and biomass. The total number of individuals and their distribution by taxonomic groups were determined in formalin-preserved samples (5% final concentration) observed under a binocular microscope. Specimens were combined in three groups related to the persistence of the species in the plankton through their life cycles and their body composition: copepods, meroplankton (larvae of molluscs, polychaetes, benthic crustaceans, and fish eggs) and gelatinous zooplankton (chaetognaths, medusae, ctenophores, siphonophores and larvaceans). Mesozooplankton biomass was measured in samples using several methods. The largest specimens of gelatinous zooplankton were removed from these samples. Dry weight (DW) was measured on unpreserved material collected on pre-ashed (500°C, 24 h) and pre-weighed Whatman GF/C glass fibre filters. The filters with the samples were rinsed with filtered sea water. Ash-free dry weight (AFDW) was measured on DW samples after combustion at 500°C for 24 h (Corral *et al.*, 1981). Displacement volume (DV) was determined on formalin-preserved aliquots stored for 6 weeks after sampling (Wiebe *et al.*, 1975). Valdés *et al.* (1991) estimated that the storage of these samples would have caused biomass losses of up to 24%. Carbon and nitrogen contents of mesozooplankton were measured using a Perkin Elmer CHN analyser on a weighted subsample of dry material after determination of DW. Only DW values were systematically determined in all samples, while the other biomass estimators were measured only in some samples.

Copepods dominated abundance numbers of mesozooplankton in almost all samples (Figure 2A). They represented >70% of total individuals counted in samples from station 2, reaching values of nearly 90% in certain months. The coastal station also exhibited a high dominance of copepods in winter, early spring and late autumn samples, but samples taken during late spring and summer displayed a significant abundance of meroplanktonic groups, mostly larvae of benthic animals (Figure 2B). Gelatinous zooplankters were generally found in low numbers at both stations, although they were more abundant at station 2. Average dominance values of ~10% occurred in May at station 4 and from August to October at station 2 (Figure 2C). These results agree basically with the dominance pattern of zooplankton in the area during 1988–1989 as described by Valdés *et al.* (1991), where more detailed taxonomic information can also be found.

Because mesozooplankton of shelf waters were dominated numerically by copepods, and to prevent the influence of meroplankton and gelatinous zooplankton in the estimations of biomass, comparisons of the different estimators were made using only samples in which the abundance of each of these groups was <10% of total individuals. A large range of zooplankton biomass values (from 0.5 to 50 mg carbon m^{-3}) was employed. Logarithmic transformations produced the highest correlations and the equations adjusted by the geometric regression model (Sokal and Rohlf, 1981) indicate a good agreement between the different estimators (Figure 3). The correlation coefficients of the log-transformed values were highly significant ($P < 0.0001$) and the variance accounted for by the regressions ranged from 67% in the relationships between carbon and nitrogen with displacement volume, to 98% in the case of DW versus AFDW. To provide more conversion factors, the relationships between AFDW and carbon or nitrogen were also studied (Figure 4), and the resulting equations explained >90% of the variance. Therefore, interconversion of these biomass estimators and reliable carbon and nitrogen estimations from other measurements are possible.

The computed logarithmic relationships would cause the ratios between different estimators to change with the absolute value of zooplankton biomass, but

