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Spatial distribution of zooplankton size spectra on the French continental shelf of the Bay of Biscay during spring 2000 and 2001

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[1] During two cruises in springtime (18 March to 13 April 2000 and 27 March to 4 June 2001), the whole French continental shelf of the Bay of Biscay was sampled to obtain an overview on the zooplankton community size structure. A laboratory optical plankton counter (OPC-1L) was used to process plankton net tow samples and estimate abundance, biovolume, and general characteristics of size spectra. In a second step, biomass estimates were extrapolated from size by using a conversion factor. Both biomass and abundance estimates show spatial patterns with a clear coastal-open sea gradient for both years. The coastal area was characterized by the highest biomasses and abundances per volume. A first analysis of the zooplankton community size spectra was made by using the slope of the normalized biomass size spectrum. Different spatial patterns of zooplankton size spectra were highlighted for spring 2000 and 2001. The highest slopes were found for the coastal zone, showing a large ratio of small organisms, although this was less marked in the springtime 2000. Stations characterized by high proportions of large organisms were located in majority in the north of the bay and at the shelf break. A second analysis using the size probability distributions of organisms revealed a nearly permanent nonlinearity of probability distributions. This implied the community structure was not in an equilibrium state during spring and this nonlinearity could be locally related to dominant species dynamics.

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1. Introduction

[2] Many authors have shown that recruitment of fish larvae is influenced by physical [Pepin, 1991; Daskalov, 1999; Borja et al., 1998] and biological [Kjørboe et al., 1988; Runge and de Lafontaine, 1996] factors. The zooplankton community is one of these biological factors because it constitutes a key trophic level as prey of pelagic fish larvae and influences fish egg production and larval mortality [O'Connell and Raymond, 1970; Michaud et al., 1996]. Several studies have thus compared indices for pelagic fishes (gut content observations, fish egg densities and larvae abundances) and various zooplankton descriptors, such as biomass, species com-

position, biovolume and growth rate [Bailey et al., 1995; Coombs et al., 1997; McFadzen and Franceschini, 1997; Plounevez and Champalbert, 1999; Horwood et al., 2000; Motos et al., 2000; Ruiz and Motos, 2000; Zhou and Tande, 2001]. However, the zooplankton size distribution has rarely been used as a zooplankton descriptor, even though it represents the size of potential prey of small pelagic fish. Moreover the size distribution is a global index that can be theoretically related to the ecosystem production capacity [Platt and Denman, 1977; Heath, 1995; Zhou and Huntley, 1997].

[3] During two cruises in springtime (2000 and 2001), the whole French continental shelf of the Bay of Biscay was sampled to obtain an overview on the zooplankton community size structure. The Bay of Biscay is an important fishery area and our sampling occurred during the period of larvae production. An optical plankton counter (OPC-1L) was used to quickly process samples and to obtain size spectrum of the mesozooplankton [Herman, 1988]. This tool has been recently used to study zooplankton community in various area and has been validated by comparisons with traditional sampling methods [Huntley et al., 1995; Zhou and Huntley, 1997; Gallienne and Robins, 1998; Beaulieu et al., 1999; Grant

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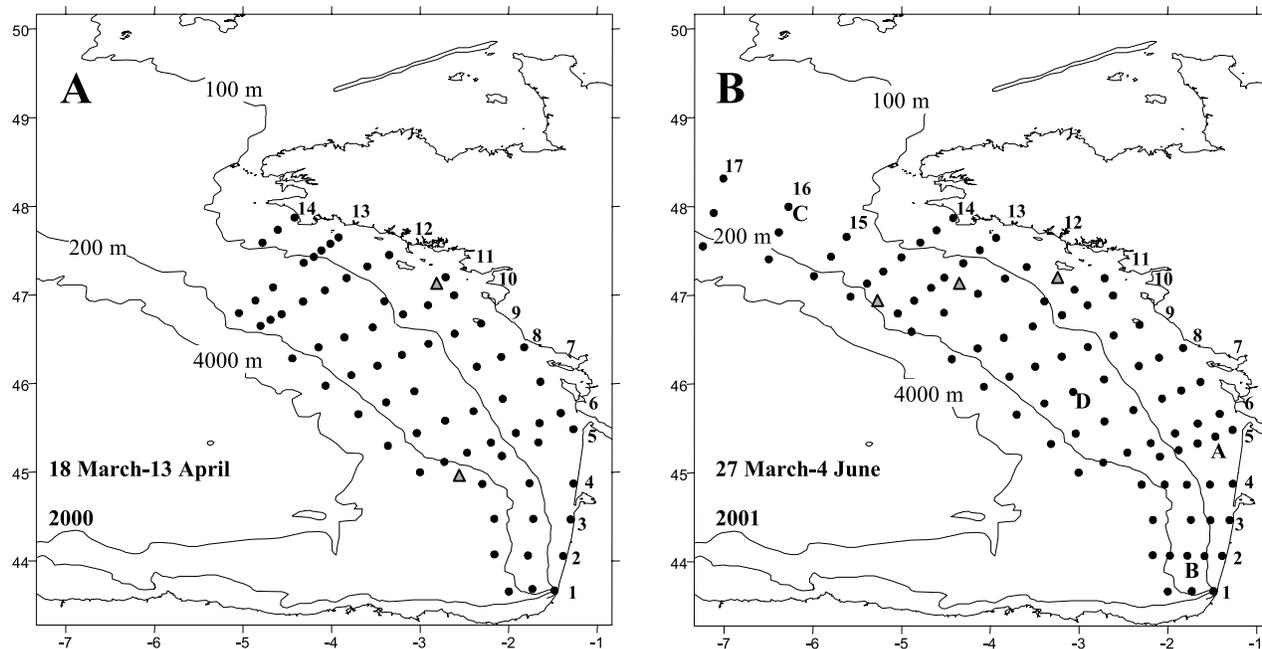


Figure 1. Sampling grids during cruises (a) PEL2000 and (b) PEL2001. Night sampling stations (solid circles) and 24 hour stations (grey triangles) sampled every 2 hours during PEL2000 and every 3 hours during PEL2001. Stations A, B, C, and D are the four stations where the size probability distributions are observed in Figure 10.

et al., 2000; Woodd-Walker *et al.*, 2000; Zhou *et al.*, 2001; Edvardsen *et al.*, 2002].

2. Materials and Methods

2.1. Sampling and Preservation

[4] Samples were collected during PEL2000 (18 March to 13 April) and PEL2001 (27 March to 4 June) cruises that covered the French continental shelf of the Bay of Biscay (Figures 1a and 1b) during the springtime. The main objective of these cruises was to study the stock of small pelagic fish in association with physical and biological environmental variables. With these constraints, zooplankton net tows were made only during the night on a grid of stations and, according to the cruises duration, sampling was realised from the beginning to the end of the spring with the highest possible frequency.

[5] A WP11 plankton net (0.25 m^2) mounted with $200 \mu\text{m}$ mesh size was used, and towed vertically over the water column from the sea bottom or 200 m depth up to the surface. Some particular stations, called “fixed stations” (at the same geographical position), were sampled during 24 hours, at two hours intervals in PEL2000 and three hours intervals in PEL2001. Collected samples were preserved in formaldehyde. They were finally processed in the laboratory by the OPC just after each cruises.

2.2. Processing Samples With the Lab-OPC

[6] The lab-OPC (OPC-1L) setup was made in accordance with the one presented by Beaulieu *et al.* [1999]. The water flow through the OPC was fixed at 18 L min^{-1} and was considered as constant during the measurements. The operator gently introduced the organisms in the water circulation system and the zooplankters were dispersed into

a large volume of water before being carried through the OPC. The light attenuation, measured over the counting time, remained constant for all samples.

