

**PARTICLE FLUX TRANSFORMATION IN THE MESOPELAGIC
WATER COLUMN: PROCESS ANALYSIS AND GLOBAL
BALANCE**

A Dissertation

by

LIONEL GUIDI

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2008

Major Subject: Oceanography

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Approved by:

Co-Chairs of Committee,	George A. Jackson Gabriel Gorsky
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ABSTRACT

Particle Flux Transformation in the Mesopelagic Water Column: Process Analysis and Global Balance. (May 2008)

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Co-Chairs of Advisory Committee: Dr. George Jackson
Dr. Gabriel Gorsky

Marine aggregates are an important means of carbon transfers downwards to the deep ocean as well as an important nutritional source for benthic organism communities that are the ultimate recipients of the flux. During these last 10 years, data on size distribution of particulate matter have been collected in different oceanic provinces using an Underwater Video Profiler. The cruise data include simultaneous analyses of particle size distributions as well as additional physical and biological measurements of water properties through the water column.

First, size distributions of large aggregates have been compared to simultaneous measurements of particle flux observed in sediment traps. We related sediment trap compositional data to particle size (d) distributions to estimate their vertical fluxes (F) using simple power relationships ($F = A \cdot d^b$). The spatial resolution of sedimentation processes allowed by the use of in situ particle sizing instruments lead to a more detailed study of the role of physical processes in vertical flux.

Second, evolution of the aggregate size distributions with depth was related to overlying primary production and phytoplankton size-distributions on a global scale. A new clustering technique was developed to partition the profiles of aggregate size distributions. Six clusters were isolated. Profiles with a high proportion of large aggregates were found in high-productivity waters while profiles with a high proportion of small aggregates were located in low-productivity waters. The aggregate size and mass flux in the mesopelagic layer were correlated to the nature of primary producers

(micro-, nano-, picophytoplankton fractions) and to the amount of integrated chlorophyll *a* in the euphotic layer using a multiple regression technique on principal components.

Finally, a mesoscale area in the North Atlantic Ocean was studied to emphasize the importance of the physical structure of the water column on the horizontal and vertical distribution of particulate matter. The seasonal change in the abundance of aggregates in the upper 1000 m was consistent with changes in the composition and intensity of the particulate flux recorded in sediment traps. In an area dominated by eddies, surface accumulation of aggregates and export down to 1000 m occurred at mesoscale distances (<100 km).

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TABLE OF CONTENTS

	Page
ABSTRACT	iii
ACKNOWLEDGMENTS.....	v
TABLE OF CONTENTS	vii
LIST OF TABLES	ix
LIST OF FIGURES.....	xi
 CHAPTER	
I GENERAL INTRODUCTION	1
1.1. What do we know about aggregate properties?	5
1.2. Aggregate sources.....	8
1.3. Processes of export and recycling of aggregate	11
1.4. Sampling techniques and flux measurements	18
1.5. Instrument	21
1.6. Instrument inter-calibration	27
1.7. Database organization.....	29
1.8. Numerical data treatment.....	32
II A NEW PROCEDURE TO OPTIMIZE THE SELECTION OF GROUPS IN A CLASSIFICATION TREE.....	33
2.1. Introduction.....	33
2.2. Procedures.....	34
2.3. Assessment.....	39
2.4. Discussion.....	46
2.5. Comments and recommendations	49
III PARTICLE SIZE DISTRIBUTION AND FLUX IN THE MESOPELAGIC: A CLOSE RELATIONSHIP.....	51
3.1. Introduction.....	51
3.2. Material and methods.....	54
3.3. Results.....	58
3.4. Discussion.....	62
3.5. Conclusion	69

CHAPTER	Page
IV PRIMARY PRODUCER COMMUNITY EFFECT ON PRODUCTION AND EXPORT OF LARGE AGGREGATES: A GLOBAL ANALYSIS	71
4.1. Introduction.....	71
4.2. Material and methods.....	73
4.3. Results.....	81
4.4. Discussion.....	90
V VERTICAL DISTRIBUTION OF AGGREGATES (>110 μ M) AND MESOSCALE ACTIVITY IN THE NORTHEASTERN ATLANTIC: EFFECTS ON THE DEEP VERTICAL EXPORT OF SURFACE CARBON	96
5.1. Introduction.....	96
5.2. Materials and methods	98
5.3. Results.....	101
5.4. Discussion.....	111
VI GENERAL CONCLUSION AND PERSPECTIVE.....	119
6.1. Main results.....	119
6.2. Remaining key questions	121
REFERENCES.....	126
APPENDIX A ARTICLE A	147
APPENDIX B ARTICLE B.....	148
APPENDIX C ARTICLE C.....	149
APPENDIX D ARTICLE D	150
APPENDIX E ARTICLE E	151
APPENDIX F ARTICLE F.....	152
VITA	153

LIST OF TABLES

	Page
Table 1: Summary of parameters used for the pixel to millimeter size conversion. The water volume recorded by each image and the minimum aggregate size that each UVP generation can measure is also given.	25
Table 2: Definition of the 27 aggregate size classes used in this work.	30
Table 3: Description of the main field used in the UVP database. Additional variables are not mentioned in this listing. When an instrument is composed of two cameras, fields ending in ‘0’ for the first camera have sisters fields ending in ‘1’ for the second camera.	31
Table 4: Comparisons of the Calinski and Harabasz index and, RST method sensitivity to 4 different cluster analyses, (S) simple link, (C) complete link, (U) UPGMA and, (W) Ward’s minimum variance procedure, considering the number of groups in the datasets. The total number of tested dataset by clustering analyses and number of groups is 27. ‘-1’ and ‘-2’ denote that the method detected one or two groups in less in comparison to the true number of groups while ‘+1’, ‘+2’ and ‘+3’ mean that the method identified one, two or three or more groups in more in comparison to the true number of groups	42
Table 5: Two examples showing the effects of outliers on Calinski and Harabasz index (C&H) and RST technique using the dataset generated by the algorithm of Milligan and Cooper (1985). The example a) is composed by 4 clusters whereas the example b is composed by 3 clusters. Both examples contain 50 observations and 10 outliers (20%) in the dataset. The real clusters of data are shown in the first part of the table and the corresponding results obtained with the C&H index and the RST are shown in the second and third part of the table, respectively.	43
Table 6: Non exhaustive literature review on the determination of the number of cluster using Fisher’s dataset.	48
Table 7: List of parameters and their dimension (M for mass, L for length, T for time)	52
Table 8: Definition of the size range and volume sampled characteristics of the 3 different Underwater Video Profilers (UVP) used in this study.	54
Table 9: Location, position, and duration of the deployments of the sediments trap used in this study. References: A- (Guieu et al. 2005); B- (Stemmann et al. 2002); C -Miquel and Gasser, submitted.	56

Table 10: Coefficient (A) and exponent (b) and their associated standard deviation (STD) of the empirical relationship between the aggregate size and their related mass, particulate organic carbon (POC), particulate inorganic carbon (PIC) and particulate organic nitrogen (PON) fluxes determinate by minimization of the fluxes estimation by the Underwater Video Profiler (UVP) and the sediment traps measurement, $n=118$	60
Table 11: Distribution of profiles within clusters for each cruise. The numbers in the C columns indicated the number of profiles that fall into the cluster.....	78
Table 12: Spearman correlation between 4 parameters of the aggregate size distribution ($n=410$), all correlation were significant.....	81
Table 13: Phytoplankton size structure (% of f_{micro} , f_{nano} , f_{pico}) and integrated chlorophyll a content (B_a) in the Z_e compared to the total aggregate flux below the euphotic layer at 400 m: F400.....	86
Table 14: Components from PCA of descriptors, sorted by their decreasing r^2 , correlation with the flux at 400m; r^2 values and probability (p) associated. Component selected for the PCR are in bold. Model's coefficient and their confidence interval after the multiple regression between the 7 descriptors (f_{micro} , f_{nano} , f_{pico} , B_{micro} , B_{nano} , B_{pico} , B_a) and the aggregate flux at 400m (F_{400}) summarized in the 2 last columns.....	90
Table 15: Cruises and UVP characteristic uses for all profiles	100
Table 16: Spearman correlation coefficient between integrated aggregate concentrations and integrated pigment concentrations in the 40-60 m layer.....	109

LIST OF FIGURES

Page

Figure 1: Biological pump and processes regulating the flux of particles in the ocean. CO ₂ fixed during photosynthesis by phytoplankton can be transferred below the surface mixed layer via three major processes, (1) passive sinking of particles, (2) physical mixing of particulate and dissolved organic matter, and (3) active transport by zooplankton vertical migration. The remineralization returns carbon and nutrients to dissolved forms (Figure from Buesseler et al. 2007a).....	3
Figure 2: UVP video images with macrozooplankton groups; appendicularians (App.), Thaliacae (Thal.; salp and doliolid), Fish, Haliscera spp medusa (Hal.), Solmundella bittentaculata (Sol.), Aglantha spp. (Agl.) Aeginura grimaldii (Gri.) and ‘other medusae’ (Med.), chaetognath (Chaet.), lobate ctenophore (Lob.), cydippid ctenophore (Cyd.), siphonophore (Siph.), crustaceans (Crust.; decapod and amphipod), single cell sarcodine grouped by four (RadioCS.), colonial radiolarians (RadioC.), colonial radiolarians with double line (RadioCD.), Phaedorian (Phaeo.), single cell sarcodine with spines (Spine.), double cell sarcodine with spines (Spine2.), spheres (Sphere.) and sarcodine with hairs (Stars.). The scale bar represents approximately 1 cm. Additional images can be viewed at http://www.obs-ovfr.fr/LOV/ZooPart/Gallery/ . (Figure from Stemmann et al. Accepted).....	4
Figure 3: Floating sediment trap deployment during the BIOSOPE cruise in the Southeastern Pacific	18
Figure 4: Illustration of the last version of the Underwater Video Profiler.....	22
Figure 5: Example of data used for the calculation of the conversion equation from pixel to millimeter size measurement. Each color corresponds to an object type.....	24
Figure 6: Example of curve of light intensity registered at one point of the grid used for the calculation of the water volume sampled by one image.....	25
Figure 7: Complete set of light intensity curve obtained at every point of the grid. The greens curves correspond to the light intensity spectrum from the stroboscope 1. Reds light intensity spectrum came from stroboscope number 2. Blue curves correspond to the sum of the 2 stroboscopes.	26

Figure 8:	Mean aggregate size distribution obtained with 4 UVP generations between 75 and 150 m. A) Combined profiles made by UVP 4a and 2c. B) Aggregate size distribution from the DYFAMED site in the Mediterranean Sea in May 1995 for UVP 2a and May 2003 for PVM 4a. C) Aggregate size distribution from the DYFAMED site from UVP 3b deployment in October 1993 and from UVP 2a in October 1993 and 1994.....	28
Figure 9:	Profiles location of UVP (black circles), CTD (red dots), and pigment profiles (green squares)	32
Figure 10:	Schematic representation of the successive steps of the Random Simulation Test (RST).....	37
Figure 11:	Result of the Calinski and Harabasz stopping rules applied on the Iris dataset between 2 and 21 clusters solutions.	39
Figure 12:	(A) Frequencies distribution of the number of cluster for the ecological dataset of Beaugrand et al. (2002). (B) Dendrogram of calanoid copepod species resulting from the flexible hierarchical clustering method used by Beaugrand et al., (2002). Underlined taxa have indicator value inferior to 25%. Groups (at the distance cut-off level of 1.152) are indicated in pale grey. Subgroups (distance cut-off level of 0.53) are indicated in dark grey. Numbers underlined and in italic represent the number of taxa for each group. Some characteristics of each group are given in grey and italic. Underlined species are species rarely collected by the Continuous Plankton Recorder survey. The dashed grey lines are cut-off levels empirically chosen by Beaugrand et al. (2002). Dark lines are the cut-off levels determined by the Random Simulation Test (0.56 and 0.45).....	45
Figure 13:	Location of all Underwater Video Profiler (UVP) profiles (red crosses) and associated sediment trap deployments (black stars). There were 1254 total profiles and 11 associated sediment trap locations.	55
Figure 14:	Comparison of measured sediment trap mass flux with that calculated using size spectra and Alldredge and Gotschalk (1988) relationships (n=118). Symbols represent trap deployments depths: 100 m - open squares, 200m - open circles, 300m - open stars, 400m - black dots and 1000m - crosses.....	58

- Figure 15: Measurement of the mass (A), particulate organic carbon (POC: B), particulate inorganic carbon (PIC: C) and particulate organic nitrogen (PON: D) fluxes by sediment traps, compared to the estimation of the mass, POC, PIC, PON fluxes using the UVP and the relationships between the aggregates size and the previous fluxes (cf Eq. 15,16,17 and 18) $n=118$. Symbols represent trap deployments depths: 100 m - open squares, 200m - open circles, 300m - open stars, 400m - black dots and 1000m - crosses..... 59
- Figure 16: Ratio of estimates and measurements of the A) mass fluxes, B) POC fluxes, C) PIC fluxes, D) PON fluxes as function of the depth of sediment traps..... 61
- Figure 17: Residual error ΔF as a function of values of A, b for the mass flux F_m . The best fit values were $A=109.5$ and $b=3.52$. Darker regions represent greater values for ΔF in $\text{mg m}^{-2} \text{d}^{-1}$. The crosses correspond to the values calculated during the jackknife error analysis. They are all located in the area where the residues are the smallest. 62
- Figure 18: A) Particle settling speed function of particle diameter measured by different authors (from Stemmann et al. 2004b). Circle: (Smayda 1970), triangle: (Shanks and Trent 1980), diamond: (Carder et al. 1982), square: (Azetsu-Scott and Johnson 1992). Empirical relationships, 1—(Alldredge and Gotschalk 1988), 2—(Alldredge and Gotschalk 1989), 3—(Syvitski et al. 1995), 4—(Diercks and Asper 1997). Settling speeds calculated using the coagulation model (Stemmann et al. 2004b) with different parameter values (5— $\Delta\rho = 0.08$, $D=2.33$; 6— $\Delta\rho = 0.01$, $D=1.79$) are also reported. The regression line 7 is the settling speed predicted by Stokes Law. The dashed line 8 is the settling speed calculated in this paper. B) Typical number spectrum from the UVP database profiles. C) Normalized cumulative flux calculated on the number spectrum (B) with the mass flux relationship Eq. 20, the black line represents the 50% of the mass flux..... 66
- Figure 19: Sediment trap mass flux measurement below the euphotic zone in $\text{mg m}^{-2} \text{d}^{-1}$ along 150°W (black asterisk) redrawn from (Raimbault et al. 1999) compared to estimated mass flux from aggregates size distribution along 180°W (gray bars)..... 68

Figure 20: Estimation of the mass flux for a radial 180°W in the Equatorial Pacific Ocean, based on the size aggregate distribution. $A=109.5$ and $b=3.52$ for the size to mass flux relationship (Table 10). The dots correspond to the sampling grid.	69
Figure 21: Samples location of UVP (black circles), CTD (red dots), and pigment profiles (green squares)	74
Figure 22: Comparison of different measures of the number distribution: b (slope of the number distribution), d_{25} (Equivalent spherical diameter (ESD) relative to 25% of the cumulative volume distribution), d_{50} (ESD relative to 50% of the cumulative volume distribution), d_{75} (ESD relative to 75% of the cumulative volume distribution). An example of measurements on one distribution (A and B), the 4 measurements correspond to 1 point in C). A) Cumulative volume distribution. B) Number spectrum n from which b was calculated. C) Relationship between b and d_{25} , d_{50} , and d_{75}	76
Figure 23: Slope profiles based on the particle size distribution, divided into 6 patterns. The Euclidean distance and the flexible link were used for the classification. Number of clusters were selected with the random simulation test (RST) (A to F for clusters 1 to 6).....	83
Figure 24 : Location of the 6 patterns of the slope profiles based on the particle size distributions of aggregates in the water column (A to F for clusters 1 to 6).....	84
Figure 25: Phytoplankton size classes related to the estimated flux at 400 m. A) Micro-phytoplankton fraction (f_{micro}) in color: chlorophyll a integrated over Z_e (B_a) versus total flux at 400 m (F_{400}). B) Same parameters for nano-phytoplankton (f_{nano}) in color. C) Same parameters for pico-phytoplankton (f_{pico}) in color.	87
Figure 26: Flux in the mesopelagic zone. A) Ternary plot of total aggregate flux at 400 m (F_{400}) B) Ternary plot of the aggregate mass flux fraction estimated at 1000 m compared to the estimated aggregate mass flux below Z_e . Both calculation are related to the phytoplankton structure in Z_e (f_{micro} , f_{nano} , f_{pico} in fractions).....	88
Figure 27: Selected components (C) of PCA for PCR. The solid line corresponds to the coefficient of determination R^2 of the multiple regression. The dashed line corresponds to the R^2 progression by successive component addition.	89
Figure 28: Flux measurement vs flux modeled by the PCR, $n=193$	91

Figure 29: Study area in the Northeastern Atlantic. The dashed line is the approximate location of the zone of discontinuity of the winter mixed layer associated with subduction of mode water masses. 98

Figure 30 : Sampling grid during the three POMME cruises. Locations of CTDs, shown by open circles, UVP stations by closed circles, and long stations and sediment traps by open squares. 99

Figure 31: Geopotential anomalies at 300m calculated from hydrographic data during (A) winter, (B) spring, and (C) summer calculated from the sampling grid. The squares represent the locations of the UVP profiles. The black circles represent the positions where high stocks of aggregates were observed in the mesopelagic layer during winter and spring. These positions correspond to the locations where the 400-800 m integrated concentrations exceeded 5 times the surrounding integrated concentrations. These calculations were not performed for the summer cruise because of the lack of data deeper than 500 m. 101

Figure 32: 3D maps of density field during (A) winter, (B) spring, and (C) summer and vertical sections of sea-water density in (D) winter, (E) spring, and (F) summer as inferred from all the CTDs. The MLD is marked by the black continuous line in both the section and 3D maps and the mode water is located between the 2 white continuous lines. The station numbers where the UVP was deployed are given above each section. The ship tracks are given on the maps on the left of each section. The continuous and dotted lines on each map are repeated under each section in order to help the reader to localize itself. The arrows point at the start of the track. 103

Figure 33: Median vertical profiles, and first and third quartiles, of aggregate mass during the three cruises: winter (n=36), spring (n=43) and summer (n=41). Note that for the summer profiles, median values deeper than 500 m were calculated using only 6 available UVP profiles. 105

Figure 34: 3D maps of seasonal changes in the vertical distribution of aggregates in (A) winter, (B) spring, and (C) summer, and vertical sections of aggregate distribution along the ship tracks in (D) winter, (E) spring, and (F) summer, in mg dry wt m⁻³. The station numbers where the UVP was deployed are given above each section. The color scale emphasizes variability at the lower end of the concentration range. The depth of the isomass of aggregates 8 mg m⁻³ is given by the white line. The ship tracks are given on the maps on the left of each section. The continuous and dotted lines on each map are repeated under each section in order to help the reader to localize itself. The arrows point at the start of the track. 107

- Figure 35: Vertically integrated concentrations of aggregates as a function of vertically integrated Chl a in three phytoplankton groups during the different cruises for the 0-200 m layer. 108
- Figure 36: Integrated concentration of total Chl a (mg Chl a m^{-2} , 0-200 m) during (A) winter, (B) spring, and (C) summer calculated from the sampling grid. Squares represent the locations of the UVP profiles. The black circles represent the positions where high stocks of aggregates were observed in the mesopelagic layer during winter and spring. These positions correspond to the locations where the 400-800 m integrated concentrations exceeded 5 times the surrounding integrated concentrations. These calculations were not performed for the summer cruise due to the lack of data deeper than 500 m. 110
- Figure 37: Figure modified from Guidi et al. (in revision). Comparison between UVP potential mass fluxes and mass fluxes from sediment traps at (A) 400 m and (B) 1000 m. Potential fluxes from UVP using Alldredge and Gotschalk (1988) in black circles and using relationship presented in chapter III in red circles. The sediment traps were corrected for trapping efficiency, which was estimated to range from 20 to 50% (Guieu et al. 2005). 111
- Figure 38: From Uitz et al. 2006. Phytoplankton community composition for June 2000 (SeaWiFS composite): (a-c) phytoplankton fractions (fmicro, fnano and fpico in %) within the 0-1.5 Ze layer, and (d-f) integrated contents within the same layer (Bmicro, Bnano and Bpico in mg m^{-2}). Coastal areas (less than 200 m deep), large lakes and inland seas are represented in white. 123

CHAPTER I

GENERAL INTRODUCTION

Understanding the effect of food web dynamics on biogeochemical cycles is the central issue of the international IMBER (Integrated Marine Biogeochemistry and Ecosystem Research) program. The subjects developed in this PhD dissertation are central to this goal, dealing with the transfers of matter across oceans interfaces. Biogeochemical processes differ among environments such as continental slopes, regions with active convection, regions with dynamic mesoscale features enhancing local biological production and oligotrophic central gyres. There is a general agreement that the response of the biogeochemical cycles to environmental changes needs to be understood better. Studies that compare processes impacting the characteristics and the vertical transfer of particulate matter in different environments may significantly ameliorate our knowledge on the fate of the surface biological production.