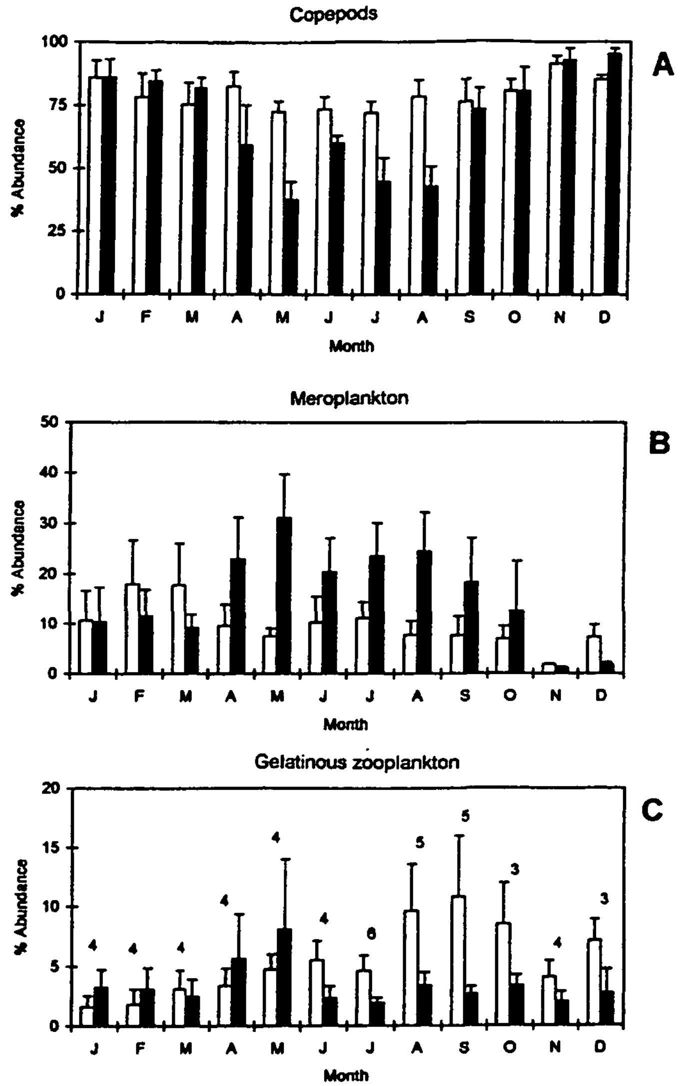

Fig. 2. Monthly average (+ SEM) abundance values (%) of the main groups of mesozooplankton at station 2 (white bars) and station 4 (filled bars) from 1990 to 1993. (**A**) Copepods. (**B**) Meroplankton (including larvae of benthic polychaetes, molluscs, bryozoans, crustaceans and fish eggs). (**C**) Gelatinous zooplankton (including chaetognaths, siphonophores, medusae and larvaceans). The number of cases averaged for each month is the same for all graphs and is indicated above bars in the lower graph (C).

such change would cause significant errors only if the value of the slope of the regression was different from one. To determine the statistical significance of these errors, we tested the significance of the differences between the values computed for the slopes (b in Figures 3 and 4) and the value $b = 1$ with Student's t-tests. Only the slopes of the equations for interconversion between DW and C,