[7] Particle coincidence in the beam depends directly on the count rate, which varies according to water flow and particle concentration. The count rate of detecting particles by the OPC (Nopc) in relation to the real frequency of

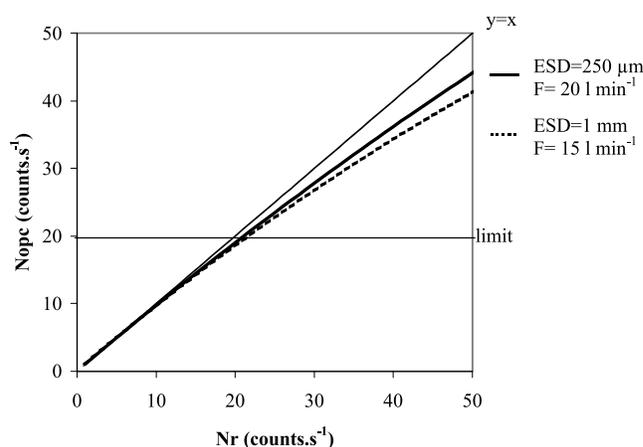


Figure 2. Effects of the water flow and the equivalent spherical diameter (ESD) of the particles on the coincidence estimated by Sprules *et al.*'s [1992] model. All combinations of ESD and flow values within these ranges ($250 \mu\text{m}$ and 1 mm of ESD; 20 and 15 L min^{-1} of flow) give curves comprised between two extreme curves presented on the graph. The limit of 20 count s^{-1} is the maximal frequency acquisition which is controlled by the operator.

particles into the beam (N_r) was realized as made by *Woodd-Walker et al.* [2000] (Figure 2). The model of *Sprules et al.* [1992] was used to estimate the probability of particles to cross the beam as a function of their the average concentration. During measurement, the organisms flow through the OPC was controlled by the operator to give count rate less than 20 counts s^{-1} , a limit value for which nearly zero coincidence occurs. The constraint with this speed limitation is the duration of processing samples. Samples were thus fractionated with a Motoda box [*Omori and Ikeda*, 1984] and a minimum counting of 1000 particles was imposed to get the spectra.

[8] The counting of nonzooplankton particles can produce bias in the estimated zooplankton size spectrum. Phytoplankton cells are the most important problem because they can aggregate in large particles (with sizes larger than 250 μm) inside of the net collector. To minimize this bias, the largest agglomerates were eliminated manually from the samples fractions before sample processing. For the smallest agglomerates and the detrital particles, we assumed, as supposed by *Beaulieu et al.* [1999], that the mixing due to the water flow in the OPC set up was sufficiently important to break the most of them.

2.3. Preliminary Test

[9] Two tests were performed to check the efficiency of size and abundance estimates. In a first test, 100 adults of copepods were selected in one sample after a preliminary filtration on 500 μm . They were measured under a microscope, and were next measured by the optical counter. In a second test, another sample was divided into 64 subsamples with a Motoda box splitter. 32 subsamples were next measured by the counter to check the counting stability over the whole size range.

2.4. Size Measurement Processing

[10] Copepods were the most abundant organisms of the zooplankton in this area, comprising 70 to 90% of total numbers of particles (personal observation). An average length/width ratio was considered equal to 3 for all the particles, following *Mauchline* [1998]. Because of the random orientation of organisms in the light beam, ESD estimations were initially increased by 15%, in agreement with *Herman* [1992] and *Beaulieu et al.* [1999], to compensate the underestimation in size. Equivalent spherical diameter (ESD) was converted in length and in weight (as carbon) by using relationships established by *Herman* [1992] and *Rodríguez and Mullin* [1986] as used by *Huntley et al.* [1995] and also by *Zhou and Huntley* [1997], respectively.

2.5. Size Spectra Analysis

[11] Two approaches were used to define and to compare characteristics of the size spectra.

[12] The first approach was based on the slope estimation of the normalized biomass size spectra (NBSS, in the sense of *Platt and Denman* [1977]) and the second was based on the probability distribution of organisms size, which could be represented by a Pareto function [*Vidondo et al.*, 1997].

[13] For the first approach, the OPC initial size classes were grouped in larger size classes. The size range was

divided regularly in a geometrical way into i intervals. The NBSS ($b(w_i)$) for each class i is estimated by

$$b(w_i) = \frac{w_i H(w_i)}{\Delta w_i} = \frac{B(w_i)}{\Delta w_i} \quad (1)$$

where $H(w_i)$, $B(w_i)$ and Δw_i are the abundance, the biomass, and the weight interval of particles in each weight class i , respectively. The nominal weight w_i for each class is the geometric mean of the weight interval. The slopes of the function $f(\log(b(w_i)), \log(w_i))$ for each station were next estimated.

[14] We know that slope estimations are also strongly influenced by the general conversion relationships, the type of scale size division (linear, geometrical or unregular), and the nominal weight for each class (e.g., mean value, upper limit, lower limit) [*Blanco et al.*, 1994]. For our analysis, we choose a constant total size interval of significant measurements.

[15] The significance of the abundance estimates in each class was implicitly related to the total number of measured particles, the scale size interval and its division. Empty classes at the end of data processing introduce distortion, because the zero values are eliminated during the log transformation. As a consequence, a few data in higher size classes, called “unexpected cases” by *Blanco et al.* [1994], distort the size distribution and strongly influence slope values of the NBSS. We thus assumed that the first empty class, in a fixed interval size with a fixed division, was the maximum limit of the classes abundance estimates.

[16] To describe the general trend of the size distribution, a number of 10 classes was chosen. The minimum limit was the detection limit of the counter and could be fixed at 270 μm (see test results). The maximum limit of the size interval was searched by an iterative method to obtain the highest size interval with any empty class in the spectra for all the stations of the two cruises. The constant size range then covered from 270 μm to 1.7 mm of ESD.

[17] The second approach, using the probability distributions, requires no class grouping, no data conversion and is not altered by the “unexpected cases” in the higher size classes. This method was used to verify if the linearity assumption of the size distribution was always correct. For comparison with the NBSS, the data were, however, converted in weight by the previous general equations [*Rodríguez and Mullin*, 1986; *Herman*, 1992]. The probability distributions were estimated by the simple relation

$$\text{prob}_i(\text{weight} > w_i) = \frac{N_{\text{weight} > w_i}}{N_{\text{tot}}} \quad (2)$$

where prob_i and w_i are the probability and the nominal weight, respectively, of each class i . N_{tot} is the total number of measured particles.

[18] Initially, an undersampling was assumed in the small classes and the second model (3), presented by *Vidondo et al.* [1997], was fitted to the spectrum by an iterative nonlinear method:

$$\log[\text{prob}_i(\text{weight} \geq w_i)] = c \log(w_i + D) - c \log(w_i + D) \quad (3)$$