One of the results of international programs studying vertical fluxes, such as VERTEX and Joint Global Ocean Flux Study (JGOFS), was that an average of 10% or more of the surface oceanic production is exported below the mixed layer depth. The main export is by large particulate matter, notably aggregates with diameters > 100 μm . However, only 1 to 10% of this matter falls below 1000 m depth, where is isolated from the surface for long periods (Berelson 2001; Martin et al. 1987; Suess 1980).

Marine aggregates are a key factor of the ocean's carbon cycle at different scales. At the macroscale, marine aggregates are an important means of transferring carbon downwards to the deep ocean by the way of the biological pump. At the microscale, they provide dissolved and particulate food to micro and macro-organisms living in the aphotic layer of the ocean (Alldredge 2000; Lampitt et al. 1993b). Aggregates are an especially important nutritional source for benthic communities that are the ultimate recipient of the flux (Buesseler et al. 2007a; Figure 1).

This dissertation follows the style of Limnology and Oceanography.

The largest fraction of exported surface production is remineralized in the meso-pelagic zone by mechanisms about which we know little (Boyd and Trull 2007; Buesseler et al. 2007b; Stemmann et al. 2004b). Most coupled climate biogeochemical models do not consider the interaction between dissolved matter, colloids, aggregates, and organisms. They use empirical parameterizations which ignore the importance and details of physical and biological processes involved in the carbon cycle. Climate simulations are very sensitive to such parameterizations (Gehlen et al. 2006). One of the most important parameters is particle length, which can determine settling speed. As a result, the international modeling community is working to develop more realistic models of sub-euphotic zone particle transformation processes. Several models of vertical fluxes suggest that coagulation, zooplankton feeding on aggregates, and bacterial degradation, play important roles in particle transformation and flux reduction (Gehlen et al. 2006; Jackson 2001; Quere et al. 2005; Stemmann et al. 2004b). However they all lack data to constrain the model structures or to adjust their parameters values.

Despite progress resulting from multiple international programs, important questions remain.

- *What are the settling velocities of in situ aggregates and how can they be related to their sizes? Can aggregate size be related to aggregate flux?*

Characteristics of surface aggregates are quite well known; however, little information is available on the nature of deeper particles. Our best tool for collecting deep particles has been the sediment trap, which integrates over many types and settling velocities of particles and provides information about bulk material rather than those of individual particles. Making it more difficult to characterize particles is that most aggregates are fragile and difficult to sample individually.

- *What mechanisms are responsible for aggregate production, transformation and export in the water column?*

Processes of aggregate production and degradation are essential to understand. Efficiency of carbon sequestration to the deep ocean is related to these processes. Large uncertainties on mechanisms responsible for aggregate transformation remain.

- *What is the spatial variability of carbon flux? Does it need to be taken into account in order to obtain more realistic estimation of carbon flux at global scale?*

The global and regional variability of the carbon export to the deep ocean is not well understood. Its importance in assessing carbon export at the global scale is not well appreciated.

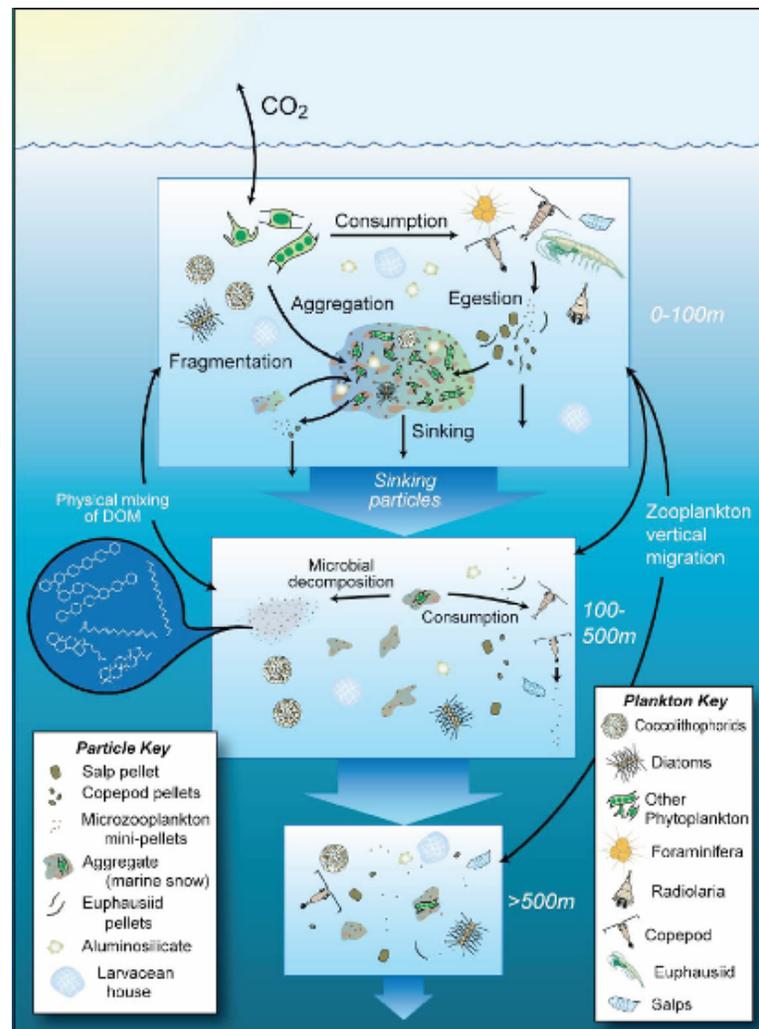


Figure 1: Biological pump and processes regulating the flux of particles in the ocean. CO_2 fixed during photosynthesis by phytoplankton can be transferred below the surface mixed layer via three major processes, (1) passive sinking of particles, (2) physical mixing of particulate and dissolved organic matter, and (3) active transport by zooplankton vertical migration. The remineralization returns carbon and nutrients to dissolved forms (Figure from Buesseler et al. 2007a).

One way to address the problems of *in situ* size estimation of particles is the use of optical methods. These methods allow a detailed description of the aggregate size spectra but do not allow their physical sampling. Here we are using results collected during the last two decades by an instrument built at the Laboratoire Océanologique of Villefranche sur mer called the Underwater Video Profiler (UVP). The instrumented platform acquired data simultaneously on physical and biological properties, particles size and macrozooplankton distribution (Figure 2).

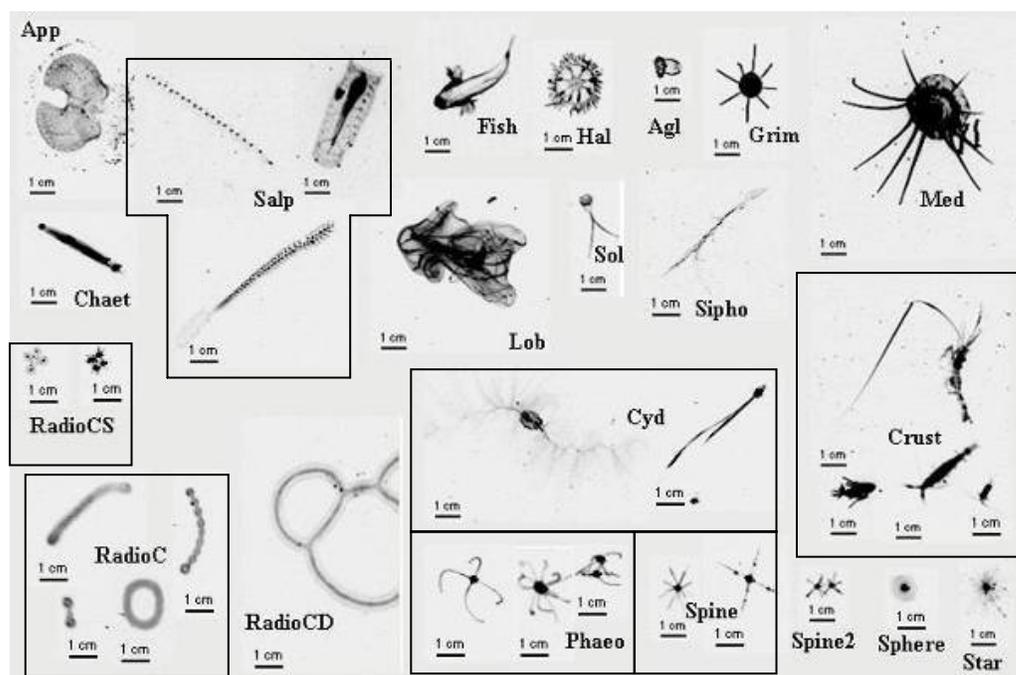


Figure 2: UVP video images with macrozooplankton groups; appendicularians (App.), Thaliaceae (Thal.; salp and doliolid), Fish, Haliscera spp medusa (Hal.), Solmundella bittentaculata (Sol.), *Aglantha* spp. (Agl.) *Aeginura grimaldii* (Gri.) and ‘other medusae’ (Med.) , chaetognath (Chaet.), lobate ctenophore (Lob.), cydippid ctenophore (Cyd.), siphonophore (Siph.), crustaceans (Crust.; decapod and amphipod), single cell sarcodine grouped by four (RadioCS.), colonial radiolarians (RadioC.), colonial radiolarians with double line (RadioCD.), Phaeodarian (Phaeo.), single cell sarcodine with spines (Spine.), double cell sarcodine with spines (Spine2.), spheres (Sphere.) and sarcodine with hairs (Stars.). The scale bar represents approximately 1 cm. Additional images can be viewed at <http://www.obs-vlfr.fr/LOV/ZooPart/Gallery/>. (Figure from Stemmann et al. accepted).

The objective of my PhD work has been to describe large aggregate size distributions in the oceans. These distributions were used to highlight important mechanisms at the origin of aggregate formation and export at global and regional scale. The current knowledge on particle dynamics is synthesized into the following paragraphs. Following the introduction, the manuscript will be divided in a methodological chapter and three additional chapters addressing the 3 previous questions on particles characteristics, formation and fate in the upper kilometer of the ocean. The last chapter will present a general conclusion.

1.1. What do we know about aggregate properties?

1.1.1. Aggregate size

There are many ways to characterize particle size, ranging from wet weight to carbon content to volume to radius. In this dissertation, size will usually refer to diameter (d) as determined using particle images.

Particles found in oceanic ecosystems range in diameter from 1 nm (“almost dissolved” colloids) to a few millimeters (diatom chains) or centimeters (cyanobacterial filaments). Three size classes of organic aggregates have often been distinguished in the past: macroscopic aggregates ($d > 500 \mu\text{m}$), such as macroaggregates, marine snow, and lake snow, microscopic aggregates ($1 < d < 500 \mu\text{m}$), also known as “microaggregates” and submicron particles ($d < 1 \mu\text{m}$; Simon et al. 2002). Macro- and microaggregates are generally formed by phytoplankton; their sizes can depend on the trophic state of the planktonic system, the season and the geographic region. Their compositions can vary from being individual algal cells to being composed of multiple particles embedded in a mucilaginous matrix (Alldredge and Silver 1988). The large size range covered by these organic aggregates implies that many complex physical, chemical, biological and specific microbial processes are involved in their formation and decomposition.

The aggregate size distribution is a continuum. Particle abundances in the water column can usually be described as a function of particle diameter. This relationship is not simple because aggregates are porous objects with porosity increasing with their size and because they are formed from different constituents having different densities.

Fractal scaling has been used in order to describe these relationships (Jackson 1998; Li and Logan 1995).

1.1.2. *Mathematical description of particle size spectrum*

Particle abundances as a function of size can be described using a size distribution. If $N(s)$ is number concentration of particles greater than a size s , then $n(s) = -dN/ds$. While both describe particle distributions, the terms *cumulative size distribution* and *differential size distribution* are used for $N(s)$ and $n(s)$. References to size distribution or number size distribution here are to $n(s)$. The number spectrum is usually estimated as $n(s) \approx (N(s) - N(s + \Delta s)) / \Delta s$, where Δs is a small size range. Any measure of size such as volume, diameter, or radius, can be used as the size, although the values and units do change with the measure.

Previous research has shown that oceanic particles tend to follow a power law distribution function over the μm to mm size range (McCave 1984; Sheldon et al. 1972). This kind of distribution can be translated as the following mathematical equation and is retrieved from UVP images:

$$n(d) = k \cdot d^b \quad (\text{Eq. 1})$$

where k and b are constants. The exponent (b) is also defined as the slope of number spectrum when the equation 1 is log transformed. This slope is commonly used as a descriptor of the shape of the aggregate size distribution (Brun-Cottan 1971; McCave 1975; Sheldon et al. 1972).

The information of this simple metric can be limited when the log-transformed aggregate size distribution is not linear. The importance of large aggregates in some systems can be missed using only the slope of a defined number spectrum. The number spectrum can be transformed to a volumetric or a mass spectrum that emphasizes the importance of large particles in mass distribution. Large aggregates may be negligible by number but they can represent more than 50% of the total mass of aggregates (Stemmann et al. submitted). Diameter is a useful particle descriptor because it can describe multiple particle properties such as mass and settling speed or flux (Alldredge and Gotschalk, 1988, Guidi et al in revision), rate of colonization by microbes and

zooplankton (Kjørboe 2001; Kjørboe et al. 2002) and coagulation rate (Jackson and Lochmann 1992). Biogeochemical activity such as aggregate remineralization by bacterial activity or zooplankton consumption can also be a function of the same length (Kjørboe and Thygesen 2001; Ploug and Grossart 2000).

Diameter is an important descriptor of the system and will be the common descriptor used in the following work.

1.1.3. Mathematical description of particle fractal dimension

The relationships between fractal geometry and the exponents for the diameter in the power relationships between particle mass and diameter have been used to estimate fractal dimensions (D) (Logan and Wilkinson, 1990) and the vice versa (Jackson et al., 1997). If the particle size is given by particle diameter (d), then its mass (m) is:

$$m(d) = a \cdot d^D \quad (\text{Eq. 2})$$

Calculated fractal dimensions for natural surface water and laboratory aggregates have been estimated to be between 1.3 and 3.75 (Jackson et al. 1997; Jiang and Logan 1991; Li and Logan 1995). A value of 3 indicates that the density is constant with size. Values of $D > 3$ can arise from measurement errors or use of an inappropriate model when analyzing observations. Surface marine snow typically has a fractal dimension (D) between 1.3 and 2.3. Much less is known about aggregates in the midwater layers.

Fractal geometry also allows estimation of the porosity of aggregates, which is inversely related to the fractal dimension and a function of size (Logan and Wilkinson 1990). The porosity is important in controlling the aggregate's sinking rate, the flux of water through the aggregate moving relative to the surrounding water, and the flux of nutrients and substrates to and from the microorganisms colonizing the aggregate's surface (Alldredge and Gotschalk 1988; Logan and Hunt 1987; Ploug 2001).

An innovative approach based on comparison of aggregate size distribution and flux measurement by sediment trap was developed to assess the fractal dimension of aggregates during this work and will be exposed in Chapter III of the dissertation (Guidi et al. in revision).

1.2. Aggregate sources

Settling material can exist as isolated source particles or incorporated in a more complex structure termed “marine snow” (Silver et al. 1978; Suzuki and Kato, 1953). A marine snow particle is an aggregate larger than 500 μm ; marine snow is ubiquitous in the world’s ocean. Marine snow forms a continuous rain of mostly organic detritus falling from the upper layers of the water column to the deep ocean. Its origin is related to the productive euphotic layer. Thus, the occurrence of marine snow changes with seasonal fluctuations in the upper ocean. More than a conveyor of the fixed carbon from the euphotic zone (biological pump), large aggregates play the role of small ecosystems (Grossart and Ploug 2001; Kiørboe et al. 2002; Ploug et al. 1999; Shanks and Trent 1980; Simon et al. 2002). They provide a unique chemical environment where both photosynthesis and microbial degradation can occur at higher level than the surrounding water (Alldredge and Silver 1988; Davoll and Silver 1986; Silver et al. 1978). In addition, as they transport material downward, they provide a highly rich food source for the mesopelagic zone (Lampitt et al. 1993b; Shanks and Trent 1979; Stemmann et al. 2004a; Turley and Mackie 1994).

1.2.1. Biogenic particles

Many sediment-trap studies have revealed that zooplankton fecal matter can be important components of rapid particulate flux in the sea. First evidence for this was the discovery of radionuclides at Oregon State reaching the deep benthos at the mouth of the Columbia River, below nuclear processing facilities (Percy and Osterberg 1968). Later radionuclides from the Chernobyl disaster were found in zooplankton fecal pellets in sediment traps at 200 m depth in the Mediterranean Sea. These radionuclides appeared 7 days after that the peak of radioactivity was delivered to the surface of the ocean and less

than 2 weeks after the explosion (Fowler et al. 1987). Fecal pellets can be a large fraction of aggregated material falling through the mesopelagic zone. Their sizes range from 3-50 μm when produced by protozoans to several mm when produced by large crustaceans, gelatinous zooplankton and fish. While their sizes vary, their composition and physical properties also differ from each other. Crustaceans generally produced cylindrical pellets encapsulated by peritrophic membranes. These membranes are composed of chitin that confers high resistivity to microbial degradation and biological attacks. Consequently, these dense pellets tend to settle fast and reach the sea floor with a composition comparable to their formation composition as long as they are not collected by coprophagous organisms. Other fecal pellets, such as those produced by gelatinous forms of macroplankton tend to be membrane free or the membrane may decompose rapidly. These pellets can be dense or fluffy and much less is known about their degradation and settling speed. This material is often sticky; increasing the probability it will aggregate with other particles and form large amorphous settling material (Turner 2002; Turner and Ferrante 1979).

Other sources of settling material include nonfecal pellet particles. Intact skeletons of radiolarians, coccoliths, foraminifera and diatoms have been found in particulate material at depth. This dense inorganic material can alter the sedimentation of aggregates produced at the surface by increasing their settling rates and playing a ballast role. Inorganic material as opposed to organic material is also named phytodetritus. Phytodetritus includes large aggregates composed of a wide variety of planktonic organic remains including diatoms, coccolithophorids, dinoflagellates, silicoflagellates, phaeodarians, tintinnids, and foraminifers (Beaulieu 2002). A survey of benthic material found viable cells in phytodetritus lay down on the sea bed (Lampitt 1985). This indicates a rapid sedimentation. Diatoms are the most common species found on these sea floor aggregates. Coccolithophorids represent the second type of phytoplankton forming the bulk of phytodetritus.

1.2.2. Inorganic particles

Fine inorganic particles, such as clays, come from land and sink very slowly through the oceanic water column ($\sim 0.5 \text{ m d}^{-1}$). Concentrations of these particles vary both temporally and spatially but have been estimated to be approximately $10 \mu\text{g L}^{-1}$ in the deep ocean. Different mechanisms lead to their export to the sea floor (Lal 1980). Large sinking aggregates can scavenge these fine particles and carry them downward at a faster rate. These fine particles can also be incorporated into a new aggregate as part of the feeding process of pelagic organisms.

Fine particles differ from large grain-size, sedimentary particles (coarse sediment, sand, pebbles, etc.), which commonly settle near their production source due to their high density and size. They are more abundant near shore, in high velocity currents and along bottom boundary interfaces. They are extremely rare in the ocean away from submarine canyon or iceberg regions.

1.2.3. Aggregate formation

Oceanic organic aggregates are derived from free-living primary producers and detritus in the euphotic zone of the world's oceans (Jackson 1990; Jackson and Lochmann 1992; Jackson et al. 2005). Processes leading to the transformation of single cells to aggregates are both biotic and abiotic. The biotic processes include repackaging of primary producers by zooplankton grazing activity, production of fecal pellets, filtration, and generation of discarded tissue such as larvacean houses. The abiotic processes are physical mechanisms that lead to the aggregation of small individual cells. The distinction between biotic and abiotic processes as the origin of aggregate formation is difficult because both processes can take place simultaneously.

The aggregation process by coagulation from the phytoplankton producer's community is the main mechanism responsible for aggregate formation in the surface layer (Jackson and Burd 1998; Jackson et al. 2005). These large aggregates come from complex interaction between producers, zooplankton, fishes and bacteria (Burd and Jackson 1997; Jackson 2001). Their concentration is highly variable according to their

location reflecting their variable production rates in different oceanic regions (Fowler and Knauer 1986).

Aggregate sources in the bathypelagic and mesopelagic zone may be different. With the exception of thermal vents, particle production in these ocean domains is primarily the result of particle loss (Jackson and Lochmann 1992) from the surface and deep water plankton and bacteria feeding and living on surface derived organic matter. Several studies observed a significant increase in carbon flux in the mesopelagic zone relative to the carbon flux immediately below the euphotic zone (Karl and Knauer 1984; Nodder 1997). It was assumed that the primary energy source for these *in situ* processes was most probably due to some interaction between microbial populations and the various dissolved and particulate organic carbon pools. Only a few studies have been conducted concerning the role of large particle production in the mesopelagic zone. However such particles may play a significant role in the water column concerning carbon cycling, biology and particle transport.