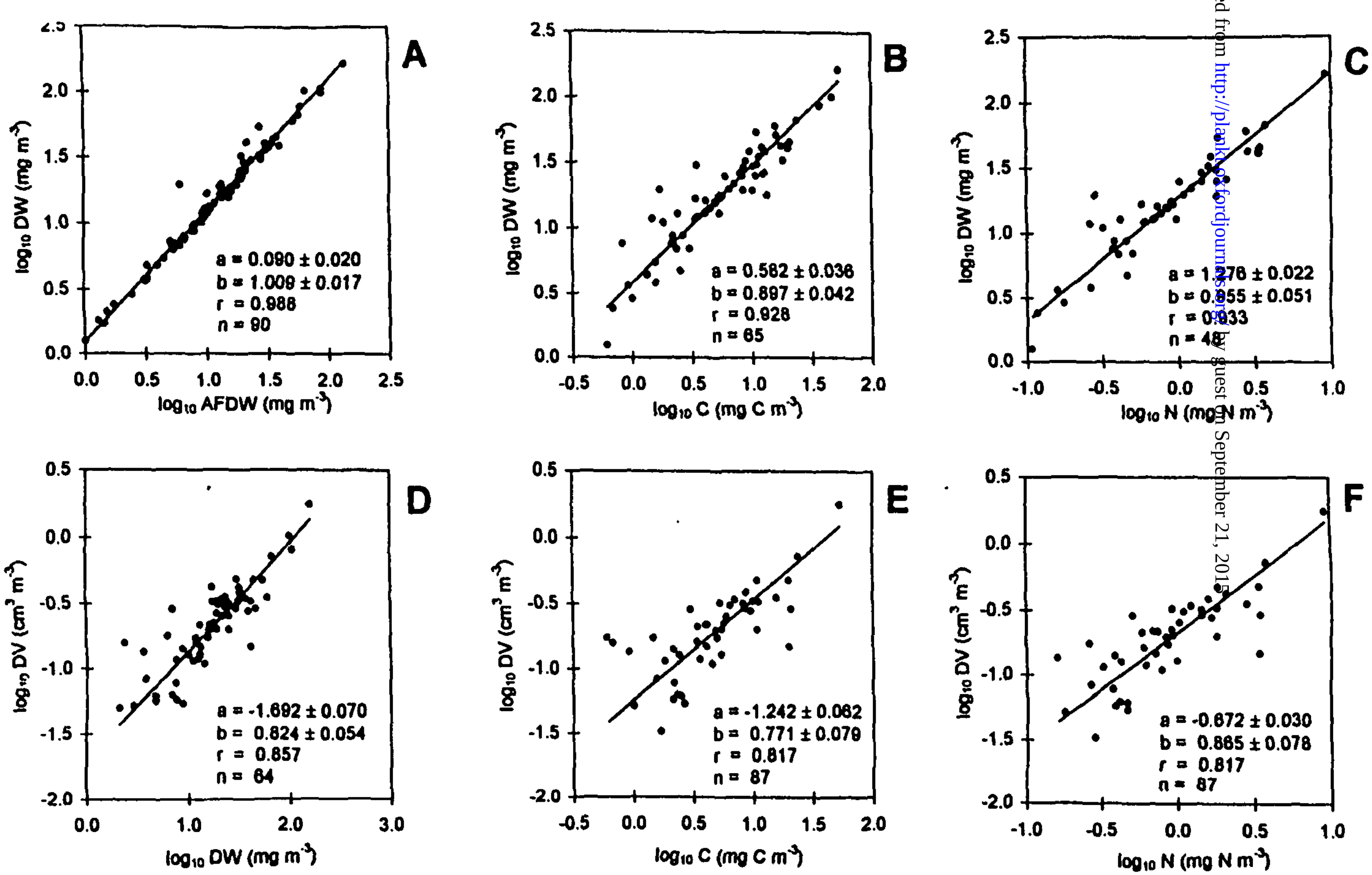

Fig. 3. Relationships between several estimators of mesozooplankton biomass. (**A**) Dry weight (*DW*; mg m^{-3}) versus ash-free dry weight (*AFDW*; mg m^{-3}). (**B**) Dry weight versus carbon (C; mg C m^{-3}). (**C**) Dry weight versus nitrogen (N; mg N m^{-3}). (**D**) Displacement volume (DV; cm^3 m^{-3}) versus dry weight. (**E**) Displacement volume versus carbon. (**F**) Displacement volume versus nitrogen. All variables were $\log_{10}$ transformed before regression analysis. The parameters (± SE) of the adjusted regression lines are indicated. *a*, constant; *b*, slope; *r*, correlation coefficient; *n*, number of data points.

and between DV and C or N, were significantly different from $b = 1$ ($P > 0.05$), indicating that the ratios between all the other pairs of estimators related by our equations can be considered constants. Nevertheless, some variation in the ratios between computed biomass variables can exist if a large range of biomass values is considered (Table I), and the differences were even higher if the resulting ratios are compared with those computed assuming linear relationships. For instance, Cushing *et al.* (1958) cited an equivalence of 1.7 mg DW mg^{-1} C, which in a range of values from 0.1 to 100 mg DW would produce carbon estimates between 1.5 and 3 times the value of the estimate that would result using our equation (from 0.02 to 38.09 mg C; Table I). More correspondence appears between our estimations and those obtained using values of the DW:C ratio of 3.1 (Wiebe *et al.*, 1975), 2.9 (calculated from the results obtained in the Galician rias and published by Corral *et al.*, 1981), or those measured in zooplankton of the Galician shelf (DW:C = 3.0, Franco *et al.*, 1981; DW:C = 3.2, Braun *et al.*, 1990). The ratio between DW and C varies from 5.8 to 2.6 along a DW range from 0.1 to 100 mg m^{-3}, and from 4.1 to 2.3 if both variables were estimated from DV values between 0.01 and 10 cm^3 m^{-3} (Table I). These values were equivalent to a change of ~20% in the carbon content of DW over four orders of magnitude of the latter, and were not far from the values of carbon content of copepods in various environments compiled by Parsons *et al.* (1977) that varied >34% of DW. The relatively low carbon content that resulted from the estimations using the computed equations for DW at low biomass values may be due to the weight of salts retained on the filter during DW determinations, while this weight would be less important when zooplankton biomass was high. When DV was employed at low biomass values, the sensitivity of the device used to measure the volume of the sample would limit the reliability of the estimations.