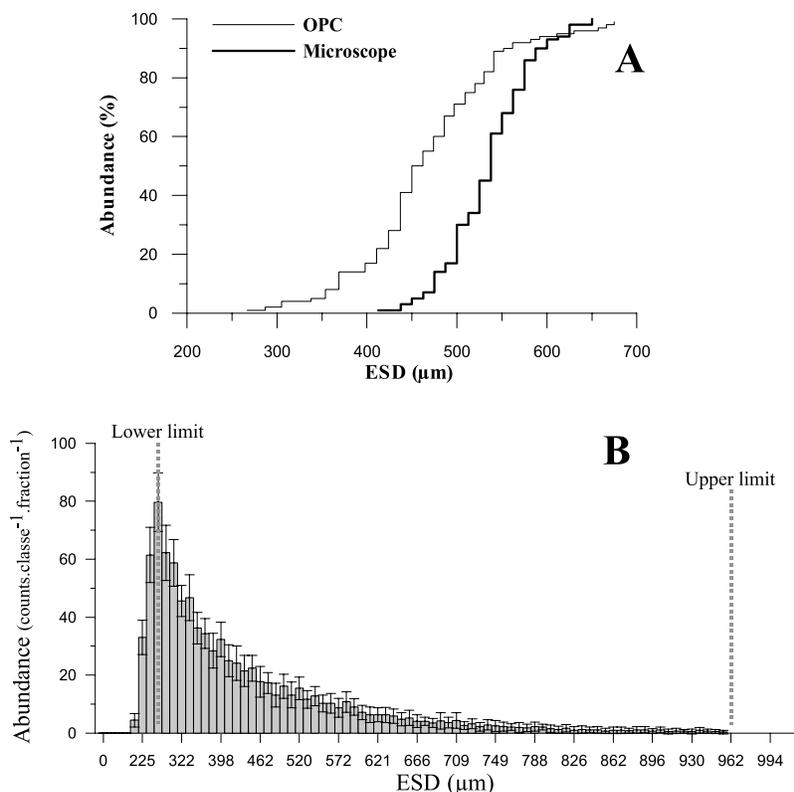


Figure 3. (a) Cumulative abundances according to ESD (μm) counted by the OPC (line) and by a microscopic observation (thick line). OPC counted 99% of the 100 counted copepods measured with a microscope. (b) Estimated average abundances in each ESD class with the original size resolution of the OPC. The 32 fractions of the same sample were measured, and the average total abundance was 920 with a standard deviation of 5%.

where c , K , and D are model parameters and the parameter c is the unbiased estimator of the slope. Theoretically, if the size distributions are linear after the log transformation, the slope estimates by the two methods (equations (1) and (3)) should converge.

3. Results

3.1. Validation of the Measurements Quality

[19] During the first test, the OPC counted 99% of the copepods. At 50% of the cumulative abundance distribution (Figure 3a), the average ESD, measured with the OPC, was also 16% lower than the average ESD estimated from length and width microscope measurements. The second test using 32 fractions of a same sample shows the stability of the total number of counted particles and the size spectra shape (Figure 3b). The average number of the total measured particles over the size spectra was equal to 920 individuals with a standard deviation of 5% over the 32 fractions. The mode was always located in the ESD class of 270 μm for all the fractions and all the samples. Thus we choose this 270 μm ESD class as the minimum limit of the computed size range.

[20] In a third test, the fixed stations of the PEL2000 cruise were taken as reference for comparing microscope and OPC counts. The comparison revealed again the good validity of abundance estimates with the lab-OPC (Figure 4). The OPC estimates in the coastal station

appeared slightly over the 1:1 line and those in the oceanic slightly below.

3.2. Temporal Stability of the NBSS

[21] The temporal variability of size spectra is presented in Figure 5 for the 24 hour coastal station during PEL2001. In this station, the total density varied between 5800

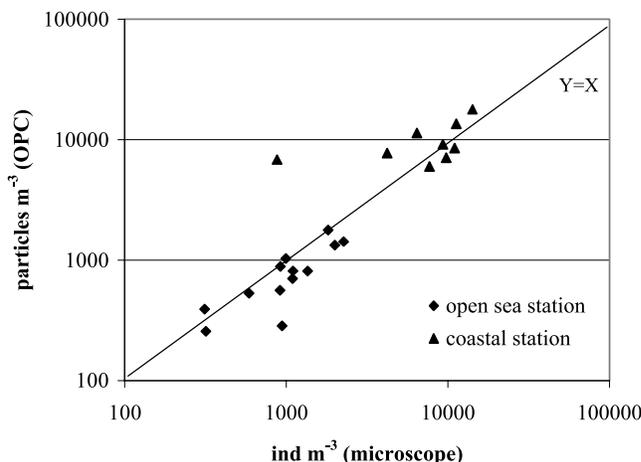


Figure 4. Comparison between OPC and microscope counts for the PEL2000 fixed stations.

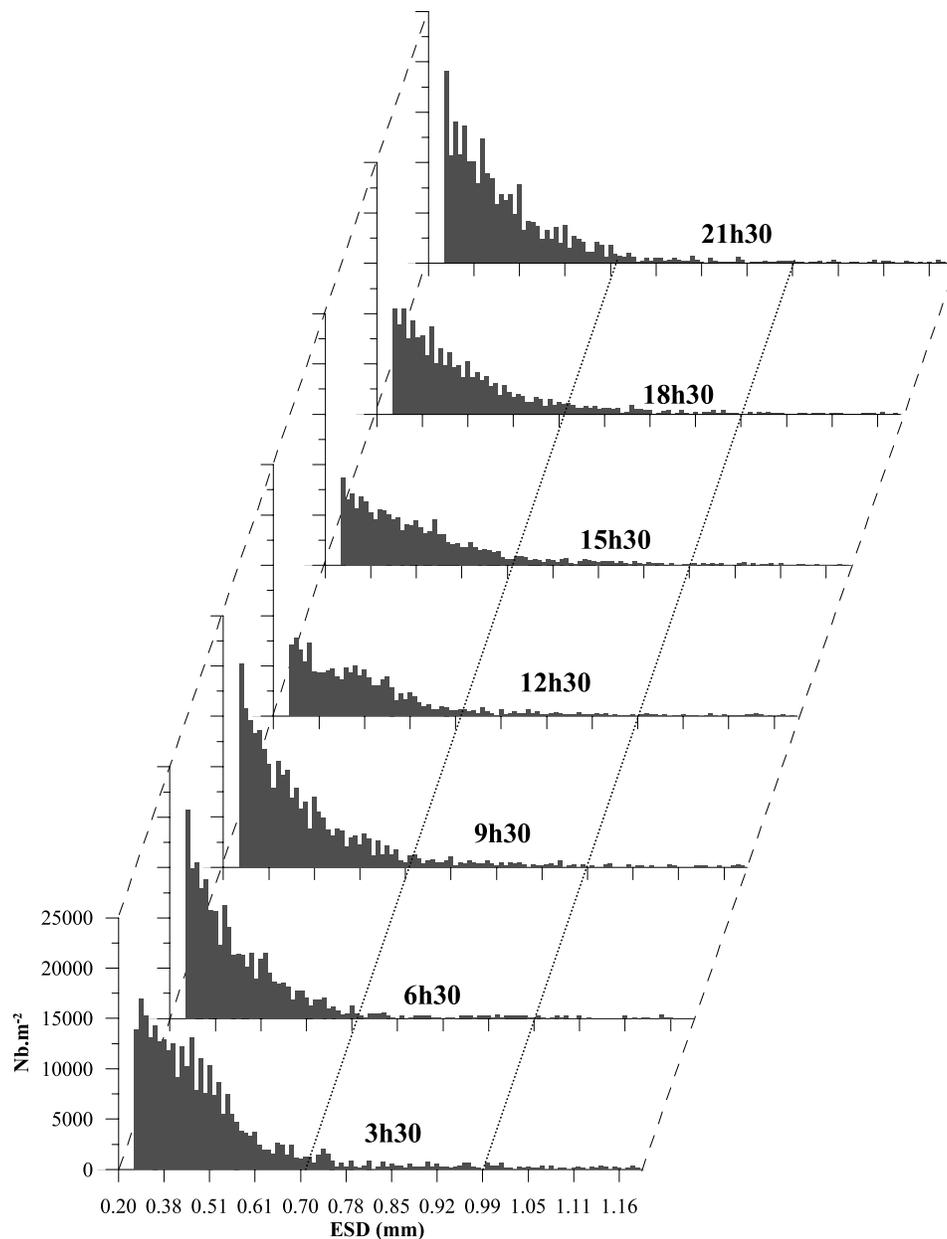


Figure 5. Temporal variation of size spectrum at the coastal 24 hour station of PEL2001 (hours UT).

individuals m^{-3} at 1230 UT and 21,540 individuals m^{-3} at 0330 UT. These density variations are linked to strong changes of the organisms size distribution. A decrease of the densities in the small size classes was observed at 1230 and 1530 UT. We can also note that the last observed distribution (2130 UT) is close to the initial observed distribution (0330 UT).