Chapter IV of the dissertation will be focused on aggregate sources. Data from high performance liquid chromatography (HPLC) have been used to describe the producer's community and highlight relations with mesopelagic aggregate size distribution and carbon flux.

1.3. Processes of export and recycling of aggregate

Many processes governed by size are involved in aggregate export and recycling. The following part will be focused on coagulation, settling speed, zooplankton feeding strategy, and bacterial community effects. Coagulation is underlined to highlight its aggregate size dependency.

1.3.1. Coagulation

1.3.1.1. Theory

A brief overview of the coagulation theory and explanation of the different equations are provided in this section. Coagulation is the process by which two particles

are brought into contact by physical mechanisms and join together to form a single larger particle. The physical mechanisms include Brownian motion, shear and differential settling. Coagulation can have a major impact in determining the particle size distribution in the euphotic layer and may explain the rapid export of surface phytoplankton production to the midwater region and ocean bottom. The probability of a collision between two particles depends on the particle concentrations, sizes and masses, while the probability that these two particles join depends on their stickiness. Studies have shown that the stickiness can varied between 0.1 and 1 in algal cultures (Kjørboe et al. 1990). This stickiness can be affected by the amount of mucus, like Transparent Exopolymeric Particles (TEP), around particles and particle shape.

1.3.1.2. Coagulation model

The coagulation model simulates the particle size distribution resulting from collision and sticking between particles over a wide range of particle size. Particle size distributions were defined earlier. A particle size distribution in terms of particle mass m can be related to one in terms of diameter d by using the original definition and some calculus:

$$n(m) = \frac{-dN(m)}{dm} = \frac{-dN(d)}{dd} \frac{dd}{dm} = n(r) \frac{dd}{dm} \quad (\text{Eq. 3})$$

Classical rectilinear approximation of coagulation theory yield in as integro-differential equation describing the evolution of n in a well mixed layer of thickness Z (Jackson 1990; Jackson 2005). More refined formulations have been described but are not presented here.

$$\begin{aligned} \frac{dn(m,t)}{dt} = & \frac{\alpha}{2} \int_0^m \beta(m_1, m - m_1) n(m - m_1, t) n(m_1, t) dm_1 \\ & - \alpha n(m, t) \int_0^\infty \beta(m, m_1) n(m_1, t) dm_1 \\ & - \frac{w(m)}{Z} n(m, t) + \mu(m) \end{aligned} \quad (\text{Eq. 4})$$

where $\beta(m, m_1)$ is the coagulation kernel and provide the probability for collision between particles with masses m and m_1 , α is the probability that the two particles stick

together or stickiness, w is the particle settling velocity, μ the particle input rate or growth rate. In the previous equation, the four terms represents

1. The rate at which collision form new particles with mass m
2. The rate at which particle are loss from the same mass range by the coagulation process
3. The loss rate due to particle sedimentation out of the mixed layer depth Z
4. The input term corresponding to a constant division rate of single particle.

The previous equation is expressed in terms of particle mass but the coagulation kernel is also a function of particle radius. Hence we need a relation between the mass (m) and the radius (r) of an aggregate. This can be described using a fractal scaling (Cf Eq. 1).

$$r = \left(\frac{m}{a} \right)^{1/D} \quad (\text{Eq. 5})$$

where D is the fractal dimension and a is a constant (Logan and Wilkinson 1990)

The coagulation kernel can be written as following if the different terms (Brownian motion, shear and differential settling) are assumed to be independent.

$$\beta(r_i, r_j) = \beta_{br}(r_i, r_j) + \beta_{sh}(r_i, r_j) + \beta_{ds}(r_i, r_j) \quad (\text{Eq. 6})$$

The Brownian motion leads to collision of particles due to particle diffusion. It is only important for particles $< 1 \mu\text{m}$. The Brownian motion kernel can be mathematically expressed:

$$\beta_{br}(r_i, r_j) = 4\pi(D_{f,i} + D_{f,j})(r_i + r_j) \quad (\text{Eq. 7})$$

where the diffusion coefficient for the particle i , is: $D_{f,i} = \frac{kT}{6\pi\eta r_i}$ where k is

Boltzmann's constant, T is the absolute temperature and η the dynamic viscosity.

Particles in laminar or turbulent shear collide if the distances of their flow streamlines or eddies are smaller than the sum of the particle radii. It is important for the collision of particles $> 1 \mu\text{m}$ and is the dominant mechanism at interfaces such as at discontinuity layers in the water column, in the bottom nepheloid layer, or at tidal currents in estuaries and shallow seas. In pelagic systems, shear is one of the major factors controlling aggregation (Jackson 1990). At these interfaces, the energy dissipation rates become

important (typically 10^{-7} to $>10^{-4} \text{ m}^2 \text{ s}^{-3}$, potentially leading to disaggregation instead of aggregation (MacIntyre et al. 1995; Riebesell 1991; Riebesell 1992). The mathematical expression of shear in the kernel coagulation is presented below:

$$\beta_{sh}(r_i, r_j) = \frac{4}{3} \gamma (r_i + r_j)^3 \quad (\text{Eq. 8})$$

where γ is the fluid shear rate.

The last mechanism involved in the kernel coagulation is differential settling. Settling particles can intercept and carry more slowly sinking particles. Usually, larger, more rapidly sinking particles scavenge smaller particles by this mechanism (Jackson 1990). The mathematical translation of this mechanism is:

$$\beta_{ds}(r_i, r_j) = \pi (r_i + r_j)^2 |w_i - w_j| \quad (\text{Eq. 9})$$

where w_i and w_j are the settling velocity of particles i and j .

$$w_i = \frac{1g\Delta\rho r_i^2}{\nu} \text{ where } g \text{ is the gravitational acceleration, } \Delta\rho \text{ is the excess density,}$$

and ν is the dynamic viscosity.

We have seen that the coagulation is based on aggregate size distribution $n(m)$ and aggregate radius (r). Hence, data from the UVPs can be particularly useful for this model parameterization because $n(m)$ and r are directly extracted from each profile.

1.3.2. Settling speed

Several past studies reported particle settling speed estimations based on divers' observations, laboratory experiments, and video measurements (Alldredge and Gotschalk 1989; Asper 1987; Pilskaln et al. 1998; Shanks and Trent 1980; Stemmann et al. 2002). During the last three decades, programs such as VERTEX and JGOFS had multiple sediment trap deployments which have been used to estimate daily to weekly aggregate settling speeds between traps at different depths and fluxes at each depth. Despite improvement in our understanding of the processes that drive the carbon flux to the ocean interior, uncertainties remains on spatial and temporal variations of the

aggregate settling speed. Particle settling depends on particle mass and a length scale. Settling speeds in the surface layer increase with particle size and range from less than 1 m d^{-1} for small algae cells to several hundred m d^{-1} for marine snow and fecal pellet. Many different relationships between aggregate size and settling speed have been described (Alldredge and Gotschalk 1988; Alldredge and Gotschalk 1989; Azetsu-Scott and Johnson 1992; Carder et al. 1982; Diercks and Asper 1997; Shanks and Trent 1980; Smayda 1970; Stemmann et al. 2004a; Syvitski et al. 1995). The fact that no universal relationship exists reflects the variability of aggregate properties. Indeed aggregate shape and composition depends on the location and depth of particle production, the season, and the surrounding water biological composition and physical characteristics. The mineral aggregate content can also play a role on the aggregate settling speed variability. Vertical differences in settling speed, on average increased by a factor of 2–10 between the depth of 100 and 2000 m may result from differential mineralization (Berelson 2002).

Estimation of aggregate settling speed using aggregate size distribution and fractal scaling will be discussed in chapter III of the dissertation.

1.3.3. Zooplankton activity

Zooplankton “function” and abundance in the water column can dramatically change the size distribution and the composition of aggregates in the water column (Graham et al. 2000). They may transform aggregates during their vertical migration according to their feeding characteristics. Fragmentation has been proposed to be one of several potentially important mechanisms by which sinking macroaggregates are lost in ocean surface waters (Karl et al. 1988). Fragmentation can change the aggregate size distribution, resulting in increasing the number of small aggregates and decreasing the large ones. The change in the size distribution will potentially lead to a mean decrease of aggregate settling speed and thus a decrease of the carbon flux from the surface. Consequently with a mean size reduction, an increase in the remineralization could be

observed in the mixed layer while small aggregate residence time will increase (Dilling and Alldredge 2000; Goldthwait et al. 2004).

Recent global biogeochemical models try to include plankton functional type in order to better represent their actions on the apparent carbon flux decrease with depth in the world's oceans (Quere et al. 2005). Why should details of zooplankton feeding be important for biogeochemical cycles? Appendicularians, for example, may be responsible for major flux events. Their remains can be the most abundant form of marine snow (Alldredge and Madin 1982; Hansen et al. 1996). Their discarded feeding structures are rapidly incorporated into aggregates, significantly modifying the downward carbon flux while they enclose rich food resources. Pteropods could have a similar impact on the carbon flux when they renew their net feeding structures. Thus different mechanisms, potentially essential to understanding the carbon cycle, have been proposed according to the organisms' feeding strategy (Jackson 1993; Jackson and Kiørboe 2004; Stemann et al. 2004b). Organisms can wait for the food to fall into their net constructed below the sinking aggregates. This strategy has been adopted by pteropods and named flux feeders (Jackson 1993). Organisms can also have active behavior. Distinction can be made between organisms that only filter the water and those that will actively search for aggregates. The first ones correspond to filter feeders such as appendicularian, salps and numerous crustaceans. The second ones are plume searchers; they seek out falling particle by sensing the hydrodynamic or chemical disturbance caused by them. Zooplankton not only consumes particles but also produce fecal pellets and detritus, modifying the aggregate size distribution. Consequently, their contribution to the aggregate formation and sinking flux can be substantial (Lampitt et al. 1990; Pomeroy and Deibel 1980; Turner 2002). Interestingly enough, these described zooplankton functions are size spectra based (Stemann et al. 2004b). Hence data from the UVP can be used directly with this approach. The size-spectra could force the biogeochemical models or be used to parameterize zooplankton functions in order to better represent their role in the carbon export passing through aggregates (Stemann et al. accepted).

1.3.4. Microbial activity

Microorganisms can be responsible for both aggregate formation and degradation. Aggregate formation can be mediated by the secretion of fibrillar material leading to strengthened aggregate structure (Heissenberger et al. 1996). Bacteria are also known to produce TEP, as are diatoms, in fairly high quantity. This transparent material could control the formation of large amorphous aggregates due to their stickiness or increase particle number (Engel 2000; Ploug et al. 1999). Bacterial communities also colonize phytoplankton and may disturb their growth, mortality and secretions that are correlated to aggregate formation (Azam 1998; Brussaard and Riegman 1998; Grossart 1999).

While microorganisms are involved in aggregate formation, they also contribute to aggregate transformation during the settling process. Bacteria concentrations in aggregates are generally greater by up to a factor of 1000 relative to the surrounding water (Alldredge and Silver 1988; Davoll and Silver 1986; Silver et al. 1978; Turley and Mackie 1994). Concentration of aggregate attached bacteria is elevated because aggregates are rich in resources. Bacteria can metabolize and solubilize the aggregate particulate organic matter. Both mechanisms lead to a loss of particle mass. However, only solubilization provides food to the surrounding water, allowing aggregates to be detected by zooplankton following their chemical plumes. Besides the loss of mass, aggregates geometry could change while they become older. Their porosity could be particularly affected, leading to a change in the relationship between aggregate size and settling speed.

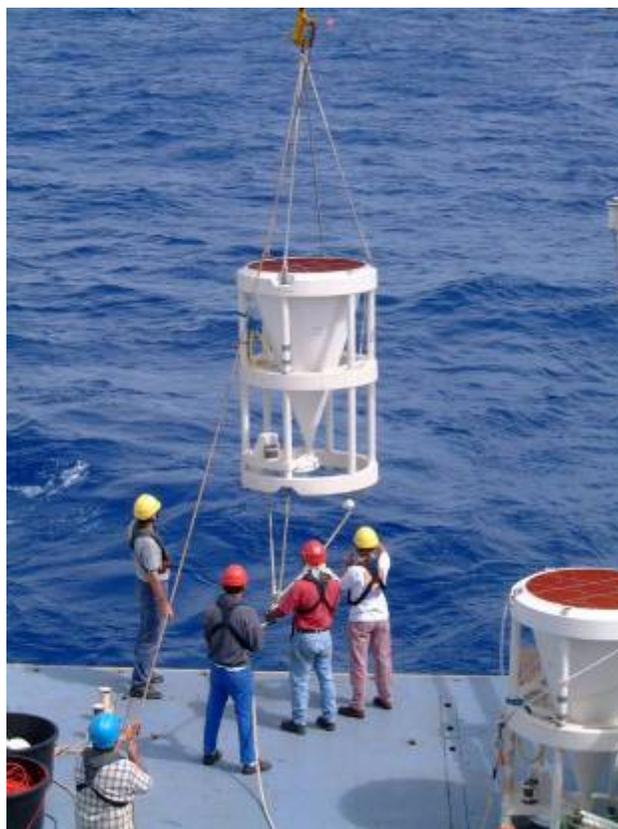


Figure 3: Floating sediment trap deployment during the BIOSOPE cruise in the Southeastern Pacific.

1.4. Sampling techniques and flux measurements

1.4.1. Sample collection

Aggregates have been collected and characterized by a variety of techniques, including collection of individual particles sampled *in situ* by scuba diving. A range of instruments, mainly based on light attenuation, have been developed in order to determine particle size distributions. Instruments such as the Coulter Counter Multisizer (Sheldon et al. 1972), the Elzone particle counter, and the HIAC/Roxio have been used in order to get the size distribution of aggregates smaller than 100 μm in diameter (Li and Logan 1995, Stemmann et al. submitted). Aggregates have also been sampled by Niskin bottles and brought to the surface for processing on a marine vessel or at a shore-based laboratory. However, extraction of the aggregates from bottles can disrupt them. Large

aggregates are extremely fragile and are easily destroyed. Deep aggregates have also been collected by submersibles, allowing undisturbed aggregates to be brought back to the surface for individual chemical analyses (Youngbluth et al. 1988).

Several attempts have been made to estimate distributions of large aggregates, their chemistry and their vertical transport through the use of large volume filtration or *in situ* pumps (Bishop and Edmond 1976; Buesseler 1998; Moran et al. 1999). POC estimates from samples collected in Niskin bottles are often higher than those from *in situ* pumps. Two hypotheses have been put forward to explain this discrepancy. The “underestimation” by the pump could be explained by the higher pressure differential across pump filters causing some material to be disrupted by the pumps and some undetermined problems with some pump design (Gardner et al. 2003). In contrast, there could be “overestimation” by bottles samples caused by DOC adsorption to filters when POC concentrations are $< 2\mu\text{M}$ (Moran et al. 1999). The idea that particles may form during bottle filtration and that “swimmers” may be caught by bottles has also been proposed to explain concentration differences observed during the MEDFLUX experiment (Liu et al. 2005).

During the 30 last years, moored and floating sediment traps were undoubtedly the most deployed instruments used to evaluate particle flux by collecting sinking material (Figure 3). Advances in understanding the ocean’s biological pump can be partially attributed to their use. However there are three processes that can highly impact trap measurements. The trap collection efficiency depends on how a trap interacts with the water flowing around it and collects aggregates in a hydrodynamic environment (Gardner 1980 a and b). Swimmers are another source of sample ‘contamination’. The third perturbation corresponds to the possible resolubilization or remineralization of aggregate caught in the traps. These two last biases lead to elemental modifications of samples, potential loss of mass or sample corruption by organisms’ molts or fecal pellets. Finally even with a perfect sediment trap it’s hard to identify an aggregates source in a dynamic context because of the large scale path that a particle takes to arrive at a given location. Models have been developed in order to take into account the

oceanic circulation and calculate the approximate source of the aggregate rain. This problem is known as the statistical funnel (Siegel and Armstrong 2002; Waniek et al. 2000).

Attempts to resolve these biases have been made by improving the design and deployment of trap devices. Thus neutral buoyant sediment traps were developed in order to decrease the hydrodynamic effect. The velocity relative to the surrounding water of these traps is quite small (Stanley et al. 2004; Valdes and Price 2000). The particles collected in a sediment trap occur over a range of sizes and settling rates when suspended in the water column but lose their individuality in the sediment trap aggregation. This loss of identity has been partially overcome by the use of a polyacrylamide gel in the collectors, which allows the determination of size distributions of these aggregates (Jackson et al. 2005; Kjørboe et al. 1994; Waite and Nodder 2001). Settling velocity traps have also been developed in order to sort particles by their settling properties. Thus caught particles are redistributed according to their settling speed allowing chemical analyses of each size class (Peterson et al. 2005).

Development of radiometric techniques such as $^{234}\text{Th}/^{238}\text{U}$ disequilibrium to calibrate the collection efficiency of sediment traps has been helpful in constraining flux variability measured with traps. This is due to several factors. ^{238}U is soluble in seawater and behaves conservatively with salinity. Thorium strongly adsorbs onto particles. Finally, the ^{234}Th half-life of 24.1 days allows the study of processes occurring over a time scale of weeks. However this measurement in the water column is very time consuming, making it difficult to implement simultaneously with routine sediment trap measurements (Buesseler et al. 2007a; Buesseler et al. 2006). In addition, biases associated with aggregate size and Thorium absorption, has been demonstrated (Burd et al. 2007; Burd et al. 2000).

1.4.2. Optical measurements

The availability of imaging sensors and computer systems to analyze their observations has led to the development of *in situ* photographic and video systems that can be used to produce profiles of aggregate size distribution and abundance (Asper

1987; Davis and Pilskain 1992; Gorsky et al. 1992; Gorsky et al. 2000; Honjo et al. 1984). These instruments allow the description of aggregate size distribution at resolution close to the resolution of physical oceanic captor. Despite their ability to provide detailed particle size distributions with high spatial resolutions, imaging systems cannot describe aggregates' chemical composition without more information about the relationship between particle size and composition (Burd et al. 2007; Burd et al. 2000).

Chapter V of the dissertation will describe a UVP application in the North Atlantic that allowed description of mesoscale horizontal and vertical aggregate size distribution and related carbon fluxes in a dynamic context (Guidi et al. 2007).

1.5. Instrument

The Underwater Video Profilers (UVPs) were constructed in the Laboratoire d'Océanographie de Villefranche sur mer, France (UPMC/CNRS) with the support of the CNRS (Centre National de la Recherche Scientifique) and the European MAST II and III programs. The UVPs have been developed for the study of large-particle ($> 60 \mu\text{m}$) abundance and size distribution and zooplankton data from 0 to 1000 m. Different models have been constructed since 1990 (Gorsky et al. 1992; Gorsky et al. 2000). They were designed to minimise the disturbance of the illuminated volume in order to reduce disruption of imaged particles. All models are autonomous and can be lowered on any regular sea wire. The latest digital model is described here.

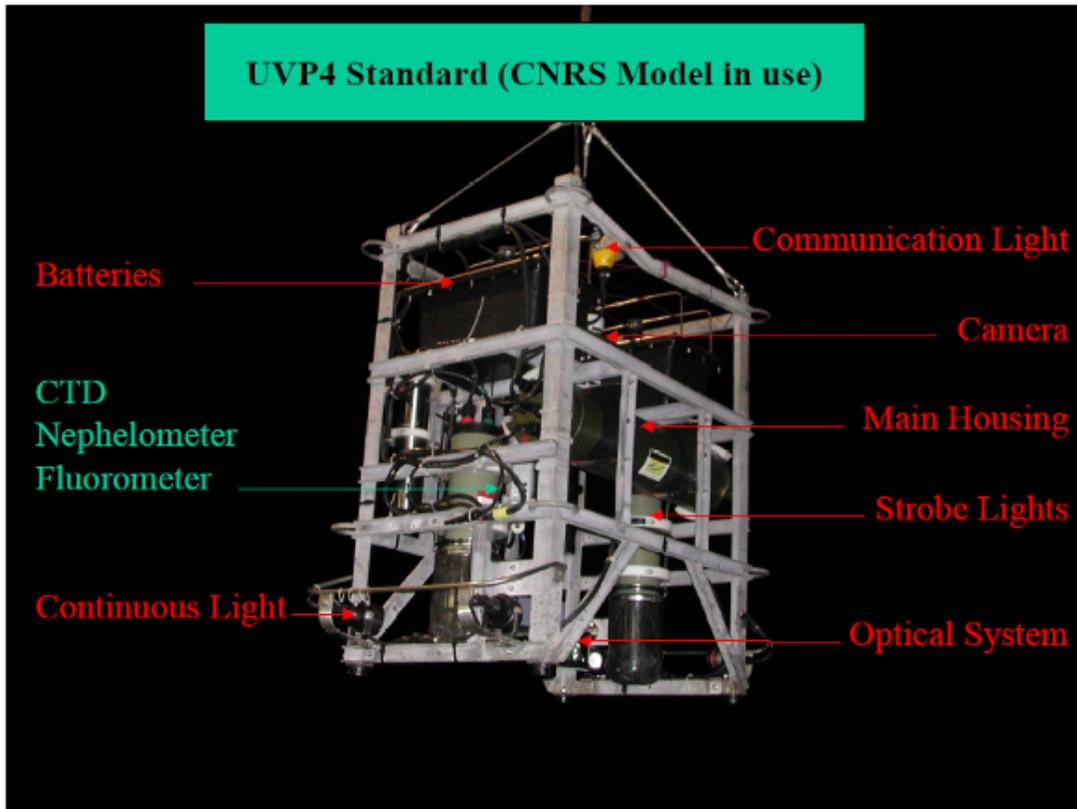


Figure 4 : Illustration of the last version of the Underwater Video Profiler.