Similarly, C:N ratios computed in Table I varied between 4.2 and 6.6 when both C and N were computed from DW, but between 3.6 and 9.4 when DV was employed. While the former range of C:N values agrees well with published results of zooplankton from the Galician shelf (Franco *et al.*, 1981) and from copepods in general (Parsons *et al.*, 1977), the C:N values produced by estimations from DV at high biomass concentrations seem to be too high for zooplankton.

Table I. Comparison of estimations of mesozooplankton biomass from DW or DV using the computed equations and the resulting ratios between them. All biomass figures were in mg m^{-3}, except for DV which were in cm^3 m^{-3}

DW	AFDW	C	N	AFDW:C	DW:C	C:N
0.10	0.08	0.02	0.004	4.8	5.8	4.2
1.00	0.81	0.22	0.046	3.6	4.5	4.9
10.00	7.98	2.92	0.514	2.7	3.4	5.7
100.00	78.16	38.09	0.514	2.1	2.6	6.6
DV	**DW**	**C**	**N**		**DW:C**	**C:N**
0.01	0.42	0.10	0.029	-	4.1	3.6
0.10	6.92	2.06	0.418	-	3.4	4.9
1.00	113.08	40.82	5.982	-	2.8	6.8
10.00	1849.23	808.93	85.694	-	2.3	9.4

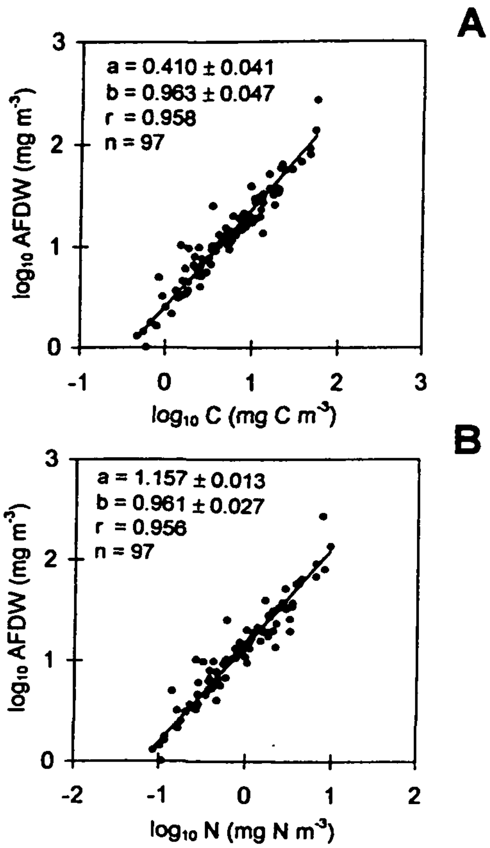

Fig. 4. Relationships between ash-free dry weight (AFDW) and (**A**) carbon (C; mg C m^{-3}) or (**B**) nitrogen (N; mg N m^{-3}). All variables were $\log_{10}$ transformed before regression analysis. The parameters (± SE) of the adjusted regression lines are indicated. *a*, constant; *b*, slope; *r*, correlation coefficient; *n*, number of data points.

These high C:N ratios may result from the lower statistical significance of the equations using DV and from the inclusion of large particles like phytoplankton chains or detritus with a large carbon content that cannot be easily separated from zooplankton in some samples. In samples where phytoplankton are clearly abundant, their contribution to total biomass collected by the zooplankton net can be determined from the chlorophyll content of a subsample and the carbon:chlorophyll ratio of sestonic particles other than mesozooplankton. In any case, we recommend that the required biomass variables are measured directly or computed using the most close relationship, as shown in Figures 3 and 4, since the use of ratios between estimators may cause large errors.