[22] Despite this temporal variability, the OPC abundance estimates (Figures 6a and 6b) and the NBSS slope values (Figures 6c and 6d) to allow a differentiation between a coastal structure and an oceanic structure. The mean density and the NBSS mean slope value at the PEL2000 oceanic station were 830 individuals m^{-3} and -0.71 , respectively. By comparison, the coastal station of the same cruise was characterized by the highest organisms concentrations,

12665 individuals m^{-3} , and the most negative mean slope -1.05 . The coastal and oceanic areas were also different in 2001 but less so. The density at the coastal and the oceanic station was estimated at 3702 and 1621 individuals m^{-3} , respectively; and the slope value was estimated at -0.91 and -0.64 , respectively. The coastal zone was thus characterized by the highest organism densities and the highest slopes (e.g., the most negative).

[23] As indicated before, an oscillation of the NBSS slope value and the density was observed with a cycle of 24 hours at the coastal station during PEL2001 (Figure 6d). However, the oscillation existence is not verified for all the stations (Figure 6c, coastal station) and the oscillation duration is not constant (Figure 6c, open sea station).

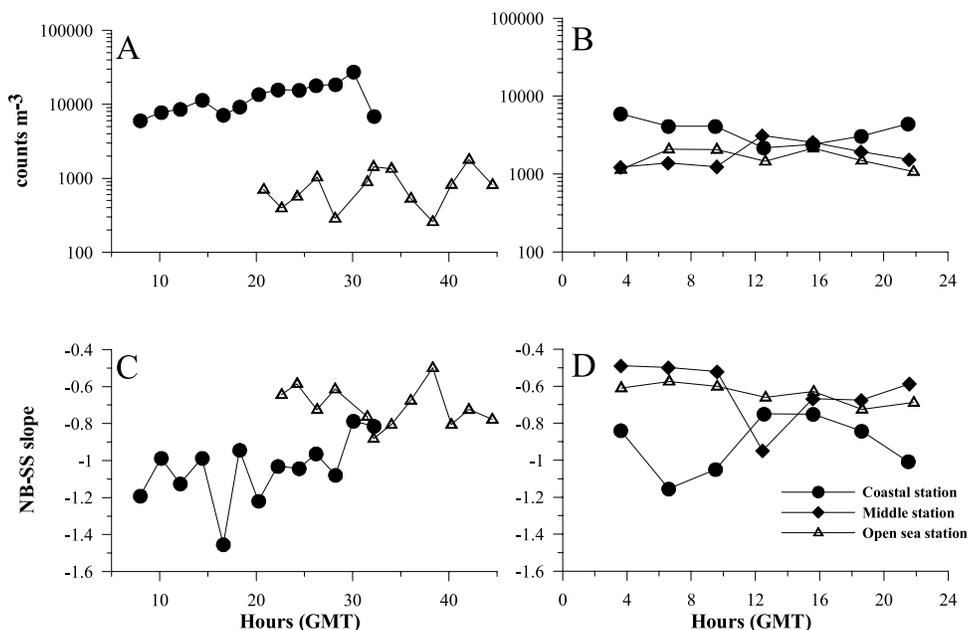


Figure 6. (a and b) Abundances and (c and d) NBSS slopes according to time (UT) for the fixed stations of PEL2000 and PEL2001, respectively. The circles, the diamonds, and the triangles represent the estimates at the samples of the coastal, the middle, and the oceanic station (see Figure 1), respectively.

3.3. Spatial Variation of the NBSS Slope at the Scale of the Bay of Biscay

[24] The spatial distribution of the OPC abundance estimates show a coastal/open sea gradient during the springtime with highest abundances in the coastal area for both years (Figure 7). This pattern appeared, less marked in 2000 than in 2001. In 2000, some high

concentrations were observed at the centre of the shelf and particularly on the transect in front of the Gironde estuary (transect 6). The 2000 spring time was also characterized by higher average concentrations (>30 individuals L⁻¹) than in 2001 (<10 individuals L⁻¹). In the north of the Bay of Biscay (transects from 12 to 17) the coastal/open sea gradient appeared also less marked with high

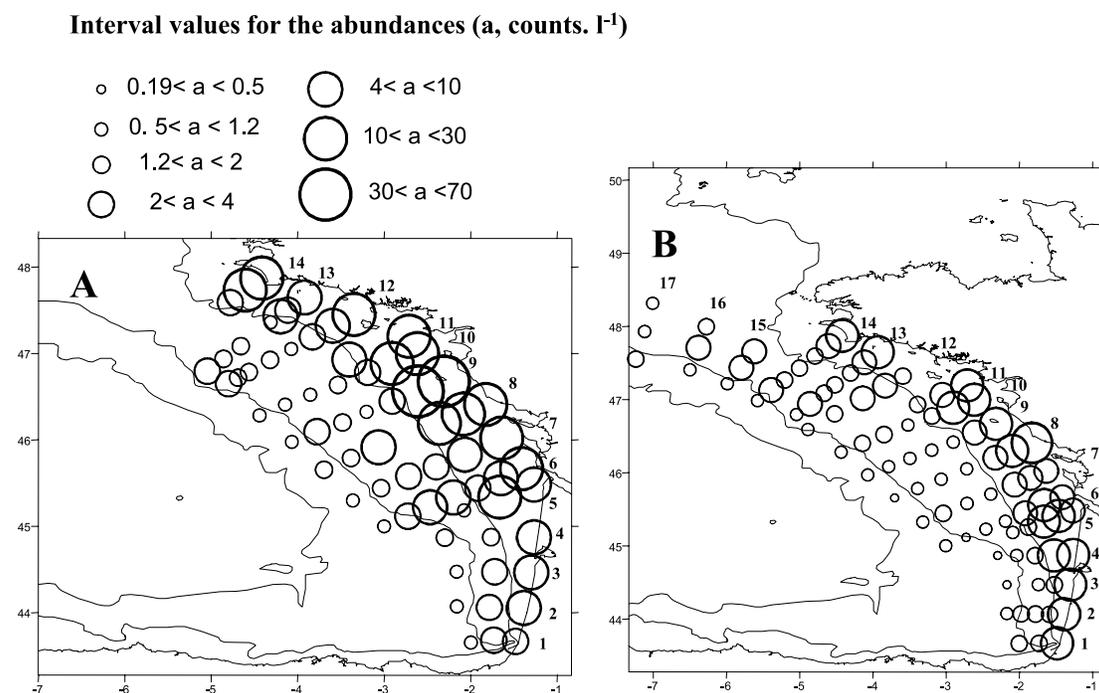


Figure 7. Abundances (counts L⁻¹) estimated by the OPC for each stations during (a) PEL2000 and (b) PEL2001 cruises.