The UVP model IV (Figure 4) is a vertically-lowered instrument mounted on a galvanized steel frame (1.1 x 0.9 x 1.25 m). The lighting is based on two 54W Chadwick Helmuth stroboscopes. Two mirrors spread the beams into a structured 8 cm thick slab. The strobes are synchronized with two full frame video cameras with 12 and 8 mm C-mount lenses. The cameras are positioned perpendicular to the light slab and they record only particles illuminated against the dark background. The short flash duration (pulse duration = 30 μ s) allows a fast lowering speed (up to 1.5 m/s) without the deterioration of image quality. Four 100 W spotlights can be used instead of the stroboscopes for continuous observations of a larger but less structured water volume. In this case the lowering speed is slower. Depth, temperature and conductivity data are acquired using a Seabird Seacat 19 CTD, with fluorometer and nephelometer (both from Chelsea Instruments Ltd.). The system is powered by two 24 volts batteries and is piloted by a

powerful computer. The data acquisition can be time or depth related and programmed prior to the immersion. The UVP is well adapted to count and measure fragile aggregates such as marine snow as well as delicate zooplankton.

Daylight can modify the optical properties of particles in the upper 0-60 meters. The depth range of the affected layer depends on the characteristics of the sunlight penetration. Therefore, data analysis starts at a depth where the measured background value of daylight remains identical to that of night profiles or to that of deep layers, not influenced by changing light regimes. This depth is automatically computed for each profile using a customized algorithm.

Processing of images obtained by the UVP in the structured light beam is performed automatically by the system during recovery using customized software. The objects in each image are detected and enumerated. The area of every individual object is measured in pixels. Data are stored in an ASCII file and can be combined with the associated CTD, fluorometer and nephelometer data using Seasoft Software (Sea-Bird Electronics Inc., Washington, USA). Vertical profiles can be printed out onboard immediately after the recovery of the UVP.

Two calibrations steps need to be done in order to make meaningful measurement:

- Particle sizing need to be transformed from pixel to international metric units (meters).
- Image volume must be computed to derive quantitative particle count per volume unit.

Explanations on these calibrations are given in the following sections.

1.5.1. Size measurement: From pixel to millimeter

Aggregate sizing is performed on images recorded by the underwater video profilers. Hence, the size is given in number of pixels. The conversion in metric units has been done in laboratory using different biologic objects including opaque objects such as fecal pellets and transparent aggregates such as eggs, large aggregates (marine snow), and appendicularian houses. Individual objects were first measured under the

binocular microscope and then injected in a dark test tank filled with 3 m³ filtered (20 μm) sea water. The relation between the two measurements is non-linear and follows a power law (Figure 5).

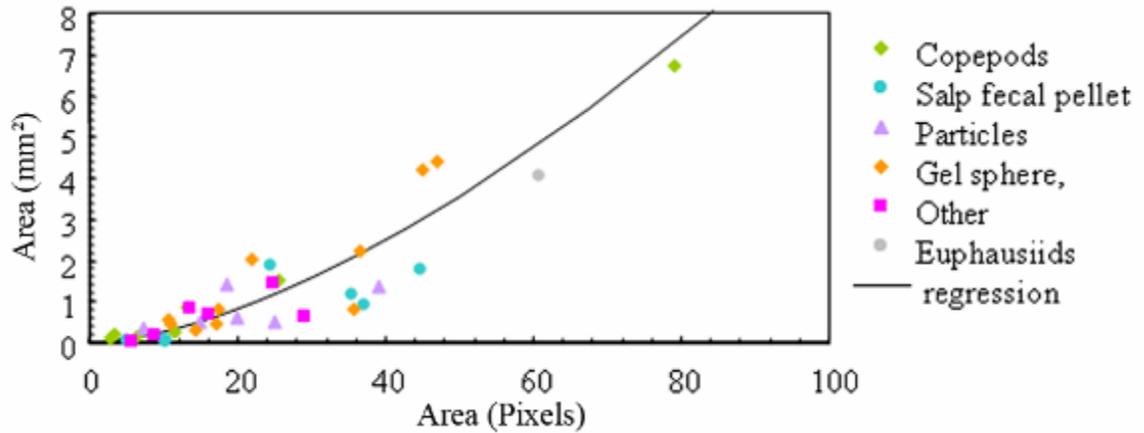


Figure 5 : Example of data used for the calculation of the conversion equation from pixel to millimeter size measurement. Each color corresponds to an object type.

Different instrument generations have been used since the first *in situ* deployment. The same calibration protocol has been applied to each system. The latest UVP (4a) is composed of 2 cameras with different resolution in order to cover a large size range. The following model has been used for all size conversions

$$S_{IS} = A \cdot S_p^B \quad (\text{Eq. 10})$$

where S_{IS} is the object surface area in millimeter square and S_p the object surface area in pixels. The values of A and B are obtained by minimization.

Table 1: Summary of parameters used for the pixel to millimeter size conversion. The water volume recorded by each image and the minimum aggregate size that each UVP generation can measure is also given.

UVPs	<i>A</i>	<i>B</i>	Volume in liters	Minimum ESD mm	Number of profiles
2a	0.0014	1.4300	0.28	0.203	515
2c	0.0028	1.1207	0.23	0.089	115
3a	0.02	1.1370	1.33	0.483	168
3b	0.0024	1.3728	0.6	0.089	79
4a (25 mm)	0.0024	1.4959	1.25	0.060	377
4a (8mm)	0.0149	1.6100	10.53		

A summary of all coefficients and exponents used for different UVP generation is given in Table 1. Finally, the object area is converted to equivalent spherical diameter (ESD) corresponding to the diameter of the measured cross-sectional area of the object assuming a spherical shape. Then, the ESD is used to calculate the corresponding object solid volume (ESV).

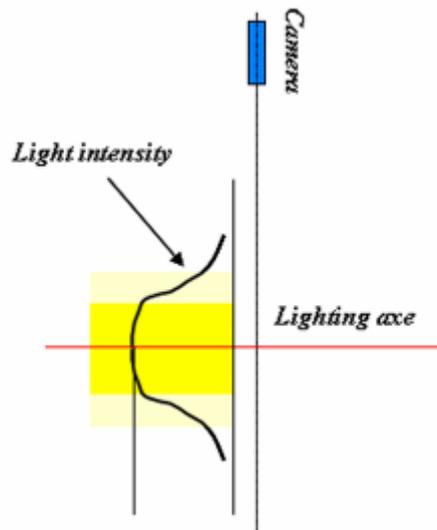


Figure 6 : Example of curve of light intensity registered at one point of the grid used for the calculation of the water volume sampled by one image.

1.5.2. Volumetric issue

The aggregate count per volumetric unit is not possible without a good estimation of the water volume “sampled” in each image. The estimation was performed in laboratory condition identical to those of the size calibration. The volumetric estimation was obtained using a grid facing the camera. The light intensity was measured at each point of the grid using a photodiode. A light intensity spectrum was obtained for each point of the grid (Figure 6). A three dimension shape was then calculated combining individual light intensity spectrum. Different volumes could be estimate according to a specific light intensity.

Finally a light intensity threshold was chosen in order to get a water volume homogeneously lighten. For the last UVP generation (4a) the threshold was chosen at 45 (Figure 7) corresponding to a volume of 10.53 for the 8 mm and 1.25 liter for the 25 mm camera. A summary of calculated volumes for each instrument is given in Table 1.

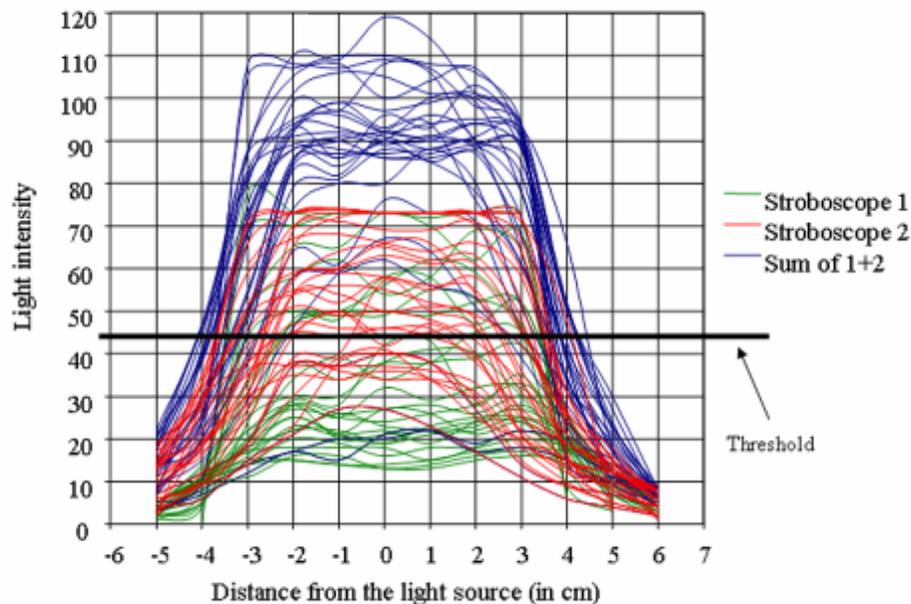


Figure 7 : Complete set of light intensity curve obtained at every point of the grid. The greens curves correspond to the light intensity spectrum from the stroboscope 1. Reds light intensity spectrum came from stroboscope number 2. Blue curves correspond to the sum of the 2 stroboscopes.

1.6. Instrument inter-calibration

As described in the above procedure, 3 parameters can affect the aggregate abundance and size measurement. These parameters are the coefficient A , the exponent B of Eq.10 and the water volume illuminated for each image. Several profiles have been done simultaneously with the 2 UVPs versions. These two UVPs were version 2c and 4a. Direct comparison of aggregate size distribution can be done using these combined profiles. Sample Volumes, A s and B s were adjusted slightly using the Matlab function *fminsearch* (The Mathworks, Inc., Natick, MA). The aim of this study was to minimize the sum of square of the differences between the 2 UVPs aggregates size spectra. The size range used for the inter-calibration is related to the instrument ability to detect small and large aggregates. The extremes parts of aggregate size spectrum with marked inflections were removed from the analysis. Values given in Table 1 are those resulting from the minimization procedure. After this adjustment, there was little difference for abundance and aggregate size distribution measurements measured by the different instruments (Figure 8A).

UVP 2c and 4a were the only versions deployed simultaneously. The others versions cannot be compared using identical profiles. However the DYFAMED station located in the north western part of the Mediterranean Sea (Ligurian Sea) approximately 45 km south of Cape Ferrat, France, was sampled by 3 UVPs version (2a, 3b and 4a) for the same seasons but at different years. These profiles should provide similar aggregate size distributions when a seasonal cycle of aggregate size distribution has previously been demonstrated (see Fig. 4 in Stemmann et al. 2002). The minimization process presented for the comparison between UVP 2c and 4a was applied for these instruments (4a vs 2a and 2a vs 3b). These combined profiles reveal that results from these 4 instruments can be matched up (Figure 8B and C).

Unfortunately the UVP 3a could not be compared to any other UVP version; it will be excluded from all following analyses performed in this manuscript. Furthermore, the minimum size detection of UVP 3a was 0.438 mm, strongly constraining any kind of aggregate size distribution study based all the entire UVP dataset.

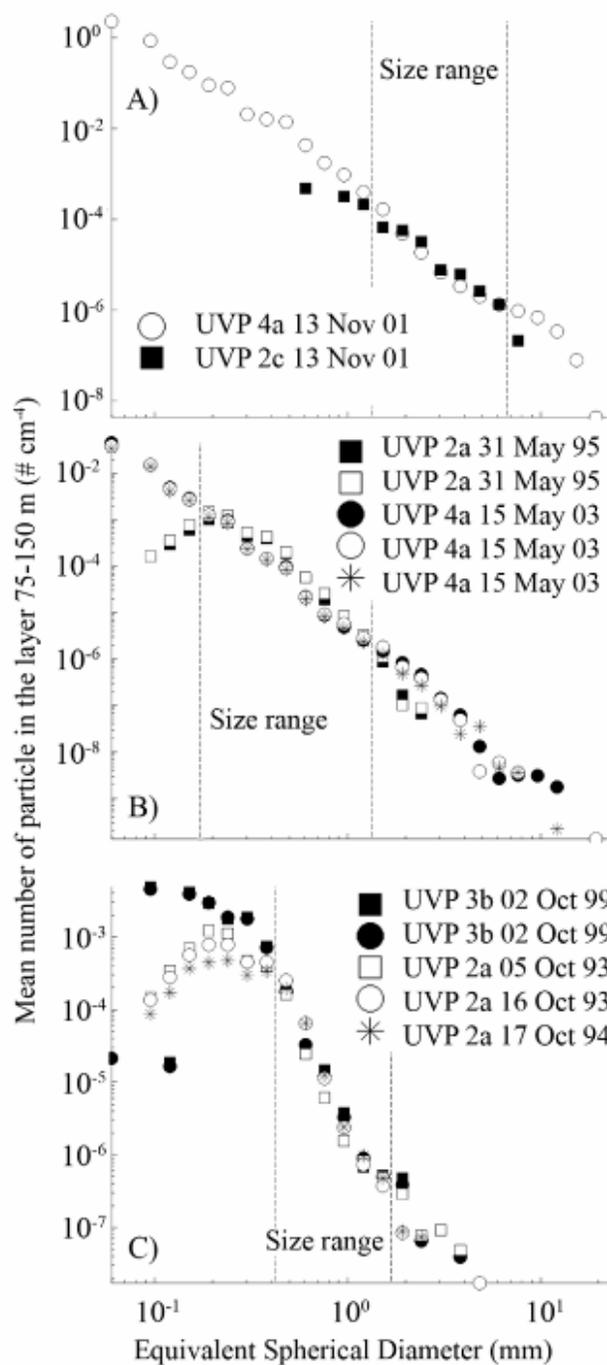


Figure 8 : Mean aggregate size distribution obtained with 4 UVP generations between 75 and 150 m. A) Combined profiles made by UVP 4a and 2c. B) Aggregate size distribution from the DYFAMED site in the Mediterranean Sea in May 1995 for UVP 2a and May 2003 for PVM 4a. C) Aggregate size distribution from the DYFAMED site from UVP 3b deployment in October 1993 and from UVP 2a in October 1993 and 1994.

1.7. Database organization

The inter-calibration performed, all profiles have been organized in a structured database organized with Matlab 6.5 (The Mathworks, Inc., Natick, MA). Output from the UVP correspond to a matrix ordered by image and object. Objects are referred to by the number of the image and their number in each image. Aggregate profiles were mostly associated with CTD sbe19 allowing image and depth association. When the sbe19 was missing, the length of the sea wire was used to estimate the depth for each image. Aggregates were then grouped by size classes and depth. At the end of the treatment, one profile corresponded to aggregate abundance (number per liter) divided into 27 size classes and grouped by layers of 5 meters. In other word, when a UVP profile is made down to 1000 m deep, the resulting file corresponds to 200 rows (200*5 meters) and 27 columns; each column equal to a certain aggregate size range. In order to have homogeneous treatment for all instruments, the smallest size class started at 0.52 μm in ESD, which is the size of one pixel of the instrument with the best resolution (UVP 4a). The next size classes were calculated on a ESV base and follow an octave progression (Table 2) as suggested by Jackson (1997).

Table 2: Definition of the 27 aggregate size classes used in this work.

Class number	Lower limits of classes (mm)	Upper limits of classes (mm)
1	0.052	0.066
2	0.066	0.083
3	0.083	0.105
4	0.105	0.132
5	0.132	0.166
6	0.166	0.209
7	0.209	0.264
8	0.264	0.332
9	0.332	0.419
10	0.419	0.527
11	0.527	0.665
12	0.665	0.837
13	0.837	1.055
14	1.055	1.329
15	1.329	1.674
16	1.674	2.110
17	2.110	2.658
18	2.658	3.349
19	3.349	4.219
20	4.219	5.316
21	5.316	6.697
22	6.697	8.438
23	8.438	10.631
24	10.631	13.395
25	13.395	16.876
26	16.876	21.263
27	21.263	26.789

Each profile is associated with metadata giving information on the data treatment, the quality of the profiles, the parameters used for size conversions, its location, the date of the deployment and others (Table 3). The metadata are particularly useful for profiles post treatment.

Several other independent variables were associated with the particles profiles during this work. These parameters correspond to phytoplankton pigments profiles from High Performance Liquid Chromatography (HPLC) and temperature, salinity, density and fluorometry profiles from the sbe19 (CTD deployed with the UVP) and/or CTD date

from the rosette. CTDs and HPLC data were added such as new field in the structured database. They have their own depth, location and time references.

Table 3: Description of the main field used in the UVP database. Additional variables are not mentioned in this listing. When an instrument is composed of two cameras, fields ending in '0' for the first camera have sisters fields ending in '1' for the second camera.

Field number	Name of the field	Description
1	histfile	Profile identification name
2	cruise	Name of the cruise
3	profile	Profile number during the cruise
4	pvmttype	UVP version
5	soft	UVP software treatment
6	sbe19	Name of the CTD sbe associated profile
7	date	Date (year/month/day)
8	time	Local time GMT (hhmmss)
9	station	Name of the station
10	depth	Bottom depth registered on board
11	ctdrosette	Name of the rosette cast
12	latitude	Latitude
13	longitude	Longitude
14	quality	Profile quality (0: doubtful)
15	bru	Name of the original file
16	minpixelsurf	Minimum surface of object conserved in the file
17	zimgprem	Depth of the first image without light perturbation
18	maxesd	Maximum surface of object conserved in the file
19	a0	Coefficient of the pixel to mm equation conversion (A)
20	exp0	Exponent of the pixel to mm equation conversion (B)
21	volimg0	Water volume of 1 image
22	minor	Inferior limit of the first size class in volume
23	maxor	superior limit of the last size class in volume
24	step	Factor of the power progression (2 when octave)
25	datem	Date in Matlab format

Finally, 39 cruises were organized in the database, corresponding to 1300 aggregate size distribution profiles, more than 500 corresponding CTD profiles and 230 HPLC profiles, each HPLC profile corresponding to at least 25 pigments (Figure 9).

1.8. Numerical data treatment

Several methods have been used during this work and they will be described in the following chapters. However chapter II is dedicated to the development of an innovative classification technique that determines the true number of clusters in a natural ecological dataset. Common rules used to select the right number of clusters in a classification tree are particularly sensitive to the high variability which is always present in ecological data. This new method, called the Random Simulation Test (RST), has been tested against computer generated data and natural ecological datasets. Performance and weakness of RST will be discussed. This RST is applied to the clustering of aggregate size distribution profiles.

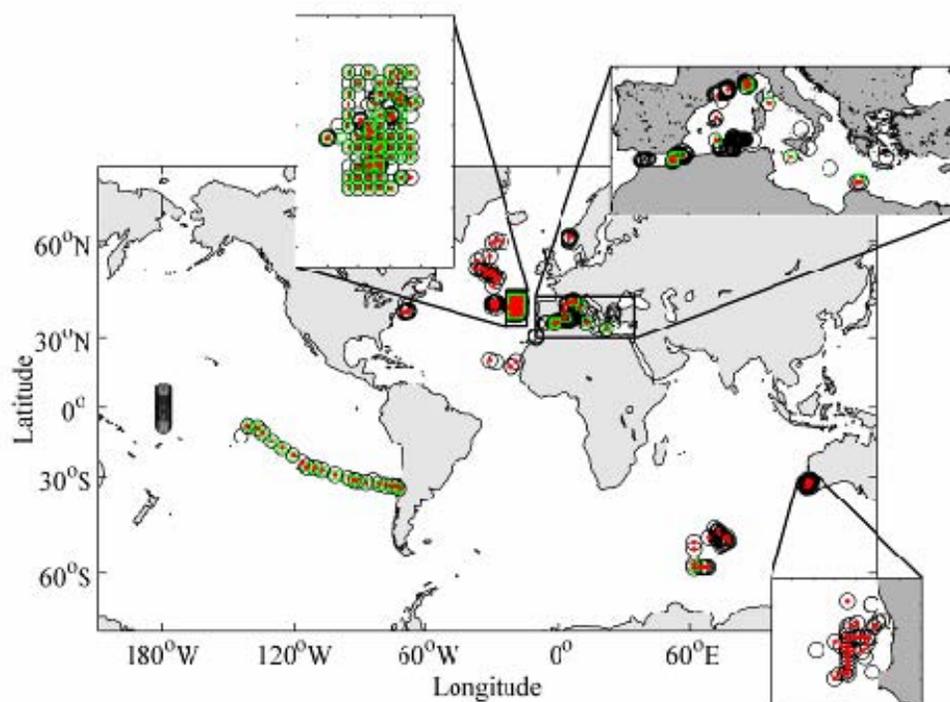


Figure 9: Profiles location of UVP (black circles), CTD (red dots), and pigment profiles (green squares).