AFDW was on average ~80% of DW, as was reported in other studies of mesozooplankton in upwelling areas (Le Borgne, 1975). However, Corral *et al.* (1981) cited average values from 51 to 79% in zooplankton of two Galician rias in different seasons. The variations found by the latter study may be due to changes in the abundance of meroplankton in the shallow waters of the rias, since meroplanktonic mollusc larvae may have a large mineral content because of their calcareous shells. The carbon or nitrogen contents of zooplankton that can be computed from AFDW using the equations provided in Figure 4 are likely to be quite accurate because of the large significance of the relationship and because the slopes of both equations are not significantly different from one ($P > 0.05$).

In contrast, carbon estimations from DV are very variable in different studies. One millilitre of DV would result in a carbon equivalent from 31 to 69 mg C using the equations computed by Le Borgne (1975) in an upwelling area, whereas the equation of Roman *et al.* (1985) gives a value of 117 mg C ml^{-1} DV. The comparison between carbon estimates from a large range of DV values using the equation of Roman *et al.* (1985) and the equation given in Figure 3E reveals that the former estimates values >10 times higher than those produced by our equation at DV concentrations of 0.01 cm^3 m^{-3}, but only 24% higher for a DV value of 10 cm^3 m^{-3} (Table II). Therefore, the carbon biomass concentrations of zooplankton given by Valdés *et al.* (1990) and Tenore *et al.* (1995), which were computed from DV using the equation of Roman *et al.* (1985), are likely to be too high for this upwelling region. This result is not surprising as the equation of Roman *et al.* (1985) was generated for zooplankton larger than 64 μm collected in mostly oligotrophic waters of the Sargasso Sea, Gulf Stream and slope waters. The overestimation of mesozooplankton carbon is of less importance if the values computed with the same equation are only used for comparative purposes between stations or cruises, as in Valdés *et al.* (1990). However, when the carbon estimations are employed in further computations of zooplankton rates, the overestimation can produce misleading interpretations of the zooplankton activity. As an example, Tenore *et al.* (1995) used estimations of zooplankton carbon from DV along with measured instantaneous specific carbon grazing rates to compute the grazing impact of the zooplankton community on the phytoplankton standing stock in several cruises. These authors estimate that zooplankton grazing can reduce up to 100% phytoplankton carbon daily during upwelling conditions, which means that zooplankton can effectively control any accumulation of phytoplankton even in the most productive conditions. However, the phytoplankton concentrations shown in the same study and the results reported in other studies of the Galician upwelling (e.g. Varela *et al.*, 1991; Varela, 1992; Bode *et al.*, 1994; Casas *et al.*, 1997) indicate that the former estimations of grazing impact are likely to be biased. Using zooplankton carbon values computed from an equation

Table II. Comparison of biomass carbon estimates from DV using the equation of Roman *et al.* (1985; C_R) and the equation obtained in this study (Figure 3E; C_S). Carbon biomass is in mg C m^{-3} and DV in cm^3 m^{-3}. Differences between both estimates ($C_R - C_S$) and relative overestimations of C_R ($100 [C_R - C_S]/C_S$) are given

DV	C_R	C_S	$C_R - C_S$	% overestimation
0.01	1.6	0.1	1.5	1410
0.10	13.5	2.1	11.5	557
1.00	116.6	40.8	75.8	186
10.00	1004.7	808.9	195.8	24

adjusted with local data, Bode and Varela (1994) estimated that biomass-specific daily mesozooplankton ingestion was <5% of phytoplankton biomass and <10% of daily primary production during upwelling conditions off Galicia.

In this study, we provide a set of equations for the computation and interconversion of various estimators of mesozooplankton biomass in the upwelling area of NW Spain. AFDW, carbon and nitrogen can be computed from easily measured variables like DW and DV. The use of direct measures of carbon or DW to obtain values of zooplankton biomass is recommended, but if these measurements are not available for a particular study, they can be calculated using the equations provided. The use of the DV cannot be recommended because of the large uncertainties associated with the estimation of other variables from it, and the equations computed in this study are intended mainly for comparative purposes with previously published results for the Galician upwelling. Most of the computed relationships could be applied to the zooplankton of similar upwelling areas, as the use of equations from other environments may introduce large errors in subsequent computations using the biomass estimates.

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