Interval values for the NB-SS slopes (s)

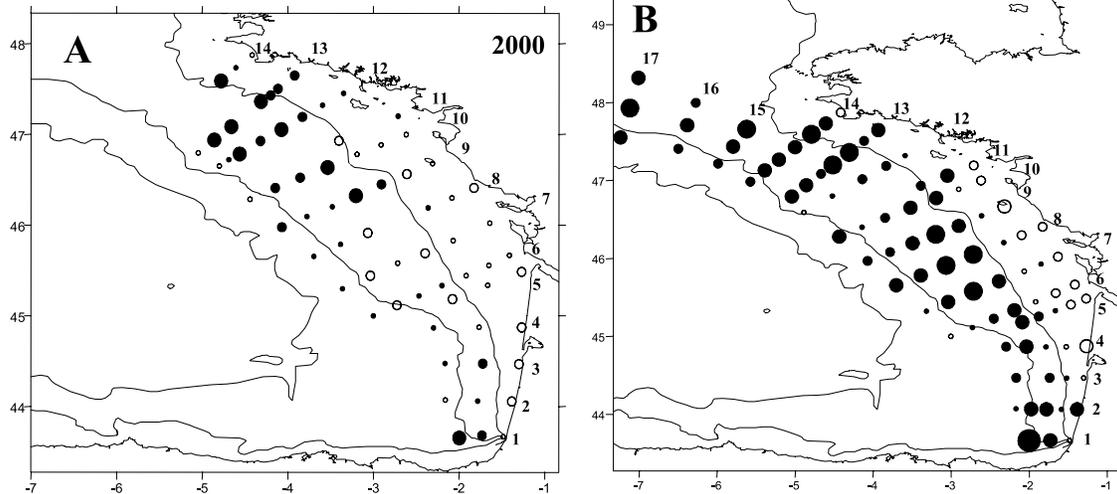
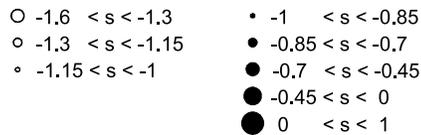


Figure 8. Values of the NBSS linear slopes for each station during (a) PEL2000 and (b) PEL2001 cruises.

concentrations near from the shelf break in 2000 and 2001 (2–4 individuals L^{-1}).

[25] Spatial patterns were also observed with the slope of the NBSS (Figure 8). The two spring time periods show a coastal/open sea gradient. The slopes were higher at the coastal stations (i.e., the proportion of small organisms was higher), and this fact was illustrated with the transect 8 of PEL2001 (Figure 9). The north of the bay (transects from 12 to 17) was also always characterized by low slope values all along the transects (<1 in 2000 and 2001) during the two cruises. The Capbreton Canyon (transect 1) was characterized by an important gradient. The slopes values varied around -1.1 in the coastal station to -0.7 in the open sea station for the 2 years. This result indicated a strong relation between bathymetry and the NBSS slope in this area.

[26] Some differences can be also highlighted between the two cruises. The slope values were higher during PEL2000 and notably in the middle of the shelf where no gradient was visible (transects 5 to 9).

3.4. Study of the Probability of Size Distributions

[27] Some linear distributions were observed (e.g., Figure 10a), but in most cases, the probability distributions of the size spectra show a nonlinearity with different dome (Figure 10b) or polynomial shapes (Figures 10c and 10d). This fact disagrees with the initial assumption of linear decrease that is a direct result of theoretical models. Within this size range and with a such size resolution, the community structure was thus far from an equilibrium state. By assuming an underestimation of the abundance in the small size classes, the second model (equation (3), Figure 11a) fitted thus better than that of a linear regression. Consequently, the estimates of the slope parameter were higher than the estimates determined for the NBSS. However, the

polynomial forms shown also that the shapes of the probability distribution were not only the result of an underestimation in the small size classes. The comparison of the two methods (NBSS and probability distributions) show also that this nonlinearity was obviously less visible when size classes were grouped (Figure 11b), even if the residuals of regression on the NBSS remained significantly autocorrelated for 95% of samples (tests result not presented).

4. Discussion

4.1. Measurement Quality

[28] The observed underestimation of the copepod ESD by the OPC, compared to binocular observations, was linked on the first hand with the random orientation of the copepod oblong shape in the beam and, on the other hand, with their transparency. This underestimation (16%) is in agreement with the results of *Herman* [1992] and *Beaulieu et al.* [1999], who noted a difference closed to 15% for the copepods. It justifies the ESD correction of 15% of ESD increase during the data processing. The density estimations are also reasonable by examining the preliminary tests results. The slight underestimation of the densities with the OPC at the coastal station could be explained by the smallest size of organisms in the coastal area compared to offshore stations and by the random orientation of the organisms body. However, the efficiency of abundance estimates by the OPC is already well known [*Herman*, 1992; *Sprules et al.*, 1992; *Beaulieu et al.*, 1999; *Wood-Walker et al.*, 2000]. We can thus assume that the variability of concentration estimates at fixed stations (Figure 4) is linked to differences in the subsampling required for the two methods (OPC and microscope) rather than to a problem of abundance estimate by the OPC. Size and abundance OPC

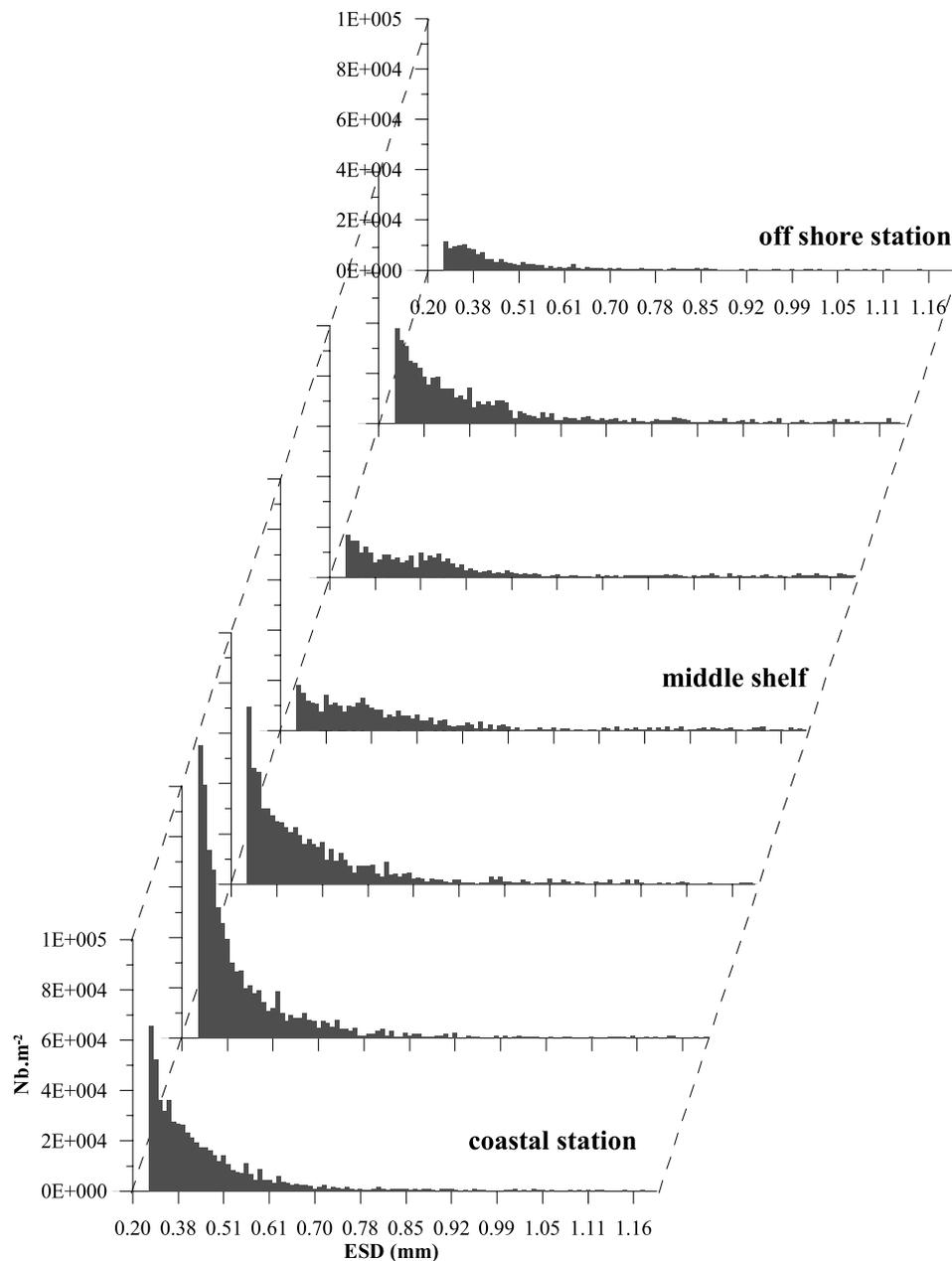


Figure 9. Spatial variation of size spectrum along the transect 8 of PEL2001.