CHAPTER II

A NEW PROCEDURE TO OPTIMIZE THE SELECTION OF GROUPS IN A CLASSIFICATION TREE

2.1. Introduction

Cluster analysis is a technique widely used in oceanography which is useful in several types of exploratory pattern analysis, including data mining, document retrieval, image segmentation, and pattern classification. It provides a powerful tool allowing observations or descriptors to be partitioned into subsets. Many algorithms have been proposed (see Legendre and Legendre 1998 for a review). Among them, the hierarchical agglomerative technique maybe the one most commonly used in natural sciences. This technique leads to a dendrogram describing the relation between objects or descriptors.

Although the hierarchy of the classification represents important information *per se* for such methods, biologists and ecologists have often searched for optimal selection of the partitioning level. The level of selection of groups is often set empirically, combining a visual examination of the dendrogram with the knowledge of the systems or processes under consideration. This is not an objective way to choose the partitioning level and some algorithms have been proposed to evaluate the validity of the clusters. Reviews of techniques can be found in Gordon (1996); Halkidi et al. (2001); Jain et al. (1999); Lozano and Larranaga (1999). One of the most popular statistical techniques is the *k*-means approach proposed by Fisher (1958). Unfortunately the method requires a preliminary choice of the number of existing groups, which introduces some subjectivity. A more effective procedure for the identification of the number of clusters in a dataset is the Cubic Clustering Criterion (CCC, Sarle 1983). The index estimates the number of clusters for methods that search to minimize the within-cluster sum of squares, such as the Ward's minimum variance or the *k*-means method. Milligan and Cooper (1985) recommended the Calinski and Harabasz index (hereafter referred as C&H; Calinski and Harabasz 1974). For varying cluster group simulations, this index led to better results than the CCC procedure (Milligan and Cooper 1985). However

despite the existence of some stopping rules, Xu and Wunsch (2005) stated that no established method was available for determining the optimal number of clusters. This is especially true for environmental data which often exhibit pronounced variability.

The goal of this paper is to describe a new procedure, named the Random Simulation Test (RST), to select the optimal level of partition of a dendrogram. The technique is derived from a method proposed by Ibanez (1973) to select the right number of axes in principal components analysis. The method is presented and then evaluated using three different ways. First, the procedure is evaluated on the widely used iris dataset published by Fisher (1936). Second, the technique is applied on simulated datasets with known number of groups using the Milligan and Cooper (1985) procedure. Results are compared with outputs from the different cluster analyses applied on these data and the technique is judged against the stopping rule technique proposed by Calinski and Harabasz (1974). Third, the technique is used on a calanoid copepod crustacean dataset analyzed by Beaugrand et al. (2002). It is argued that the technique is well adapted to data with strong variability (a condition often encountered in biological and ecological data) and can be applied in any science field that uses agglomerative cluster analysis.

2.2. Procedures

2.2.1. Random and Simulation Test (RST)

The method finds its origin in a procedure proposed by Ibanez (1973) to identify meaningful principal components. The author proposed to generate a random variable, which was then included among descriptors to identify informative eigenvalues. The Random Simulation Test (RST) is a modified version of this technique for the case of the segmentation of a classification tree but including a simulation procedure. The algorithm belongs to the group of external criteria that tests whether the objects are randomly structured or not (Milligan 1981). The method is described for a classification of the objects in the space of the descriptors (Q mode). However, the algorithm is usable

for the classification of the descriptors in the space of the observations (R mode), providing that the distance coefficient is suitable for the data.

Let $X(n,m)$ be a matrix with n observations in rows and m descriptors in columns. The Random Simulation Test (RST) generates a supplementary observation we call r (with $0 < r \leq 1$), corresponding to m variables extracted from a uniform random distribution. Then, this random observation r is scaled according to the range of each of the m variables. This is accomplished by the following transformation:

$$\varepsilon_{n+1,j} = r_j (X_{j(\max)} - X_{j(\min)}) + X_{j(\min)}, j = 1, 2, \dots, m \quad (\text{Eq. 11})$$

A classification tree of the $n+1$ observations is built in order to determine the level (cut-off) from which ε is included in a group. The result is tested by generation of a large number of classifications, each simulation using a new ε , leading to a distribution of the cut-off levels. Figure 10 shows the successive steps involved in the analysis. At Step 1, a distance matrix is calculated between the $n+1$ observations (original objects + ε). At Step 2, a dendrogram is built. During Step 3, the position of ε on the dendrogram is identified. The selected level of partitioning corresponds to the highest distance for which ε appeared alone on the dendrogram (3 in the example). Step 4 takes place after the second iteration (I) and gives the frequency distribution of the solution. This frequency distribution corresponds to the percentages of the number of times that ε came out with a specific number of clusters. Steps 1 to 4 are repeated, with the frequency distribution updated after each iteration. For example, if after 150 iterations, ε gives 15 times 3 clusters in X , the frequency for the “solution” 3 clusters is $15/150 \cdot 100 = 10$. At the end of the simulations (we advice 10000 simulations), the highest frequency of the potential solutions indicates the most probable number of clusters in the dataset (step 5). In some cases, the frequencies distribution can be multimodal. In Figure 10 (step 5, and Figure 12A hereafter) a case with a bimodality is presented, which indicates the possibility of 2 different solutions for the number of clusters in X . Note that it is not necessary to calculate all distance coefficients among the $n+1$ observations for each simulation because the distances between the n observations are already known. At each iteration, only the distance values between ε and the n original observations need to be

computed. When the data are very well partitioned, the algorithm rapidly converges towards the correct number of groups. If the frequency distribution point out the same solution for a consequent number of simulations (100 for example), the algorithm can be stopped before the end. In other words, the more compact the groups are, the fewer the number of iterations required. Of course, if the structure is entirely random, the histogram will never be stable and no clear mode is likely to be identified on the histogram.

2.2.2. *Data and tests*

The method was evaluated by performing three tests on different sets of data.

2.2.2.1. Test 1: use of the Iris dataset of Fisher (1936) and comparison with results from the literature

The so-called *Iris* dataset collected in the Gaspé Peninsula (eastern Québec) was used. This dataset was created by the botanist Edgar Anderson of the Missouri Botanical Garden, who gave permission to Fisher (1936) to publish and use the raw data. The dataset consists of 50 samples of flowers, each with four numerical descriptors: length and width of both *sepal* and *petal* expressed in centimeters. Using the four descriptors, data should be classified into 3 classes of Iris flowers corresponding to the species *Iris setosa*, *Iris versicolor*, and *Iris virginica*. This dataset was used because it is maybe the best known dataset in the literature that deals with clustering and pattern recognition.

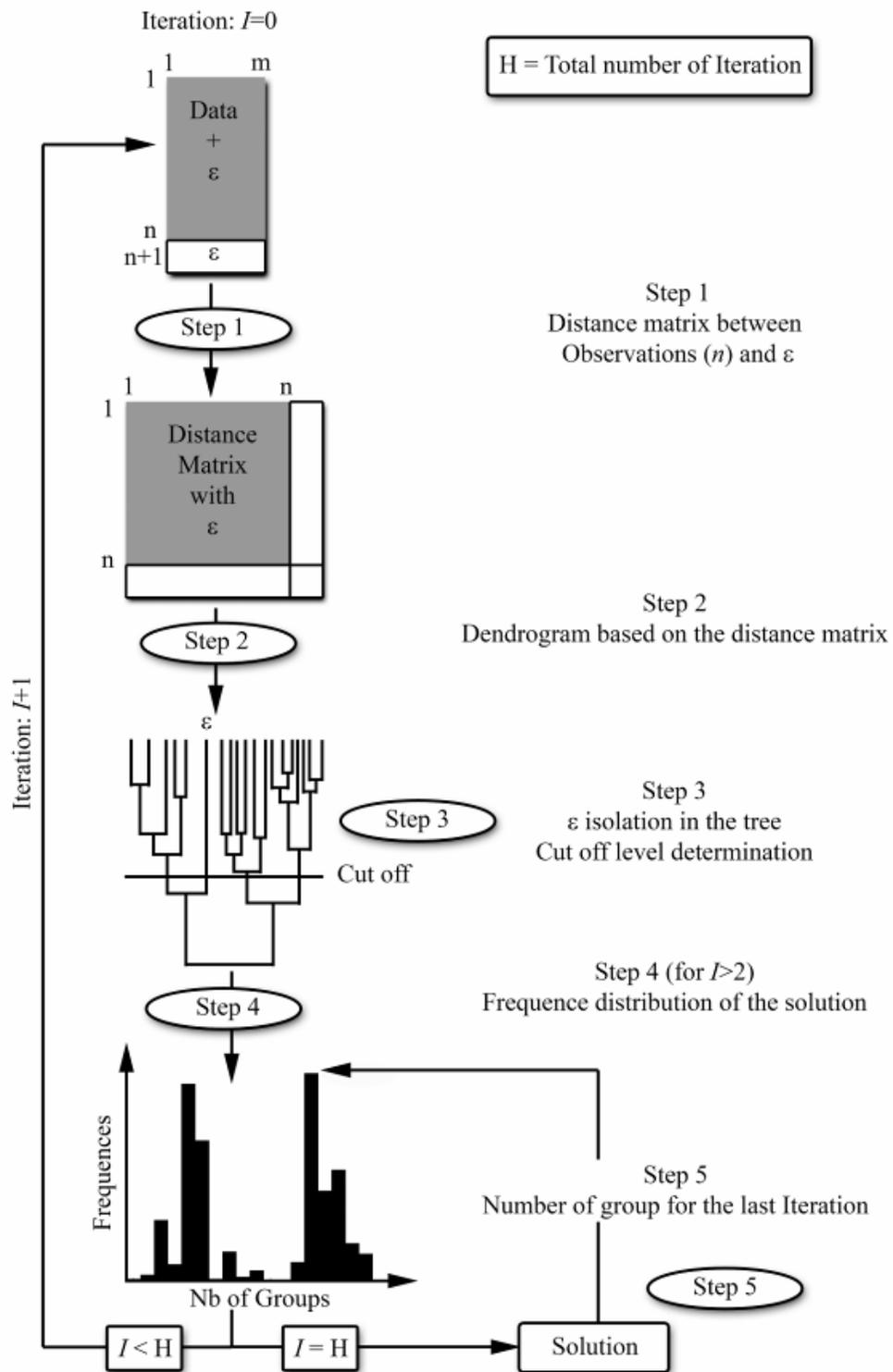


Figure 10: Schematic representation of the successive steps of the Random Simulation Test (RST).

2.2.2.2. Test 2: test using a simulated dataset with an *a priori* known number of groups

The simulations were generated using the program of Milligan and Cooper (1985). Datasets were built by varying three factors: (1) the number of clusters (2) the number of variables and (3) the number of observations in each cluster, called density level. The third factor was set by one of three values. The first parameter assumed an equal number of observations in each cluster. The second required that one cluster always contained 10% of the observations. The third parameter specified that one cluster encompassed 60% of the observations, with other observations distributed as equally as possible across the remaining clusters. For each simulation the same number of observations (50) was selected while the clusters were expected to be composed of 4, 6, or 8 objects. A systematic rule was fixed by Milligan and Cooper (1985), as never an overlap of cluster boundaries occurs with the first dimension of the variable space. The authors noted that the actual distribution of the points within clusters followed a truncated multivariate normal distribution. Overall 36 datasets (4 fixed numbers of cluster x 3 number of variables x 3 density levels) were generated, each replicated three times. This produced a total of 108 datasets. These basic 108 datasets were modified by adding outlier observations at a rate of 20% or 40% or by slightly modifying the coordinates of the observations. It is also possible to generate only noisy data (i.e. no compact clusters). These perturbed data were used to test the robustness of our algorithm.

2.2.2.3. Test 3: example using marine ecological data published and interpreted in Beaugrand et al. (2002)

Beaugrand *et al.* (2002) recently decomposed diversity of the marine calanoid copepod crustaceans (108 taxa) into species assemblages by means of a method called the indicator value (Dufrene and Legendre 1997) and multivariate analyses. One step involved in the identification of the species assemblages was the analysis of a matrix of indicator values (87 species by 44 indicator values corresponding to 44 identified regions). This matrix was first transformed into a distance between-species matrix using

the Bray and Curtis coefficient. Then, the hierarchical flexible clustering method (Lance and Williams 1967) was used to detect species assemblages. The resulting dendrogram was analysed considering the distance cut-off levels 1.152 and 0.530. These two levels were selected because they represented the best compromise between high distance levels in the dendrogram where groups still included heterogeneous taxa and low distance levels for which the differences between groups were due to minor change in the geographical distribution of species. The Random Simulation Test is used here to find out if the two levels selected empirically in this study also had a statistical basis.

2.3. Assessment

2.3.1. Test 1: Iris dataset of Fisher

Iris setosa is linearly separable from *Iris versicolor*, but *Iris virginica* cannot be linearly distinguished. To cluster this dataset, the Euclidean squared distance coefficient was computed and the flexible link for hierarchical clustering method proposed by Lance and Williams (1967) was applied in order to be consistent with the ecological data treatment performed by Beaugrand et al. (2002), test 3 below.

The partition and the estimation of the number of species using the Calinski and Harabasz (1974) index were not satisfactory. The actual number of clusters is three, corresponding to the three known species. However, using the C&H stopping rule, only two species were identified (Figure 11).

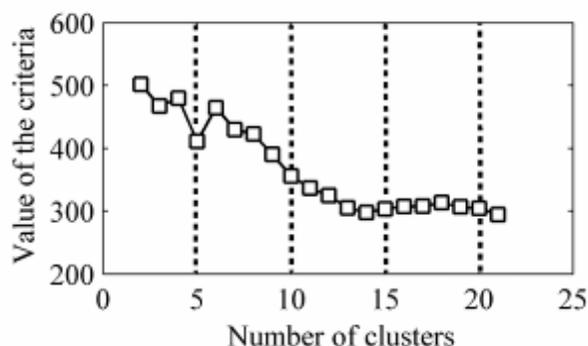


Figure 11: Result of the Calinski and Harabasz stopping rules applied on the Iris dataset between 2 and 21 clusters solutions.

The stopping rule was not able to distinguish *Iris versicolor* from *Iris virginica*. The third group, *Iris setosa* was correctly isolated. This result might be explained by the high variability of the Iris dataset and the overlapping descriptors of *I.versicolor* and *I.virginica*. Our technique identified correctly the three species from the biometric measurements contained in the dataset. Furthermore, only 6 flowers are misclassified, leading to 96% of correct classification of the *Iris* data. The natural variability of the dataset did not perturb the RST algorithm compared to C&H stopping rule. Several studies have also reported satisfactory results but they were generally based on supervised techniques, for which the result is dependent on the learning dataset.

2.3.2. Test 2: simulated datasets with an a priori known number of groups

These datasets were previously used by Milligan and Cooper (1985) in order to test 30 stopping rules with 4 hierarchical clustering methods. The same classification techniques have been used in this study in order to facilitate the comparisons with the results reported in Milligan and Cooper (1985).

For each dataset, a dissimilarity matrix between observations based on the Euclidean squared distances was computed in order to increase the distance among observations. From each distance matrix, four hierarchical clustering methods were applied: single link, complete link, unweighted pair group method with arithmetic mean (UPGMA) and Ward's minimum variance procedure. A total of 432 classification trees were generated (108 datasets x 4 types of cluster analysis). The datasets were tested by comparing results using the proposed Random Simulation Test and results from a stopping rule proposed by Calinski and Harabasz (1974) and recommended by Milligan and Cooper (1985). The index I_{CH} is calculated as (Calinski & Harabasz 1974):

$$I_{CH} = \frac{[\text{trace } B / (k - 1)]}{[\text{trace } W / (n - k)]} \quad (\text{Eq. 12})$$

trace refers to the sum of squared Euclidean distances between each observation and their centroid, n is the total number of entities and k the number of clusters in the solution. The B and W terms are the between and pooled within clusters sum of squares and cross products matrices, respectively.

Whatever the hierarchical clustering method used, the C&H stopping rule found 410 out of 432 simulated groups, a percentage of 95% of clusters (Table 4). The recovery of groups with RST was only 341, which represented 79% of group recovery (Table 4). The method performed badly when only two groups should be detected. However, our technique enables the distribution of the possible number of groups in a dataset to be displayed, which is not so for the C&H technique. When the two modes of the distribution are considered (10% of the datasets), the number of group recovery increased to 380/432, therefore a percentage of 88%. The use of a second mode, when present, was reasonable because it indicated that the method could not choose between 2 different solutions close in probability. Furthermore, the technique performs as well as or better than the C&H stopping rule when the number of groups increase, for example with 106 groups recovery against 103 for the C&H technique in the case of 4 groups (Table 4).

The number of cluster recovery was 101/108 for the Ward's minimum variance procedure, 102/108 for the simple link, 103/108 for the complete link and, 104/108 for UPGMA (Table 4) for the C&H index. The C&H index performed generally better than RST. The number of cluster recovery was 85/108 for the Ward's minimum variance procedure, 74/108 for the simple link, 90/108 for the complete link and, 92/108 for UPGMA (Table 4). However, when the first two better solutions are considered, results are better and there are cases for which our technique had a better group recovery. Indeed the Ward's minimum variance procedure provided excellent results for datasets with large number of clusters (4 or 5 clusters) and reached 100% of group recovery instead of 92% when the C&H index was applied (Table 4). However the results are still unsatisfactory for the single link method for which only 68% of the groups were recovered. RST performed better than the C&H index when the number of cluster increased and when the Ward's or UPGMA links were used (Table 4).

Table 4: Comparisons of the Calinski and Harabasz index and, RST method sensitivity to 4 different cluster analyses, (S) simple link, (C) complete link, (U) UPGMA and, (W) Ward's minimum variance procedure, considering the number of groups in the datasets. The total number of tested dataset by clustering analyses and number of groups is 27. '-1' and '-2' denote that the method detected one or two groups in less in comparison to the true number of groups while '+1', '+2' and '+3' mean that the method identified one, two or three or more groups in more in comparison to the true number of groups.

Number of true cluster	2					3					4					5					Total
	S	C	U	W	sum	S	C	U	W	sum	S	C	U	W	sum	S	C	U	W	sum	
Calinski and Harabasz index																					
-2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
-1	0	0	0	0	0	1	1	1	1	4	1	1	1	1	4	0	0	0	0	0	8
correct level	25	25	26	25	101	24	26	26	26	102	26	26	26	26	104	27	26	26	24	103	410
1	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0	0	1	1	3	5	7
2	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2
3	2	1	1	1	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
Not found	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RST (The highest number of group frequency)																					
-2	0	0	0	0	0	1	0	0	0	1	4	0	0	0	4	7	1	3	0	11	16
-1	5	0	0	0	5	6	0	2	0	8	3	1	2	0	6	5	2	4	0	11	30
correct level	19	16	23	7	65	20	24	24	24	92	20	26	25	27	98	15	24	20	27	86	341
1	1	0	1	2	4	0	1	1	1	3	0	0	0	0	0	0	0	0	0	0	7
2	0	2	0	4	6	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0	8
3	1	7	2	11	21	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	22
Not found	1	2	1	3	7	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	8
RST (Two highest number of group frequencies)																					
-2	0	0	0	0	0	1	0	0	0	1	2	0	0	0	2	3	1	3	0	7	10
-1	2	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	3
correct level	23	17	23	9	72	26	25	26	25	102	25	27	27	27	106	23	26	24	27	100	380
1	0	0	1	2	3	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	4
2	0	2	0	3	5	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0	7
3	1	6	2	10	19	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	20
Not found	1	2	1	3	7	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	8

Table 5: Two examples showing the effects of outliers on Calinski and Harabasz index (C&H) and RST technique using the dataset generated by the algorithm of Milligan and Cooper (1985). The example a) is composed of 4 clusters whereas the example b) is composed of 3 clusters. Both examples contain 50 observations and 10 outliers (20%) in the dataset. The real clusters of data are shown in the first part of the table and the corresponding results obtained with the C&H index and the RST are shown in the second and third part of the table, respectively.

Real clusters of data					
a)	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Outliers
	1-12	13-24	25-37	38-50	50-60
b)	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Outliers
	1-16	17-33	34-50	-	50-60
Calinski and Harabasz					
a)	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Outliers
	1-12 + (51,52)	13-24 + (53,54,60)	25-37 + (55,56,57)	38-50 + (58,59)	-
b)	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Outliers
	1-16 + (51,52)	17-33 + (53,54,55,56)	34-50 + (57,58,59,60)	-	-
RST					
a)	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Outliers (in 8 clusters)
	1-12	13-24	25-37 + (55)	38-50 + (58)	51,52,53,54,56,57,59,60
b)	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Outliers (in 6 clusters)
	1-16	17-33	34-50 + (57,58)	-	51,52,53,54,55,56,59,60

The software developed by Milligan allowed the simulation of data with three different perturbations, increasing the variability in the clusters. First, 20% and 40% of outliers were added to the original dataset. Table 5 shows results from two examples, first with 4 clusters and second with 3 clusters, both with 20% of outliers. The C&H index did not isolate the outliers while the RST algorithm isolated 80% of these in external groups and the actual groups were only slightly perturbed. It should be noted

that such cases with a significant amount of outliers are widely met in ecological datasets.

For the first example with 4 clusters; clusters 1 and 2 were perfectly identified while clusters 3, and 4, included one outlier using the RST. The same example processed by the C&H index included 2 outliers in clusters 1 and 4 and 3 outliers in clusters 2 and 3, respectively. For the second example with 3 clusters, cluster 3 enclosed 2 outliers for the RST instead of 4 for the C&H index while cluster 1 and 2 are correctly isolated by RST and highly contaminated by outliers using C&H index.

Second, two levels of error-perturbed coordinates were applied to the dataset that increased the variability intra-groups. Results showed both decrease of C&H and RST cluster recovery about 50%. The C&H index tended to underestimate the number of clusters (70% of the misclassified) while the RST increased the number of groups (50 % of the misclassified) which is related to the increase of the variability of the observations.

Finally, it is possible to generate random noisy data. Due to the algorithm construction of C&H, clusters are always found. Indeed more than 50% of the simulations found that there are 2 clusters in the random dataset. By contrast, the RST found no clusters in more than 80% of datasets.

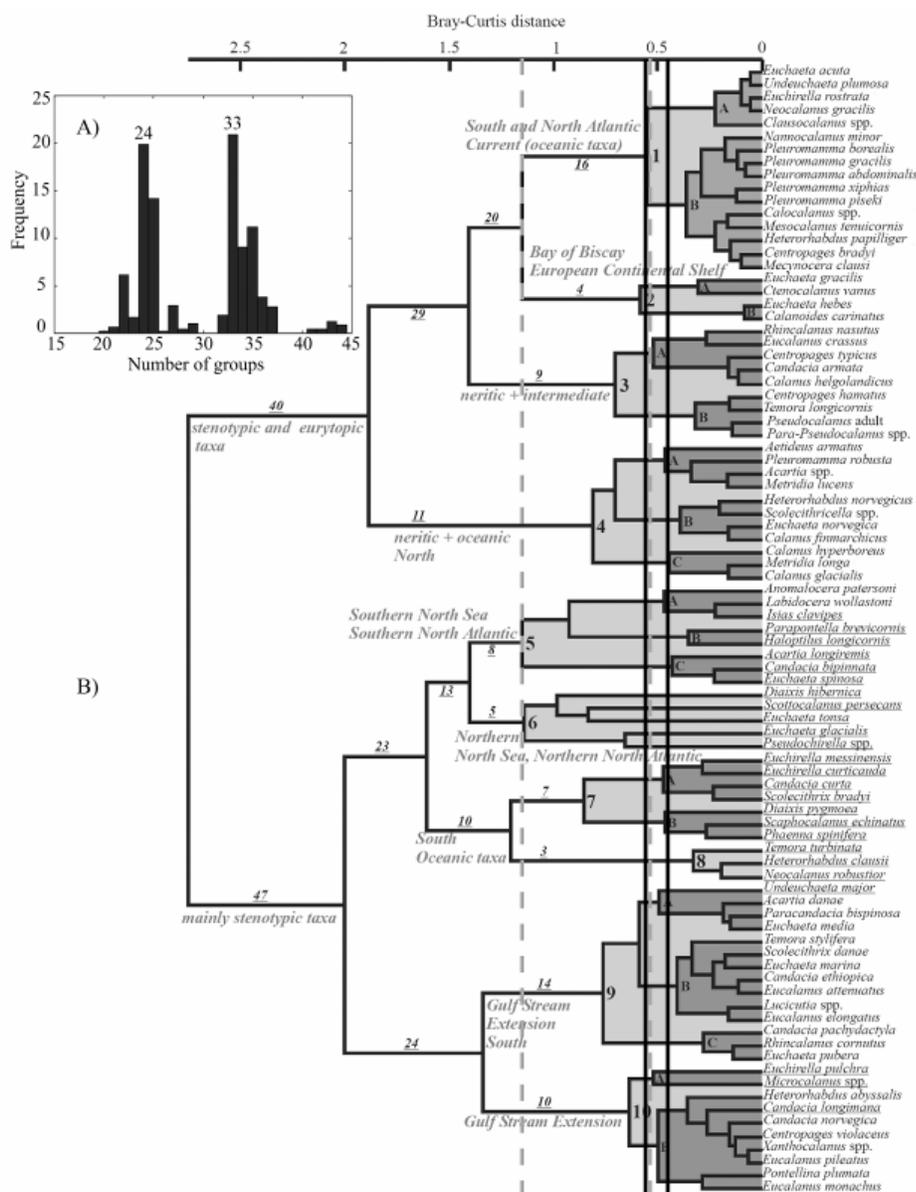


Figure 12: (A) Frequencies distribution of the number of cluster for the ecological dataset of Beaugrand et al. (2002). (B) Dendrogram of calanoid copepod species resulting from the flexible hierarchical clustering method used by Beaugrand et al., (2002). Underlined taxa have indicator value less than 25%. Groups (at the distance cut-off level of 1.152) are indicated in pale grey. Subgroups (distance cut-off level of 0.53) are indicated in dark grey. Numbers underlined and in italic represent the number of taxa for each group. Some characteristics of each group are given in grey and italic. Underlined species are species rarely collected by the Continuous Plankton Recorder survey. The dashed grey lines are cut-off levels empirically chosen by Beaugrand et al. (2002). Dark lines are the cut-off levels determined by the Random Simulation Test (0.56 and 0.45).

2.3.3. Test 3: ecological application

The histogram based on the Random Procedure Test exhibited two modes, suggesting the presence of two optimal cut-off levels in the dendrogram (Figure 12A). The first mode suggests the presence of 24 groups while the second mode, with the highest amplitude, suggests 33 groups. The first level detected in our study is very close to the partition empirically chosen by Beaugrand *et al.* (2002). The second mode, identifying 33 groups, allowed the detection of finer relationships between species. New groups were formed on the basis on subtle difference in the spatial distribution of species at a seasonal scale. For example, group 3A was divided into two small groups, *Eucalanus crassus* and *Rhincalanus nasutus* being rarer than the two other species. The species *Eudeuchaeta major* was removed from group 9C (Figure 12B). Such species also belongs to species rarely sampled by the continuous plankton recorder (CPR) survey.

The use of RST on data analysed by Beaugrand *et al.* (2002) confirmed their choice of the partition level of the dendrogram. However another threshold was detected. It is likely that the second threshold was influenced by the increased chance of the random variable to be included in a group when the variable goes towards the origin of the dendrogram. Therefore, the priority should be given to the mode that corresponds to the highest distance in the dendrogram. This threshold corresponded well with the selected level by Beaugrand *et al.* (2002). These authors selected a cut-off level of 0.53 while the procedure found two optimal levels (0.56 and 0.45). The procedure therefore provided satisfactory results for this noisy dataset.

2.4. Discussion

A cluster analysis partitions data into a number of subsets (Everitt *et al.* 2001). In the last 50 years, many different stopping rules have been proposed to determine the number of clusters in a dataset (Gordon 1996; Milligan 1981; Podani 1998). Unfortunately, none of them performed well in all conditions. Dubes (1993) calls this difficulty to select a cut-off level of a dendrogram the fundamental problem of cluster validity. Xu and Wunsch (2005) have recently listed four different approaches used currently to identify the level of partition in a dendrogram. The visualization of dataset

(first approach) can be applied only for simple datasets, which can be projected onto a plan using multivariate analyses such as Principal Components Analysis (PCA) or Multi Dimensional Scaling (MDS). The construction of indices (stopping rules, second approach) compare variations inter and intra clusters. Milligan and Copper (1985) tested 30 criteria and the Calinski and Harabasz index achieved the best performance for 432 simulated datasets. It is important to bear in mind that the success of an index depends largely on the data utilized to test it. The use of a synthesis of different techniques is recommended to get the right number of clusters (Everitt et al. 2001). The optimization of some criterion functions under probabilistic mixture-model framework is a third approach. Such a technique can be compared to an optimization parameter procedure that fits a statistical model with observed data. A statistical test can help to chose among competing cluster models objectively (Anderson and Clements 2000). A large number of criteria have been proposed in the literature including the Akaike's information criterion (AIC; Akaike 1974) or the Bayesian inference criterion (BIC; Pelleg and Moore 2000; Schwarz 1978). The use of constructive clustering algorithms (neural network) is the fourth approach (Getz et al. 2000). This technique is flexible and the number of clusters is dynamically adjusted (Blatt et al. 1997). However, even if the problem of the determination of the number of cluster is avoided, the problem of variable selection remains, influencing the number of clusters. Chon et al. (2000), analysing benthic invertebrates, developed a model patterning the community dynamics of several species. Input data were simply monthly changes in density and species richness. Two artificial models were tested, the Adaptive Resonance Theory (ART) and the Kohonen network. Species were grouped into selected taxa to reduce their number and also the noise inherent to the series. The authors recognized that each configuration after convergence may be different, depending upon the initial training. The main problem is to appreciate how correctly the learning method perceives the dynamic behaviour of input data.

Table 6: Non exhaustive literature review on the determination of the number of cluster using Fisher's dataset.

Technique	Number of clusters	References
Bayesian Ying-Yang Model (BYY-HDS)	3	(Guo et al. 2002)
Bayesian Ying-Yang Model (BYY-HDS)	3	(Hu and Xu 2004)
Support Vector Machine	3	(Moguerza et al. 2002)
Akaike's information criterion (AIC)	5	(Hu and Xu 2004)
Minimum Description Length (MDL)	2	(Hu and Xu 2004)
Consistent Akaike's Information Criterion (CAIC)	2	(Hu and Xu 2004)
Krzanowski and Lai (KL)	4	(Mufti et al. 2005)
Loevinger's measures	4	(Bertrand and Mufti 2006)
Voting-k-means algorithm	2	(Fred 2001)
RST	3	This study

These studies have shown that there is still a need to improve the criteria that enable the selection of significant clusters. The RST is a new approach of the clustering question in the sense that the algorithm takes into account the variability of the data. Biological and ecological datasets are very variable and previous stopping rules are very sensitive to variability (Bertrand and Mufti 2006; Mufti et al. 2005). Cut-off level such as the C&H index, were adapted for well partitioned data (Milligan & Copper, 1985). Our results show that this index did not perform well when high variability was introduced in the data (Table 5).

Table 6 provides a non exhaustive review of the number of clusters determined by recent methods, on the well known *Iris* dataset. Only three of them found 3 clusters: Our study, the Bayesian Ying-Yang Model and the vector supervised machine. The two

latter are learning methods whereas the RST is an unsupervised technique. The neural networks are more flexible than stopping rules but they need learning sets. The efficiency of the method is highly related to the quality of the learning (Chon et al. 2000). On the contrary, RST only depends on the tested dataset, which makes it a powerful tool for data with large natural variability.

The RST can detect a dataset that cannot be partitioned. This property constitutes an important improvement brought by our algorithm. When there is one cluster (all the observations pulled together), the frequency distribution of the solutions is uniform and the probability for any solution is very low, usually less than 10%. Conventional techniques test the variability inter- and intra-clusters that obviously lead to a minimum of two clusters (Milligan & Copper, 1985). Therefore, none only capable to cluster highly variable data, RST can identify the data that cannot be classified, whereas other conventional techniques would always find a number of clusters.

2.5. Comments and recommendations

The literature emphasises the existence of many criteria to determine the number of clusters but none of them has been found perfect. RST does not derogate to the rule. Two main limitations of the technique have been revealed in this study. First, the use of the simple link gives unsatisfactory results in the case of the data generated by the software of Milligan and Cooper (1985). This result can be explained by the fact that the more we go up in the dendrogram, the greater the probability that a variable be clustered with another by chance alone. In the case of the single link, only a small affinity with an observation that belongs to another cluster is sufficient to stop the algorithms that increase artificially the number of groups. Hence when observations are highly variable, we advice to use the UPGMA (or other average clustering) for which this effect is smaller or the complete link for which this effect is considerably reduced. Indeed the affinity between the random observation (ϵ) and the other observations is tested for each observation of the clusters. Furthermore for the UPGMA and the complete link, the later the random observation appears in the cluster the lower is that effect. Second, when the

dataset is composed of only two groups, the RST tend to overestimate the number of clusters. However the RST as been developed to cluster high variability ecological data that usually contain more that 2 clusters. In that case it might be better to use discriminant functions as described by Fischer (1936).

RST is highly adapted to data showing high variability, which is often the case in biology or ecology. To our best knowledge, this technique is the only one that enables the absence of cluster to be detected. RST might be preferentially used with average clustering or complete clustering to partition datasets with large number of groups. Future work may improve the technique. Two random observations, instead of one currently, could be used for example but the time of calculation would increase by a factor two. Despite some limitations revealed by this study, we think that our technique represents a new way to approach the clustering question.

This methodological chapter presents the new RST algorithm that has been developed in order to be used in the following dissertation, to cluster profiles of aggregate size distribution on a global scale. The RST will be applied in chapter IV to facilitate the grouping of oceanic sites having similar profiles of aggregate size distribution.

CHAPTER III

PARTICLE SIZE DISTRIBUTION AND FLUX IN THE MESOPELAGIC: A CLOSE RELATIONSHIP

3.1. Introduction

Large aggregates, also known as marine snow, are ubiquitous in the water column and comprise a significant fraction of particle mass and of vertical particulate organic carbon (POC) flux. More than a conveyor of the fixed carbon from the euphotic zone (biological pump), large aggregates play the role of small ecosystems. They provide a unique chemical environment where both photosynthesis and microbial degradation can occur at rates greater than in the surrounding water. In addition, by moving material downward, they provide a rich food source for the mesopelagic zone.

Although important in the ocean, large aggregates are difficult to collect and study because of their fragile nature. Sediment traps have been used widely to collect settling material, to describe vertical flux and its decrease with depth, and to document the chemical transformations of settling aggregates (Martin et al. 1987; Turley et al. 1995; Wakeham et al. 1984). The particles collected in a sediment trap occur over a range of sizes and settling rates when suspended in the water column but lose their individuality in the sediment trap amalgamation. This loss of identity has been partially overcome by the use of a polyacrylamide gel in the collectors, which allows the determination of particle size distributions of these aggregates (Jannasch et al. 1980; Kiørboe et al. 1994; Waite and Nodder 2001). Sediment traps provide an important sampling approach but do not provide the spatial coverage or the detailed descriptions of particle size distributions that are useful in mechanistic descriptions of particle dynamics.

The availability of imaging sensors and computer systems to analyze their observations has led to the development of *in situ* camera systems that can be used to produce profiles of aggregate size distribution and abundance (Asper 1987, Davis and Pilskaian 1992; Gorsky et al. 1992; Honjo et al. 1984). Despite their ability to provide

detailed particle size distributions with high spatial resolutions, imaging systems cannot describe aggregate chemical composition without more information about the relationship between particle size and composition (Burd et al. 2007).

Table 7: List of parameters and their dimension (M for mass, L for length, T for time).

Symbol	Description	Dimension
A	Constant for F_E	$M L^{-2-b} T^{-1}$
a	Constant for $m(d)$ (Eq. 18)	$M L^{-D}$
b	Constant for F_E	-
c	Constant for $w(d)$ (Eq. 19)	$L^{2-D} T^{-1}$
d	Particle diameter	L
D	Fractal dimension	-
F	Generic flux	$M L^{-2} T^{-1}$
F_E	Flux estimation using (A and b)	$M L^{-2} T^{-1}$
F_T	Sediment trap flux measurement	$M L^{-2} T^{-1}$
$F_m, F_{poc}, F_{pic}, F_{pon}$	Mass, POC, PIC and PON fluxes estimations	$M L^{-2} T^{-1}$
ΔF_c	Differences between sediment trap and spectral-estimated fluxes	$M L^{-2} T^{-1}$
g	Gravitational acceleration	$L T^{-2}$
h	Coefficient to convert particle mass to particle excess of mass	-
m	Particle mass	M
n	Particle number spectrum	L^{-4}
V	Volume of a particle	L^3
w	Particle settling rate	$L T^{-1}$
α	Constant for $m(d)$ (Eq. 14)	$M L^{-3}$
β	Constant for $w(d)$ (Eq. 15)	$L^{-1} T^{-1}$
ρ	Particle density	$M L^{-3}$
ρ_0	Fluid density	$M L^{-3}$
$\Delta\rho$	Particle excess density	$M L^{-3}$
ν	Seawater viscosity	$L^2 T^{-1}$

Particle concentrations are frequently presented as number spectra (Burd et al. 2000; Jackson 1990; Stemmann et al. 2004b). The size spectrum of a “population” of particles is usually defined in terms of the number concentration of particle (ΔC) in a given small size range (Δs): $n = \Delta C / \Delta s$. The particle mass in that size range is $m(s) n(s) \Delta s$ and the mass flux spectrum is $m(s) n(s) w(s) \Delta s$, where $m(s)$ is the mass of an

individual particle and $w(s)$ is its settling velocity. Any measure of particle size can be used for s , although particle diameter (d) is frequently used. The total mass flux (F) is the mass flux spectrum integrated over all particle sizes. Using diameter as a measure of particle size, then:

$$F = \int_0^{\infty} n(d)m(d)w(d)dd \quad (\text{Eq. 13})$$

The mass of a spherical particle is given by

$$m(d) = \alpha d^3 \quad (\text{Eq. 14})$$

where $\alpha = \pi \rho / 6$ and ρ is its average density. Its settling rate can be calculated using Stokes Law:

$$w(d) = \beta d^2 \quad (\text{Eq. 15})$$

where $\beta = g(\rho - \rho_0)(18\nu\rho_0)^{-1}$, g is gravitational acceleration, ρ_0 is the fluid density, and ν is the kinematic viscosity (see Table 7 for summary of notation).

Aggregates do not have a constant density, so Eq. 14 and Eq. 15 are not useful without more information. In fact, particle mass and settling rate are often described using relationships of the form yd^x by fitting data from observations, usually made in the surface layer (Alldredge 1998; Alldredge and Gotschalk 1988; Ploug and Grossart 2000). This is equivalent to α and β being functions of d , not constant. Note that if both $w(d)$ and $m(d)$ are given by power relationships, so is the combined quantity,

$$w \cdot m = A \cdot d^b \quad (\text{Eq. 16})$$

For the above case of constant density shown in Eq. 13, and Eq. 14, $b=5$.

To our knowledge, only a few studies relating aggregates size and flux have been made for the deep ocean (Asper 1987; Ratmeyer and Wefer 1996; Walsh and Gardner 1992). In this paper, we relate sediment trap data to particle size distributions to estimate the vertical fluxes of mass, particulate organic carbon (POC), particulate inorganic carbon (PIC) and particulate organic nitrogen (PON). This technique allows us to estimate particle fluxes with much greater vertical resolution than is feasible with

sediment traps alone. We then apply the technique to a series of profiles taken in the equatorial Pacific.

3.2. Material and methods

3.2.1. Instrument and data

We have measured particle size distributions between the surface and 1000 m depth throughout the ocean during the last 2 decades using three generations of the Underwater Video Profiler (UVP). The camera in the UVP records objects illuminated in a slab of water whose volume ranges from 0.20 to 10 L, depending on the UVP version. An image provides information about the size and shape of particles in its field of vision which can be used to calculate particle size distributions (Gorsky *et al.* 1992; Gorsky *et al.* 2000). The detection limit has improved through time, with the minimum observed particle diameter improving from 250 down to 90 μm ; the effective maximum particle size depends on the sample volume (Table 8). The UVP is lowered on a cable at a speed chosen to avoid overlapping regions in the images (1 m s^{-1}). The images are recorded digitally and processed by image analysis software to yield the projected area for each particle. The equivalent spherical diameter (ESD) of each particle is calculated assuming that the projected shape is a circle.

Table 8: Definition of the size range and volume sampled characteristics of the 3 different Underwater Video Profilers (UVP) used in this study.

Model	Size range	Vol. sampled	Reference
UVP 2a	>250 μm -1.5 mm	0.28 L	(Gorsky <i>et al.</i> , 1992)
UVP 2c	>150 μm -1.5 mm	0.23 L	(Gorsky <i>et al.</i> , 1992)
UVP 3b	>90 μm -5 mm	0.60 L	(Gorsky <i>et al.</i> , 2000)
UVP 4a	>90 μm -2 cm	10.5 L	(Gorsky <i>et al.</i> , 2000)

The instruments have been calibrated in a sea-water tank using natural particles of different aggregate types to determine the conversion between pixel and cm (Stemmann et al. 2002). Different generations of instruments have been deployed together to ensure that their measurements are consistent (Guidi et al. 2007).