measurements are thus clearly consistent and can be used to describe the size structure of the sampled zooplankton community. On a methodological point of view for the sample collection, *Gallienne and Robins* [2001] have, however, shown that the use of a plankton net with a 200 μm mesh size induces an underestimation in size classes lower than 500 μm of ESD, even though these classes represent the major part of the community in abundance term. At the difference of the in situ OPC, by using net tows we thus lose an important fraction of the zooplankton community. Furthermore, an underestimation can exist in the largest size classes due to avoidance effects. The destruction of fragile gelatinous organisms, such as appendicularians, can also introduce bias in the size structure

estimate. The biovolumes, the biomasses and the size structures estimate are also affected by the model to estimate the ESD [*Mustard and Anderson*, 2005] and the both length/width and length/carbon ratios. The biomasses and the volumes of zooplankton in the samples were, however, not compared with the OPC estimates because the first validation of ESD and abundance measurements appeared sufficient for our study. The use of the size spectrum as a zooplankton descriptor must be done cautiously by keeping in mind all these methodological problems.

[29] The nonlinear model, which was fitted with the size probability distributions (equation (3)), was used out of its initial aim because the origin of the nonlinearity was not

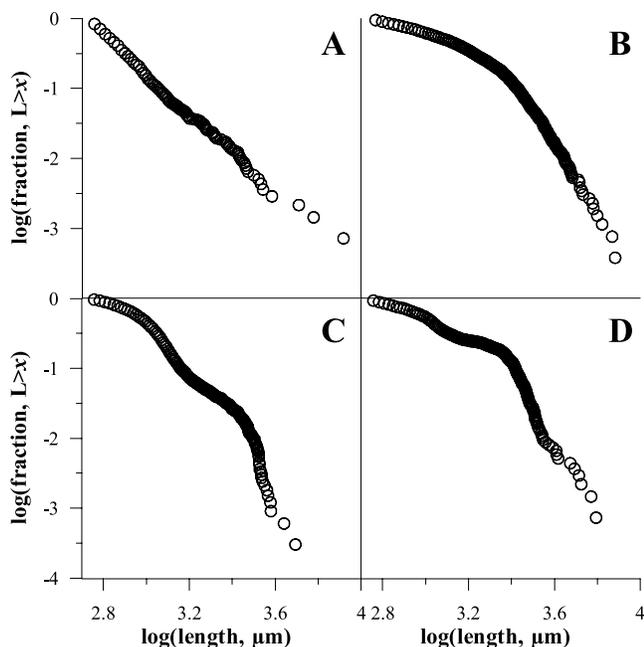


Figure 10. Patterns of length probability distributions for four stations (A, B, C, D: see Figure 1b). ESD were converted to length by assuming that the major part of the counted organisms is copepods with an average length/width ratio of 3.

only due to an underestimation of the abundance in the small size classes. The slopes were thus overestimated by this way and the estimates were not a better descriptor of the global size distribution than the values from the NBSS. Conversely to the nonlinear model, the artificial disappearance of the nonlinearity (i.e., the increase of the correlation coefficient) when grouping size classes, leads us to assume that the global information was included in the NBSS slope. The fitting of 4 order polynomial on the size probability distributions was also tested to describe the size structure. The first analyses of the parameters to

classify the spectra appeared not efficient (results not shown) and needed an extensive development.

4.2. Temporal and Spatial Variations of the Zooplankton Community Structure

[30] The temporal variations of NBSS slope at the 24 hour stations appears to be linked with fast variations of the total biomass ($\times 3$ in 2 hours). Thus these strong variations cannot be interpreted as being the result of a temporal dynamic of the same community (growth or mortality) or of day/night variation of the net capture efficiency. Finally, the vertical migration of the organisms could be responsible of the size structure variability only for the open sea stations (depth > 200 m). This is not the case in the coastal area because all the water column was sampled. Zooplankton size structure variations, observed at fixed stations are thus principally linked with advection and spatial heterogeneity. A smaller spatial and temporal study appears necessary to observe and to understand the temporal dynamics of the zooplankton community in this area characterized by a high diversity of physical events and extremely variable zooplankton communities [Poulet *et al.*, 1996].

[31] However, the spatial variability is greater than the temporal variability (Figures 6, 7, and 8). At the Bay of Biscay scale, the spatial patterns, highlighted during the two cruises, show strong characteristics of the zooplankton community. The coastal/open sea gradient of slope values and of organism densities is a constant observation and indicates important differences in the zooplankton community structure. Previous zooplankton community studies in the Capbreton area [d'Elbée, 2001] have also identified smallest (e.g., *Acartia sp.*, *Oithona sp.*, and *Oncaea sp.*) and largest copepods species (e.g., *Anomalocera sp.*, *Calanus sp.*, and *Candacia sp.*) in the coastal area and in the open sea, respectively. d'Elbée [2000] had also shown a coastal/open sea gradient of the biodiversity, as the NBSS slope in this study. In agreement with Poulet *et al.* [1996] observations, the NBSS slope thus confirms that the patterns of copepods were similar to those describe in others planktonic ecosystems of mixed and stratified waters characterizing the European shelf areas [Williams *et al.*, 1994]. The absence of this coastal gradient along the

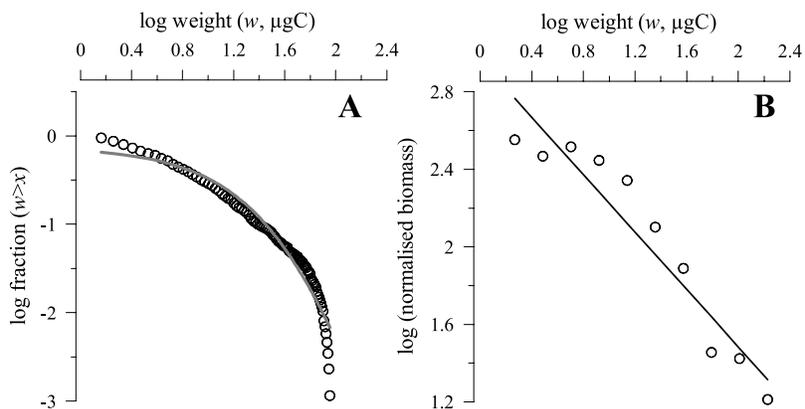


Figure 11. A size spectrum study for one sample. (a) Fitting of the nonlinear model on the probability distribution: $y = 4.8731 \times \log(-3.4464 + 55.6917) - 4.8731 \times \log(w + 55.6197)$. (b) Fitting of the linear model on the NBSS: $y = -0.7404 \times \log(w) + 2.9643$ ($r^2 = 0.9067$).