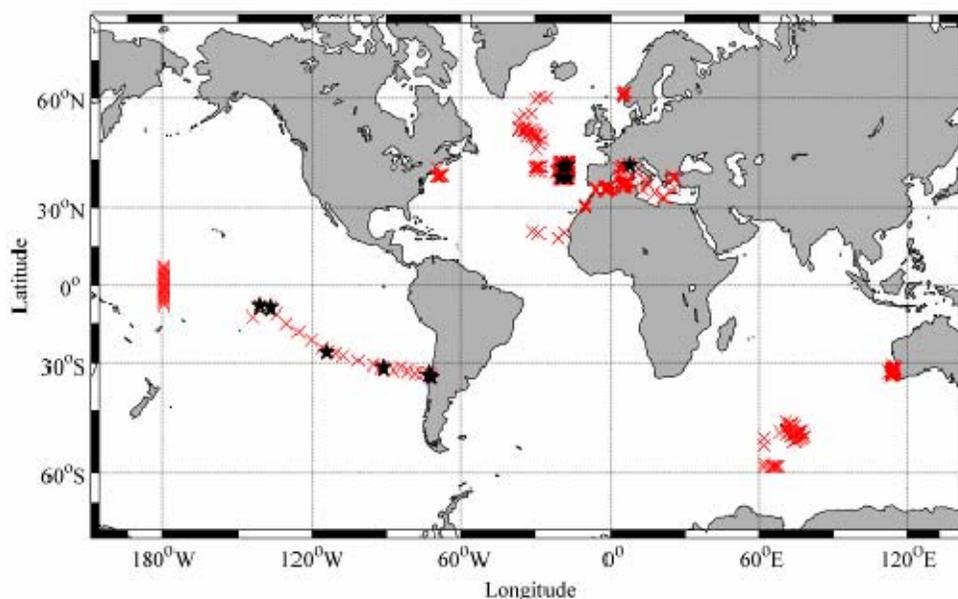


Figure 13: Location of all Underwater Video Profiler (UVP) profiles (red crosses) and associated sediment trap deployments (black stars). There were 1254 total profiles and 11 associated sediment trap locations.

We now have a database of particle size distributions from 1254 profiles for a range of seasons and locations (Figure 13). In this study, we restricted the size range of interest to 250 μm - 1.5 mm in order to use data from all UVP generations (Table 8), although we also performed the same calculations on a subset of data with the larger size range associated with UVP4a (90 μm -2 cm).

Table 9: Location, position, and duration of the deployments of the sediments trap used in this study. References: A- (Guieu et al. 2005); B-(Stemmann et al. 2002); C -Miquel and Gasser, submitted.

Location	Station	Lat.	Long.	Begin	End	Depth	Ref.
North Atlantic	NW	42.98	-19.07	2/21/01	2/6/02	400	A
North Atlantic	NW	42.98	-19.07	2/21/01	2/6/02	1000	A
North Atlantic	NE	43.83	-17.33	2/18/01	2/6/02	400	A
North Atlantic	NE	43.83	-17.33	2/18/01	2/6/02	1000	A
North Atlantic	SE	39.5	-17.25	2/18/01	2/6/02	400	A
North Atlantic	SE	39.5	-17.25	2/18/01	2/6/02	1000	A
North Atlantic	SW	39.56	-19.85	2/21/01	8/21/01	400	A
North Atlantic	SW	39.56	-19.85	2/21/01	8/21/01	1000	A
Mediterranean	DYFAMED	43.42	7.86	6/27/1987	-	100	B
Mediterranean	DYFAMED	43.42	7.86	6/27/1987	-	200	B
Mediterranean	DYFAMED	43.42	7.86	6/27/1987	-	1000	B
South Pacific	Marquise Island	-8.25	-141.14	10/26/04	10/29/04	100	C
South Pacific	Marquise Island	-8.25	-141.14	10/26/04	10/29/04	200	C
South Pacific	HNLC	-9	-136.53	10/31/04	11/2/04	100	C
South Pacific	HNLC	-9	-136.53	10/31/04	11/2/04	200	C
South Pacific	Central Gyre	-26.04	-114.02	11/12/04	11/16/04	200	C
South Pacific	Central Gyre	-26.04	-114.02	11/12/04	11/16/04	400	C
South Pacific	East Gyre	-31.52	-91.25	11/25/04	11/30/04	200	C
South Pacific	East Gyre	-31.52	-91.25	11/25/04	11/30/04	300	C
South Pacific	Chilean upwelling	-33.58	-73.23	12/6/04	12/8/04	100	C
South Pacific	Chilean upwelling	-33.58	-73.23	12/6/04	12/8/04	200	C
South Pacific	Chilean upwelling	-34.36	-72.26	12/9/04	12/11/04	100	C
South Pacific	Chilean upwelling	-34.36	-72.26	12/9/04	12/11/04	200	C

Some of the UVP profiles were made in conjunction with sediment trap deployments (PPS5, Table 9). The sediment traps were of different types, both moored (Mediterranean Sea) and drifting (Pacific and North Atlantic). Samples collected in the traps have been analyzed total mass, organic carbon, inorganic carbon, and organic nitrogen and the associated fluxes calculated.

UVP data collected within 0.2° latitude and longitude of a sediment trap location, 10 meters of its depth, and 5 days of its deployment were used for the comparisons. An average aggregate size spectrum is calculated using the pertinent UVP data if more than one profile fit the criteria. There are 118 data sets with both particle size distributions from the UVP and sediment trap flux measurements; there are only 39 for the analysis using the larger size range.

3.2.2. Flux estimation from aggregates size

If the size distribution and the values of A and b are known, then a mass flux can be calculated from a size spectra using Eq. 13 and Eq. 16. The fluxes calculated this way can be compared to matching sediment trap observations. Because we did not know the appropriate values of A and b , we used a minimization procedure to find those two values that provided the best fit between the two fluxes – sediment trap and particle size distribution-derived.

We used the Matlab function *fminsearch* (The Mathworks, Inc., Natick, MA) to find the values of A and b that minimized the log-transformed differences (ΔF_c) between sediment trap and spectral-estimated fluxes:

$$\Delta F_c = \sum_i [\log(F_{T,i}) - \log(F_{E,i})]^2 \quad (\text{Eq. 17})$$

where $F_{T,i}$ is the sediment trap flux value and $F_{E,i}$ the associated flux based on Eq. 13. for the i th observation. The logarithmic transformation was used to give equal weight to differences for small and large fluxes. Note that the sample integration is only for particles between 250 μm - 1.5 mm, not the 0 - ∞ shown in Eq. 13.

We also tested the ability of a previously determined set of relationships for w and m to match the ways of estimating fluxes. Alldredge and Gotschalk (1988)

calculated that their diatom aggregates in the surface waters off Santa Barbara, CA, followed the relationships of $m = 8.8 \cdot d^{1.125}$ and $w = 50 \cdot d^{0.26}$ (in mg m^{-3} and m d^{-1}), implying that $A = 440$ (in $\text{mg m}^{-2} \text{mm}^b \text{d}^{-1}$) and $b = 1.385$.

3.2.3. Error estimation of the parameters

The minimization procedure yields only one pair of parameter values. We used a jackknife procedure to estimate the errors of the estimates. The minimization was performed on 1000 subsamples one third the size of the original and composed of data pairs selected randomly from the original data set. The results provide us with the frequency distribution of A and b .

3.3. Results

3.3.1. Comparing size spectral flux estimates to observed fluxes

Pearson's correlation coefficient is 0.40 between the two fluxes when Alldredge and Gotschalk (1988) values for A and b are used. However, the particle size estimate of flux consistently overestimates the sediment trap fluxes, with 95% of the estimates larger than the observations (Figure 14). Furthermore the overestimation is as much as a factor of 100 greater.

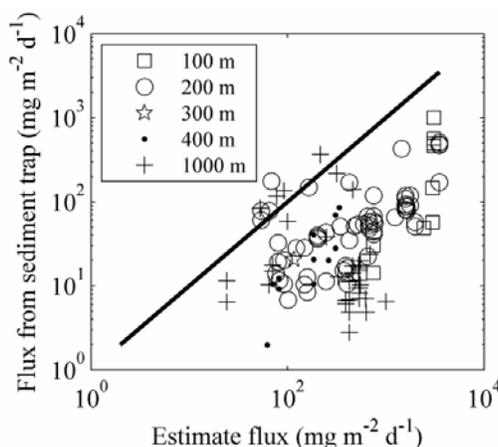


Figure 14: Comparison of measured sediment trap mass flux with that calculated using size spectra and Alldredge and Gotschalk (1988) relationships ($n=118$). Symbols represent trap deployments depths: 100 m - open squares, 200m - open circles, 300m - open stars, 400m - black dots and 1000m - crosses.

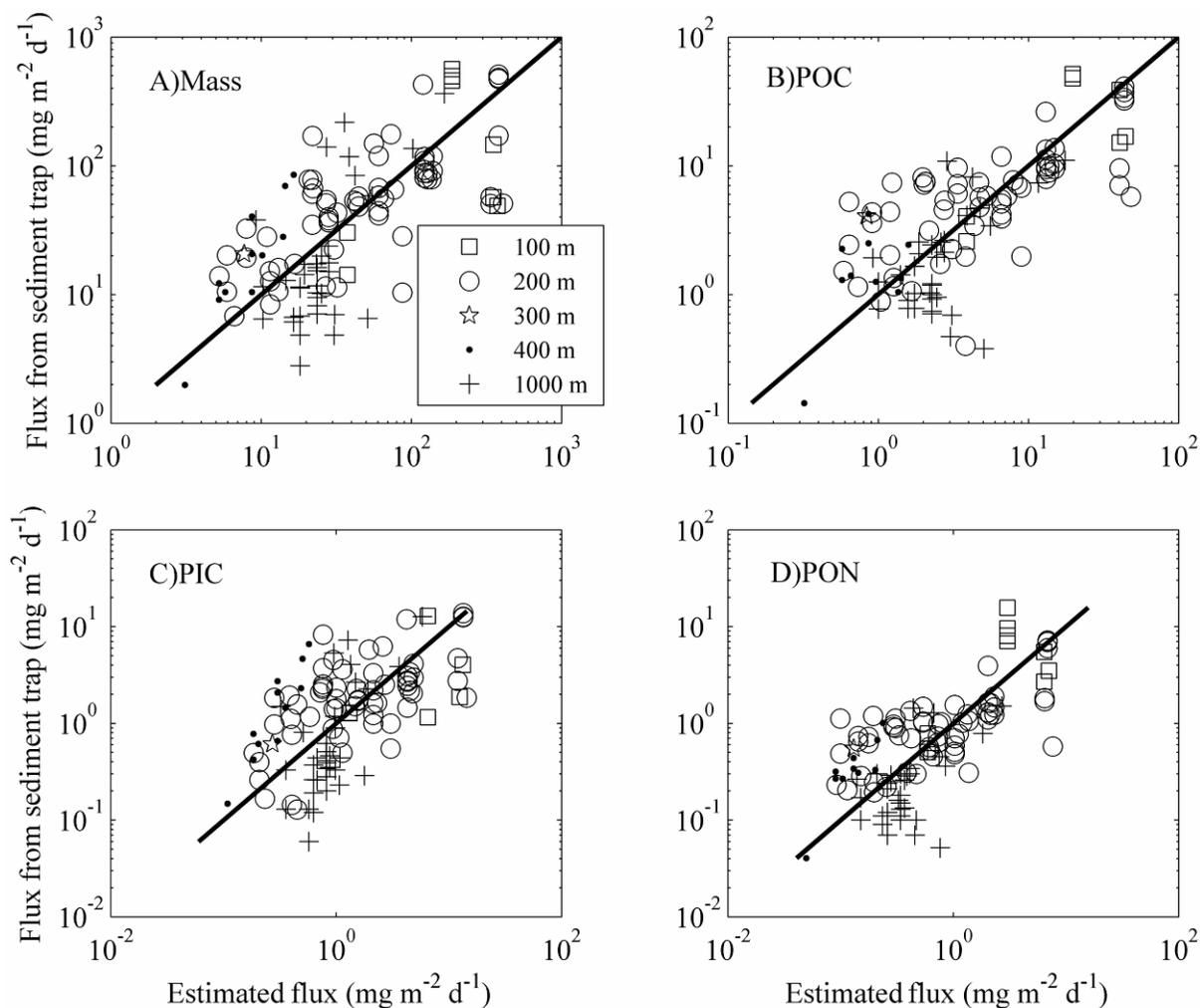


Figure 15: Measurement of the mass (A), particulate organic carbon (POC: B), particulate inorganic carbon (PIC: C) and particulate organic nitrogen (PON: D) fluxes by sediment traps, compared to the estimation of the mass, POC, PIC, PON fluxes using the UVP and the relationships between the aggregates size and the previous fluxes (cf Eq. 15,16,17 and 18) $n=118$. Symbols represent trap deployments depths: 100 m - open squares, 200m - open circles, 300m - open stars, 400m - black dots and 1000m - crosses.

The minimization procedure provided flux estimates which are better for mass (F_m), POC (F_{poc}), PIC (F_{pic}) and PON (F_{pon}) fluxes (Figure 15). Pearson's correlation coefficients between the two fluxes vary from 0.57 to 0.73 for F_{pic} and F_{pon} respectively. The values of b are quite consistent for the different fluxes, with largest differences

equal to 0.4 between F_m and F_{pon} (3.52 and 3.93). The standard deviations on the values for b estimated using the jackknife procedure, are 0.7-0.8 (Table 10). Most of the differences in the parameter values for the different material fluxes are for A and reflect the material composition. The ratio F_m to F_{poc} is about 10 and F_{poc} to F_{pon} is 6.2, similar to the Redfield ratio for C:N of 6.6 and reflecting the sediment trap measurements.

Table 10: Coefficient (A) and exponent (b) and their associated standard deviation (STD) of the empirical relationship between the aggregate size and their related mass, particulate organic carbon (POC), particulate inorganic carbon (PIC) and particulate organic nitrogen (PON) fluxes determinate by minimization of the fluxes estimation by the Underwater Video Profiler (UVP) and the sediment traps measurement, $n=118$.

Generic relationship: $F = A \cdot d^b$							
Fluxes	Symbol	A	STD A	b	STD b	R ²	P
Mass	F_m	109.5	32.6	3.52	0.72	0.70	<0.0001
POC	F_{poc}	12.5	3.40	3.81	0.70	0.73	<0.0001
PIC	F_{pic}	3.97	1.13	3.60	0.76	0.57	<0.0001
PON	F_{pon}	2.02	0.59	3.93	0.82	0.71	<0.0001

There appears to be little systematic difference in the relationship between estimated and observed fluxes within the depth range of 100 and 1000 m. Even if there is only little difference with depth, mass and PIC have similar evolution, as well as POC and PON fluxes (Figure 16). The mass flux is highly variable and ranges from 10 mg m⁻² d⁻¹ to 1000 mg m⁻² d⁻¹.

3.3.2. Error estimation

The standard deviations of A and b from the jackknife procedure are ~ 30% and ~20% of the minimization values for all of the different fluxes (F_m , F_{poc} , F_{pic} , and F_{pon} ; Table 4).

A map of ΔF for a range of parameter values provides a different perspective on the sensitivity of the residual to these parameters (Figure 17). The results show a well-defined region for the minimum. The values of A and b calculated for the 1000 subsamples in the jackknife procedure fall in the minimum region. They follow a normal distribution (Kolmogorov-Smirnov test significant at the 5% level) from which the mean and the standard deviation have been calculated (Table 10). Results for the other relationships (F_{poc} , F_{pic} , and F_{pon}) are similar but not shown.

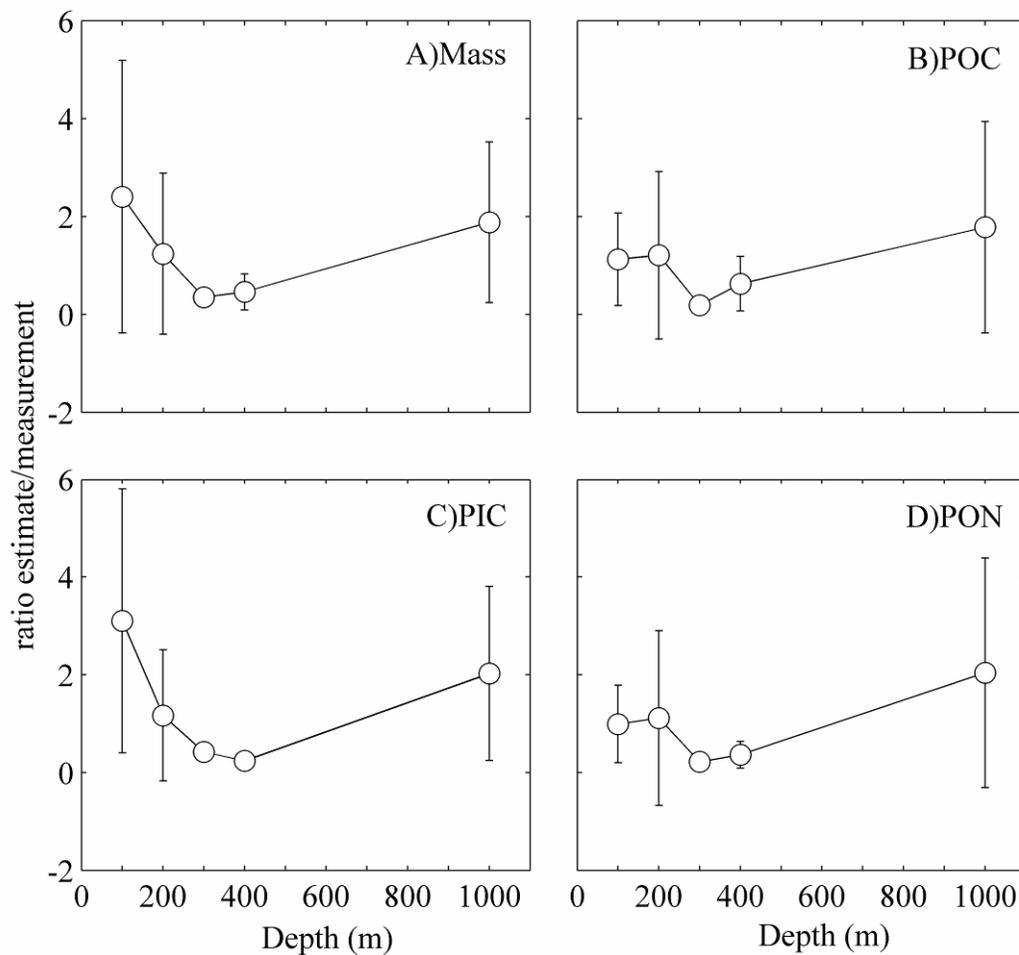


Figure 16: Ratio of estimates and measurements of the A) mass fluxes, B) POC fluxes, C) PIC fluxes, D) PON fluxes as function of the depth of sediment traps.

3.4. Discussion

The flux measurements cover three orders of magnitude, a range which can hide variations that are absolutely small but locally significant. Such variation is consistent with fluxes measured in oligotrophic and eutrophic regions (Figure 15A). Despite the variability of various flux measures, simple power relationships relate them to the particle size spectra. This has several implications.

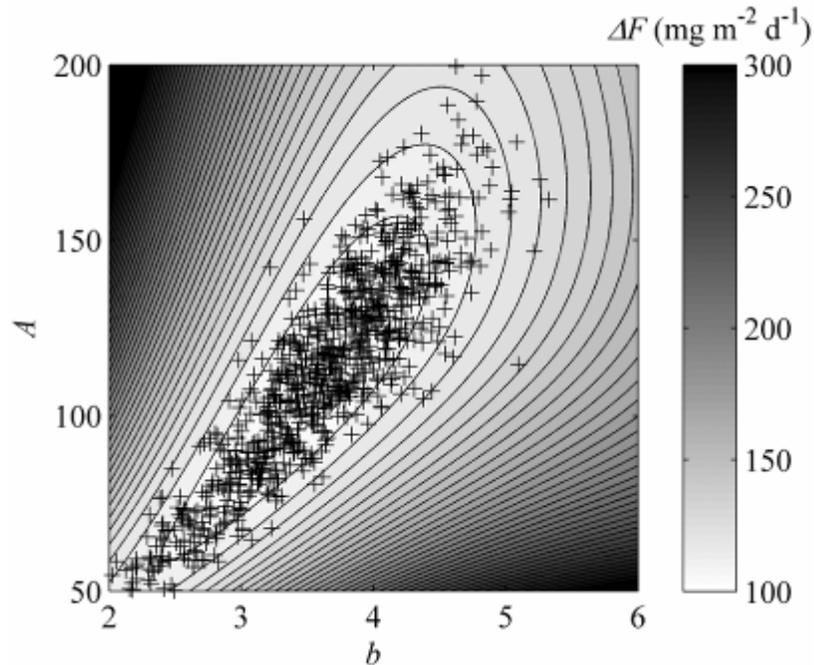


Figure 17: Residual error ΔF as a function of values of A , b for the mass flux F_m . The best fit values were $A=109.5$ and $b=3.52$. Darker regions represent greater values for ΔF in $\text{mg m}^{-2} \text{d}^{-1}$. The crosses correspond to the values calculated during the jackknife error analysis. They are all located in the area where the residues are the smallest.