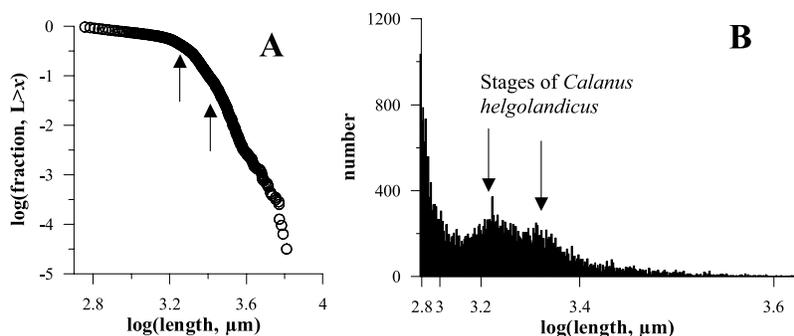


Figure 12. Detailed results for the open sea station in the Capbreton canyon: (a) sizes probability distribution and (b) abundances spectrum according to the measured organism size. The *Calanus helgolandicus* stages were determined under a microscope.

Northwest and North Iberian shelf [Nogueira *et al.*, 2004] can be explained by the short shelf. River flows and physical events thus appeared as the environment conditions acting upon the size structure of the zooplankton community.

[32] Our cruises duration have fluctuated around one month and thus first samples of each cruises were realized at the beginning of the growth season in contrast with the last samples, which were realized at the end of the growth season. In combination with the spatial variation, a temporal variation occurred in relation with the zooplankton dynamic. On the Spanish shelf of the Bay of Biscay, Villate [1991] have thus shown an increase of the average zooplankton size during the springtime. Furthermore, the sampling period was not exactly identical for the two cruises and differences in the spatial pattern between the two cruises could be also the result of temporal dynamics of the zooplankton community [Pedersen *et al.*, 2001]. This bias was, however, unavoidable, owing to the numerous constraints for such cruises (high spatial scale, numerous environment measurements).

4.3. Nonlinearity of the Size Spectrum

[33] In this study the observations of size spectra using the initial OPC resolution revealed also the nonlinearity of probability distributions. The communities were thus far from an equilibrium state according to the theoretical models [Sheldon *et al.*, 1972; Kerr, 1974; Platt and Denman, 1977; Lurie *et al.*, 1983]. The size range observed, however, was small (250 μm to 1.7 mm of ESD) compared to theoretical models assumptions, but this nonlinearity is not obvious to understand and can have several origins: methodological and biological. From the methodological point of view, the net used can introduce biases, but it should be, on the whole, constant over samples. The biological mechanisms are likely to be the main reasons of these deviations from the linearity because for particular stations, the distribution was directly related with marked population dynamics of dominant species. For the Capbreton station in the open sea (Figure 12), the dominant species, *Calanus helgolandicus*, was thus responsible of the probability distribution shape. So, there were some observable results of population dynamic inside of these size spectra even if in most of stations the distribution shapes do not have a simple explanation. The nonlinearity

also appears as additional information because it indicates abundances in particular size classes which are different from the expected densities at the equilibrium state.

4.4. Size Spectra Interpretation

[34] The measurements with the OPC-1L were faster than with a microscope but they had, however, the biases related to the sampling and processing methods as indicated above. As a consequence, an estimation of the rate of change in plankton biomass, as proposed by Zhou and Huntley [1997, equation 49], was not possible with our data. However, by assuming that allometric relationships described all the physiological rates (e.g., ingestion and respiration) [Fenchel, 1974], we can assume that the size spectrum slope is an instantaneous global descriptor of the matter flux efficiency inside of the community. Thus, with high slope values, the zooplanktonic community in coastal zone can be characterized by a lower efficiency of the matter flux than in open sea.

5. Conclusion

[35] Our results from the calibration were in agreement with previous studies [Herman, 1992; Gallienne and Robins, 1998; Beaulieu *et al.*, 1999; Woodd-Walker *et al.*, 2000] and thus our OPC measurements of both organism size and abundance appeared reliable. The OPC results highlight the nonlinear patterns of the spectra realized and also suggest that the NBSS slope is more efficient to describe the global size spectra shape rather than the use of the model parameter fitted on the probability distributions. By comparison to the standard analyses of net samples, the OPC use gives quickly a general description of the community structure. If required, and according to the general trend, the composition of particular samples can be next realized.

[36] The observed variability of the size spectra shape in the Bay of Biscay from this survey indicates some important variations of the zooplankton community structure which results from the high diversity of physical features on the French continental shelf. To understand the zooplankton dynamics in the Bay of Biscay, devoted studies with an adapted observation scale are now required. Despite their variability, our slope values, however, highlight the classical patterns of organisms size distribu-

tion which associate on the one hand large copepods, stratified waters and classical food web (diatoms-copepods), and on the other hand, small copepods, coastal mixed waters and dominated microbial food web. In agreement with several studies [Riandey *et al.*, 2006], size spectra appeared linked to environment conditions and, as suggested by Yurista *et al.* [2005], represents an interesting index for trophodynamics studies. Size spectra provided by an OPC is thus a new information quickly available and should be used regularly in the next years and introduced in databases to describe the environment.

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References

- Bailey, K. M., M. F. Canino, J. M. Napp, S. M. Spring, and A. L. Brown (1995), Contrasting years of preys levels, feeding conditions and mortality of larval walleye pollock *Theragra chalcogramma* in the western gulf of Alaska, *Mar. Ecol. Prog. Ser.*, 119, 11–23.
- Beaulieu, S. E., M. M. Mullin, V. T. Tang, S. M. Pyne, A. L. King, and B. T. Twining (1999), Using an optical plankton counter to determine the size distributions of preserved zooplankton samples, *J. Plankton Res.*, 21, 1939–1956.
- Blanco, J. M., F. Echevarria, and C. M. Garcia (1994), Dealing with size-spectra: some conceptual and mathematical problems, *Sci. Mar.*, 58(1–2), 17–29.
- Borja, A., A. Uriarte, J. Egaña, L. Motos, and V. Valencia (1998), Relationships between anchovy (*Engraulis encrasicolus*) recruitment and environment in the Bay of Biscay (1967–1996), *Fish. Oceanogr.*, 7, 375–380.
- Coombs, S., O. Giovanardi, D. Conway, L. Manzueto, N. Halliday, and C. Barret (1997), The distribution of eggs and larvae of anchovy (*Engraulis encrasicolus*) in relation to hydrography and food availability in the outflow of the river Po, *Acta Adriat.*, 38(1), 33–47.
- d'Elbée, J. (2001), Distribution et diversité des copépodes planctoniques dans le golfe de Gascogne, in *Océanographie du Golfe de Gascogne, VIIe Colloqure International, Biarritz, 4–6 Avril 2000*, coordinated by J. d'Elbée and P. Prouzet, *Ifremer Actes Colloq.*, 31, 147–156.
- Daskalov, G. (1999), Relating fish recruitment to stock biomass and physical environment in the Black Sea using generalized additive models, *Fish. Res.*, 41, 1–23.
- Edwardsen, A., M. Zhou, K. S. Tande, and Y. Zhu (2002), Zooplankton population dynamics: measuring in situ growth and mortality rates using an optical plankton counter, *Mar. Ecol. Prog. Ser.*, 227, 205–219.
- Fenchel, T. (1974), Intrinsic rate of natural increase: The relationship with body size, *Oecologie*, 14, 317–326.
- Gallienne, C. P., and D. B. Robins (1998), Trans-oceanic characterization of zooplankton community size structure using an optical plankton counter, *Fish. Oceanogr.*, 7, 147–158.
- Gallienne, C. P., and D. B. Robins (2001), Is *Oithona* the most important copepod in the world's oceans?, *J. Plankton Res.*, 23, 1421–1432.
- Grant, S., P. Ward, E. Murphy, D. Bone, and S. Abbott (2000), Field comparison of an LHPR net sampling system and an optical plankton counter (OPC) in the Southern Ocean, *J. Plankton Res.*, 22, 619–638.
- Heath, M. R. (1995), Size spectrum dynamics and planktonic ecosystem of Loch Linnhe, *J. Mar. Sci.*, 52, 627–642.
- Herman, A. W. (1988), Simultaneous measurement of zooplankton and light attenuation with a new optical plankton counter, *Cont. Shelf Res.*, 8, 205–221.
- Herman, A. W. (1992), Design and calibration of a new optical plankton counter capable of sizing small zooplankton, *Deep Sea Res.*, 39, 395–415.
- Horwood, J., D. Cushing, and T. Wyatt (2000), Planktonic determination of variability and sustainability of fisheries, *J. Plankton Res.*, 22, 1419–1422.
- Huntley, M. E., M. Zhou, and W. Nordhausen (1995), Mesoscale distribution of zooplankton in the California Current in late spring, observed by optical plankton counter, *J. Mar. Res.*, 53, 647–674.
- Kerr, S. R. (1974), Theory of size distribution in ecology communities, *J. Fish. Res. Board Can.*, 31(12), 1859–1862.
- Kjørboe, T., P. Munk, K. Richardson, V. Christensen, and H. Paulsen (1988), Plankton dynamics and larval herring growth, drift and survival in a frontal area, *Mar. Ecol. Prog. Ser.*, 44, 205–219.
- Lurie, D., J. Valls, and J. Wagensberg (1983), Thermodynamic approach to biomass distribution in ecological systems, *Bull. Math. Biol.*, 45, 287–293.
- Mauchline, J. (1998), *The Biology of Calanoid Copepods*, *Adv. Mar. Biol.*, vol. 33, 710 pp., Elsevier, New York.
- McFadzen, I. R. B., and G. Franceschini (1997), The nutritional condition of larvae of anchovy (*Engraulis encrasicolus* L.) in the outflow of the River Po (northern Adriatic), *Acta Adriat.*, 38(1), 49–64.
- Michaud, J., L. Fortier, P. Rowe, and R. Ramseier (1996), Feeding success and survivorship of Arctic cod larvae, *Boreogadus saida*, in the Northeast Water polynya (Greenland Sea), *Fish. Oceanogr.*, 5, 120–135.
- Motos, L., P. Alvarez, and A. Uriarte (2000), Distribution pattern of hake (*Merluccius* (L.)) eggs and larvae in relation to environmental conditions in the Bay of Biscay in winter and early spring 1995, *Bol. Soc. Oceanogr. Gipuzkoa*, 3, 273–292.
- Mustard, A. T., and T. R. Anderson (2005), Use of spherical and spheroidal models to calculate zooplankton biovolume from particle equivalent spherical diameter as measured by an optical plankton counter, *Limnol. Oceanogr. Methods*, 3, 183–189.
- Nogueira, E., G. González-Nuevo, A. Bode, M. Varela, X. A. G. Morán, and L. Valdés (2004), Comparison of biomass and size spectra derived from optical plankton counter data and net samples: application to the assessment of mesoplankton distribution along the northwest and North Iberian Shelf, *J. Mar. Sci.*, 61, 508–517.
- O'Connell, C. P., and L. P. Raymond (1970), The effect of food density on survival and growth of early post yolk-sac larvae of the northern anchovy (*Engraulis mardax*) in the laboratory, *J. Explor. Mar. Biol. Ecol.*, 5, 187–197.
- Omori, M., and T. Ikeda (1984), *Methods in Marine Zooplankton Ecology*, 332 pp., John Wiley, Hoboken, N. J.
- Pedersen, O., K. Tande, and D. Slagstad (2001), A model study of demography and spatial distribution of *Calanus finmarchicus* at the Norwegian coast, *Deep Sea Res., Part II*, 48, 567–587.
- Pepin, P. (1991), Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish, *Can. J. Fish. Aquat.*, 50, 133–142.
- Platt, T., and Q. Denman (1977), Organisation in the pelagic ecosystem, *Helgoländer Meeresun.*, 30, 575–581.
- Plounevez, S., and G. Champalbert (1999), Feeding behaviour and trophic environment of *Engraulis encrasicolus* in the Bay of Biscay, *Estuarine Coast. Shelf Sci.*, 49, 177–191.
- Poulet, S. A., M. Laabir, and Y. Chaudron (1996), Characteristic features of zooplankton in the Bay of Biscay, *Sci. Mar.*, 60(2), 79–95.
- Riandey, V., G. Champalbert, F. Carlotti, I. Taupier-Letage, and D. Thibault-Bota (2006), Mesoscale variability of the zooplankton distribution related to the hydrodynamic features in the Algerian Basin (western Mediterranean Sea), *Deep Sea Res., Part I*, 52, 2029–2948.
- Rodríguez, J., and M. M. Mullin (1986), Relation between biomass and body weight of plankton in a steady state oceanic ecosystem, *Limnol. Oceanogr.*, 31, 361–370.
- Ruiz, A., and L. Motos (2000), Spatial distribution of mesozooplankton in the spawning area of anchovy (*Engraulis encrasicolus*) in the Bay of Biscay. Implications on the anchovy population, *Bol. Soc. Oceanogr. Gipuzkoa*, 3, 233–272.
- Runge, J. A., and Y. de Lafontaine (1996), Characterization of the pelagic ecosystem in the surface waters of the northern Gulf of St Lawrence in early summer: The larval redfish–*Calanus*-microplankton interaction, *Fish. Oceanogr.*, 5, 19–38.
- Sheldon, R. W., A. Prakash, and W. H. J. Sutcliffe (1972), The size distribution of particles in the ocean, *Limnol. Oceanogr.*, 17, 327–340.
- Sprules, W. G., B. Bergstrom, H. Cyr, B. R. Hargreaves, S. S. Kilham, H. J. MacIsaac, K. Matsushita, R. S. Stemberger, and R. Williams (1992), Non-video optical instruments for studying zooplankton distribution and abundance, *Arch. Hydrobiol. Ergeb. Limnol.*, 36, 45–58.
- Vidondo, B., Y. T. Prairie, J. M. Blanco, and C. M. Duarte (1997), Some aspects of the analysis size spectra in aquatic ecology, *Limnol. Oceanogr.*, 42, 184–192.
- Villate, F. (1991), Annual cycle of zooplankton community in the Abra Harbour (Bay of Biscay): abundance, composition and size spectra, *J. Plankton Res.*, 13, 691–706.
- Williams, R., D. V. P. Conway, and H. G. Hunt (1994), The role of copepods in the planktonic ecosystems of mixed and stratified waters of the European shelf seas, *Hydrobiology*, 292/293, 521–530.
- Woodd-Walker, R. S., C. P. Gallienne, and D. B. Robins (2000), A test for optical plankton counter (OPC) coincidence and a comparison of OPC-

- derived and conventional measures of plankton abundance, *J. Plankton Res.*, 22, 473–483.
- Yurista, P., J. R. Kelly, and S. Miller (2005), Evaluation of optically acquired zooplankton size-spectrum data as potential tool for assessment of condition in Great Lakes, *Environ. Manage.*, 35, 34–44.
- Zhou, M., and M. E. Huntley (1997), Population dynamics theory of plankton based on biomass spectra, *Mar. Ecol. Prog. Ser.*, 159, 61–73.
- Zhou, M., and K. Tande (Eds.) (2001), *Global Ocean Ecosystem Dynamics, Optical Plankton Counter Workshop, GLOBEC Rep. 17*, 67 pp., GLOBEC Int. Proj. Off., Plymouth, U.K. (Available at <http://www.pml.ac.uk/globec/products/reports/globecrep.htm>)
- Zhou, M., Y. Zhu, S. Putman, and J. O. Peterson (2001), Mesoscale variability of physical and biological fields in the southeastern Lake Superior, *Limnol. Oceanogr.*, 46, 679–688.
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