3.4.1. Estimation of the fractal dimension of the aggregates

The relationships between fractal geometry and the exponents for the diameter in the power relationships between particle mass diameter (or settling velocity) and mass flux have been used to estimate fractal dimensions (D) (Logan and Wilkinson 1990) and the opposite (Jackson et al. 1997). If the particle size is given by particle diameter (d), then its mass is:

$$m(d) = a \cdot d^D \quad (\text{Eq. 18})$$

The sinking rate (w) of the same aggregate, derived from Eq. 15 and Eq. 18, is:

$$w(d) = c \cdot d^{D-1} \quad (\text{Eq. 19})$$

where $c = \frac{gah}{3\pi\nu\rho_0}$ and h is a coefficient to convert particle mass to particle excess of mass and $\Delta\rho = mV^{-1}$ for a volume (V) of a particle (Eq. 15). Hence, $w \cdot m = acd^{2D-1}$, and $D = (b+1)/2$. It follows that the flux of particles within a size range of d to $d+\Delta d$ is:

$$\Delta F(d) = nAd^{2D-1}\Delta d \quad (\text{Eq. 20})$$

where $A = a \cdot \alpha$.

The fractal dimensions corresponding to our results are 2.26- 2.46. Fractal dimensions of marine aggregates have been estimated to be between 1.3 and 3.75 (Jackson et al. 1997; Jiang and Logan 1991; Li and Logan 1995). Values of $D > 3$ can arise from measurement errors or use of an inappropriate model when analyzing observations. The aggregate fractal dimension derived from F_m is high compared to values of 1.125 to 1.3 reported by Alldredge (1998) for visible aggregates in a diatom-rich upwelling system off California. Our study is focused on deeper aggregates (100 to 1000 m depth). Aggregates below the surface mixed layer have been altered as they fall. An increase in fractal dimension with depth implies a decrease in porosity for a given diameter. Different mechanisms can lead to such results. The physical action of the fluid going through the aggregate as it sinks may compact them and decrease their porosity (Logan and Kilps 1995). There are a variety of processes which consume and redistribute matter in settling aggregates, including physical coagulation (Jackson 1990), microbial degradation (Kiørboe 2001; Ploug and Grossart 2000), zooplankton feeding (Graham et al. 2000; Jackson and Kiørboe 2004; Stemmann et al. 2004a), and zooplankton fragmentation (Goldthwait et al. 2004). Biological processes mentioned previously lead to a preferential removal of organic carbon relative to inorganic. These happen at different rates spatially and temporally but appear to transform the aggregate properties in a consistent way everywhere on the globe. For example, they may act to

decrease the median size of the aggregate and therefore decrease the related flux. Further investigations need to be done in order to see what mechanisms impact the porosity of the aggregates and how this porosity can change with depth.

The chemical composition and packing of the aggregates determines their mass and settling rates. We expect aggregates having the same components to result in a unique relationship. Only small changes have been observed between 100 and 1000 m (Figure 16). However the mass, POC and PON ratios change with depth (Boyd et al. 1999) suggesting that most of the aggregate transformation occurs in the first 100 m of the water column as previously shown by sediment trap data (Berelson 2001; Karl et al. 1988; Martin et al. 1987).

3.4.2. The size measurement issue

The relationships described here are based on the UVP aggregate size measurements. Many different instruments have been used these last 20 years to describe the abundance and the size distribution of aggregates. Instruments as different as the Coulter Counter (Beckman Coulter, Inc, Fullerton, CA) and the UVP measure different particle properties. The Coulter Counter measures the change in electrical resistance as a particle passes through a small orifice which is usually assumed to be proportional to the conserved particle volume (Jackson et al. 1995; Li and Logan 1995; McCave 1983). Optical imaging techniques such as the UVP determine a particle's size by measuring its projected area on a two dimensional plane. This area corresponds to the number of pixels that cover the image converted in metric units (Guidi et al. 2007; MacIntyre et al. 1995; Stemmann et al. 2002). These two examples represent a small fraction of the techniques available to obtain the size distribution of particles in the oceanic environment. Therefore, the fact that relationships described in this article can be used with different instruments is not obvious before a careful analysis of the instrument properties has been done.

Multi-instrumental comparison studies are actually available. The size spectrum and the fractal dimension of aggregates provide powerful tools to compare results from these different instruments (Jackson et al. 1995; Jackson et al. 1997). The authors found

that the size spectrum calculated by different instruments can be compared after that all measurements have been transformed to an optical diameter basis. The relationships used here could then be applied to any kind of instrument assuming that the conversion coefficients between instruments are correctly estimated.

3.4.3. Estimation of the settling speed of the aggregates

The settling speed is a function of aggregate diameter and fractal dimension:

$$w(d) = \frac{hagd^{D-1}}{3\pi\rho_0\nu} \quad (\text{Eq. 21})$$

where $a = \sqrt{\frac{A3\pi\rho_0\nu}{hg}}$ (derived from (Eq. 16, 19 and 20).

The use of Eq. 21 leads to settling rates of 1.8, 32, 248 m d^{-1} for particles of 100 μm , 1 mm and 5 mm (Figure 18A). These estimates are in the range of reported settling rates for deep estuaries (Syvitski et al. 1995).

The distribution of mass flux depends on the particle size distribution as well as the mass and settling relationships. Observations on the relative timing of sedimentation events through the water column have allowed estimates that the particles typically settle at 100-400 m d^{-1} (Berelson 2002; Fowler and Knauer 1986; Shanks 2002). More recent measurements of settling velocity at the DYFAMED site yield a median velocity for the flux of about 150 m d^{-1} (Peterson et al. 2005). Using a representative size spectrum determined using the UVP and our relationship for $w \cdot m$ (Eq. 16) as a function of d , we calculate a mean settling rate of 115 m d^{-1} , corresponding to the fall velocity of a 2.7 mm aggregate (Figure 18A, C). The flux was dominated by the large aggregates between 400 μm and 4 mm (Figure 18C). For the same size spectrum but with the Alldredge and Gotschalk (1988) relationship, the mean settling rate is 35 m d^{-1} corresponding to a median aggregate size of 250 μm . This flux would be dominated by aggregates smaller than 400 μm .

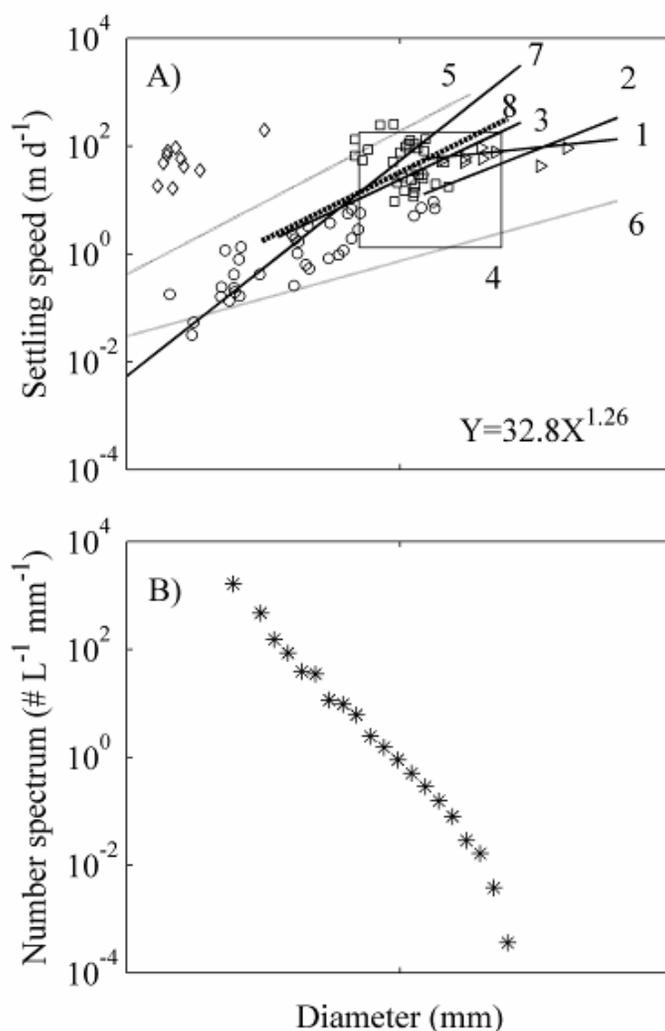


Figure 18: A) Particle settling speed function of particle diameter measured by different authors (from Stemmann et al. 2004b). Circle: (Smayda 1970), triangle: (Shanks and Trent 1980), diamond: (Carder et al. 1982), square: (Azetsu-Scott and Johnson 1992). Empirical relationships, 1—(Alldredge and Gotschalk 1988), 2—(Alldredge and Gotschalk 1989), 3—(Syvitski et al. 1995), 4—(Diercks and Asper 1997). Settling speeds calculated using the coagulation model (Stemmann et al. 2004b) with different parameter values (5— $\Delta\rho = 0.08$, $D=2.33$; 6— $\Delta\rho = 0.01$, $D=1.79$) are also reported. The regression line 7 is the settling speed predicted by Stokes Law. The dashed line 8 is the settling speed calculated in this paper. B) Typical number spectrum from the UVP database profiles.

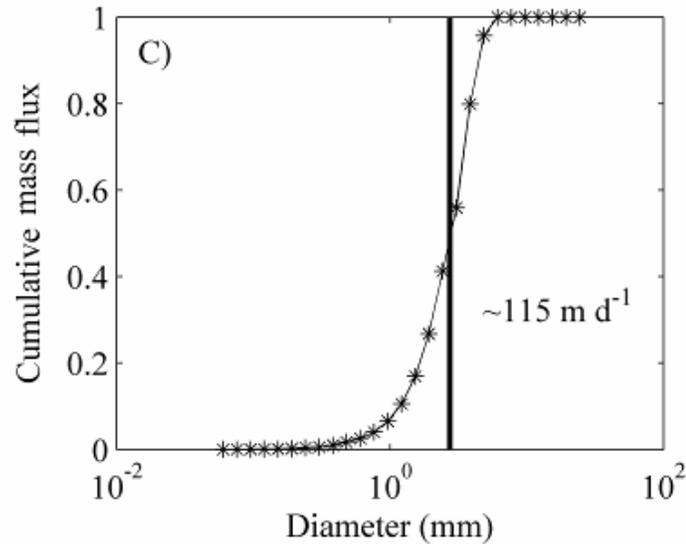


Figure 18: C) Normalized cumulative flux calculated on the number spectrum (B) with the mass flux relationship Eq. 20, the black line represents the 50% of the mass flux.

3.4.4. Using a larger size range

While the size range that we used for the size spectra covers a large range of settling particles, it does not cover all particles. We made the previous parameter estimation using spectra covering the limited 250 μm -1.5 mm size range. When we applied our technique to UVP4a size spectra profiles with the expanded 100 μm to 2 cm size range ($n=200$), the calculated fluxes averaged 2.3 times those calculated for the smaller range. Most of this increase was associated with the inclusion of larger particles. There were uncertainties in the original parameter values of 30-40%. The flux values calculated with the larger size range are comparable to the uncertainties in fluxes associated with the parameter ranges and the smaller particle size range. Interestingly, when we used the Alldredge and Gotschalk (1988) relationship, the flux was greater by a similar proportion, but most of the increase came from the greater number of small particles. While it is clear that the parameters from m and w would change if the minimization procedure were performed with a greater particle size range, the change is small compared to the large range of fluxes observed and the parameter uncertainties.

3.4.5. Application

We have used these results to map the distribution of mass flux along 180°W in the Equatorial Pacific using data of the Ebene cruise (Gorsky et al. 2003). Similar mass flux below the euphotic zone have been reported along 150°W for the same period with conventional sediment traps, bolstering the accuracy of these relationships (Figure 19).

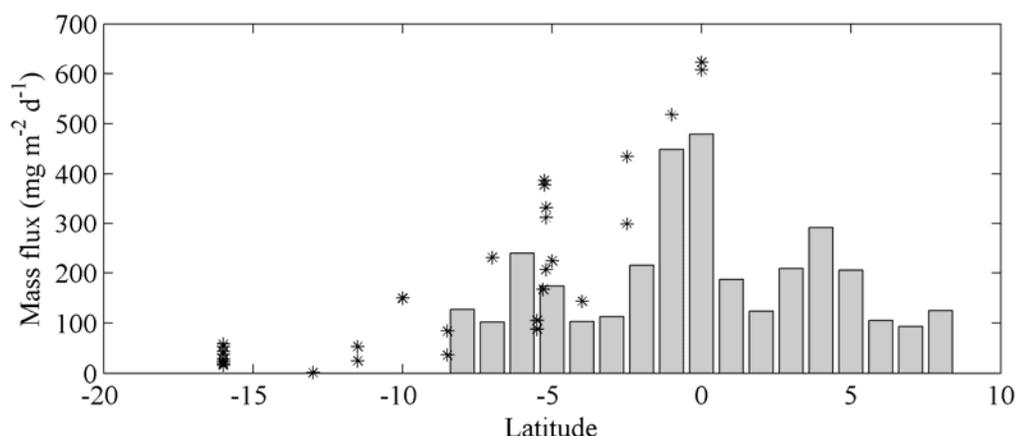


Figure 19: Sediment trap mass flux measurement below the euphotic zone in $\text{mg m}^{-2} \text{d}^{-1}$ along 150°W (black asterisk) redrawn from (Raimbault et al. 1999) compared to estimated mass flux from aggregates size distribution along 180°W (gray bars).

The high vertical and spatial resolution of the flux provides more information on its spatial variability and the processes at the origin of the export than sediment traps. The South Equatorial Current (SEC) was flowing westward at 180°, between 5°S and 4°N, and the North Equatorial Countercurrent (NECC) flowed eastward, north of 4°N. The South Equatorial Counter Current (SECC) was 6°S (Eldin and Rodier 2003). Subsurface flow consisted of the eastward flowing Equatorial Under-Current (EUC), centered at the equator below 100 m. The South and North Subsurface Countercurrents (SSCC, NSCC) also flowed eastward below 200 m south of 6°S and north of 2°N, respectively (Figure 20). The total concentration of chlorophyll *a* (*Tchl a*), was greatest between the equator and 5°N, averaging $0.21 \mu\text{g L}^{-1}$ and not exceeding $0.36 \mu\text{g L}^{-1}$. *Tchl a* maximum were localized in the 60–100-m depth strata at the equator, 4–6°S and 5–6°N (Brown et al. 2003). These strong features create physical gradients probably at the

origin of localized downward export (6°S and 5°N) of the surface production. Areas with high mass fluxes were localized immediately below the SEC, NECC and SECC with fluxes 3 to 5 times higher than in the surrounding water. Similar flux heterogeneity had been observed in the North Atlantic where mesoscale eddies were recorded (Guidi et al. 2007). Large mass flux is located between 400 and 700 m depth at the equator. Increases in particle flux with depth have been attributed to horizontal advection from boundaries (Gardner and Richardson 1992), vertical migration, and midwater biological activities (Karl et al. 1996). According to the physical field this flux increase could be the result of an accumulation of the aggregates slipping along the borders of the EUC (Gorsky et al. 2003). Unfortunately the lack of biological mesopelagic data at this location precludes a clear conclusion.

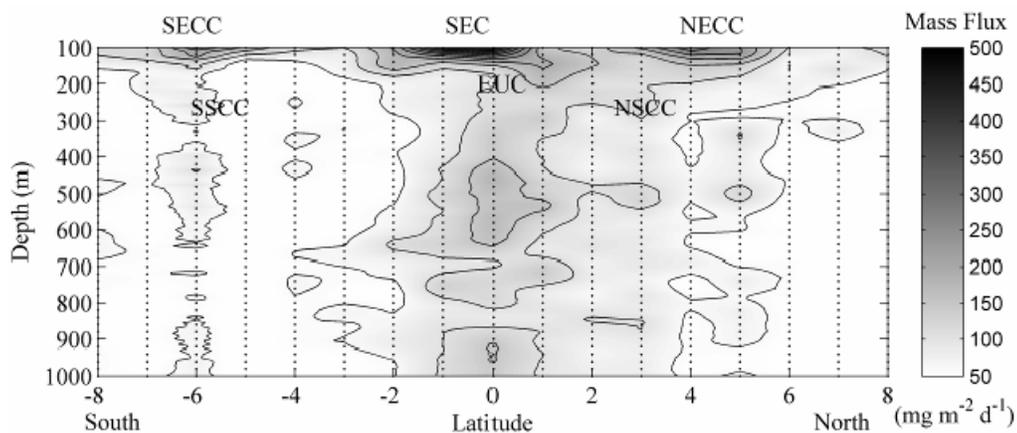


Figure 20: Estimation of the mass flux for a radial 180°W in the Equatorial Pacific Ocean, based on the size aggregate distribution. $A=109.5$ and $b=3.52$ for the size to mass flux relationship (Table 10). The dots correspond to the sampling grid.

3.5. Conclusion

The first data allowing a direct comparison between the flux measurements made with sediment traps and the instantaneous flux estimation by a camera system are presented in this article. We have shown that the size distribution of aggregates can be related to the mass, POC, PIC and PON flux measurements in the mesopelagic zone. In the future, similar procedures using aggregate size distribution, sediment trap flux

measurements and thorium/uranium profiles will probably increase the accuracy of the flux estimations.

More recently, it has been shown that vertical distribution of aggregates and the resulting carbon flux in the mesopelagic zone can be driven by the mesoscale circulation (Guidi et al. 2007; Stemmann et al. in press). In an eddy area, only a high spatial and temporal mapping of the flux can lead to a better understanding of the process that regulates the carbon flux in a dynamic ocean. The development of indirect estimates of particle flux allowed by our relationships will increase our ability to increase both vertical and horizontal resolution of maps showing fluxes in the deep ocean.

This chapter is a key step in this dissertation. Aggregate flux and settling speed can be estimated based on aggregate size. This relationship will be used in chapter IV and V to estimate fluxes and correlate them to overlaying water biology or sediment trap data at global (Chapter IV) and regional (Chapter V) scales.

CHAPTER IV

PRIMARY PRODUCER COMMUNITY EFFECT ON PRODUCTION AND EXPORT OF LARGE AGGREGATES: A GLOBAL ANALYSIS

4.1. Introduction

Processes originating carbon export to the deep ocean have been subject to considerable attention during the last 3 decades. Organic and inorganic matter is transported into the deep layers mainly by sinking particulate matter (Boyd and Trull 2007; Francois et al. 2002; Martin et al. 1987). Measuring size distributions of large aggregates in the ocean interior and relating them to the biological and physical conditions of the overlying water allows us to highlight mechanisms driving this export. Aggregate size is an important particle property which can be modified by abiotic mechanisms, such as physical coagulation, as well as biotic mechanisms, such as grazing activity, fecal pellet production, filtration, and discarded products of living organisms such as molts or larvacean houses.

Small particle size distributions (1-100 μm) have been characterized in the past (e.g., Sheldon, 1972), while horizontal and vertical variations in size distributions of large aggregates ($>100 \mu\text{m}$) remain poorly described, even though the larger particles are responsible for a significant fraction of the carbon transport to the deep ocean (Gentien et al. 1995; Lampitt et al. 1993b; Stemmann et al. 2002). The recent availability of imaging sensors and computer systems to analyze their images has led to the development of in situ camera systems that can be used to produce profiles of aggregate size distribution and abundance (Asper 1987; Davis and Pilskain 1992; Gorsky et al. 1992; Honjo et al. 1984; Wlash and Gardner 1992). Observations made with these systems suggest that a large quantity of particulate organic matter may be exported to depth in spatially limited zones where the physical conditions allow intense small-scale processes to occur (Guidi et al. 2007; Stemmann et al. in press). This spatially-focussed

export may be important for deep flux variability on small horizontal scales. However biotic mechanisms involved in the carbon export from the surface to mid waters may become important factors controlling the carbon flux variability at global scales.

Carbon export to the ocean floor is commonly believed to be related to new production by phytoplankton (Eppley and Peterson 1979). Flux of the large aggregates responsible for most of the carbon flux is usually attributed to the biggest primary producers in the euphotic layer, particularly diatoms (Smetacek 1985). The Antarctic and Arctic Oceans, as well as coastal upwelling regions, are good examples of places where such is believed to occur (Huskin et al. 2004; Kiørboe et al. 1998; Nodder and Waite 2001). Production of smaller phytoplankton size classes (pico- and nano-phytoplankton) has recently been demonstrated to contribute to the downward carbon flux by foodweb interactions (Claustre et al. 2005; Gorsky et al. 1999; Olli et al. 2007). Oligotrophic regions, where small cells dominate the production, contribute significantly to the global carbon flux. In the equatorial Pacific Ocean, picoplankton can be responsible for 87% of the particulate organic carbon (POC) export via detritus (Richardson and Jackson 2007). The size-fraction of the producer appears to be an important factor that needs to be taken into account in order to understand the process of atmospheric carbon sequestration in the ocean.

In this paper, we analyzed profiles of large aggregates ($>100 \mu\text{m}$) recorded all over the world with the Underwater Video Profiler (UVP). Different patterns of the variation of the size distribution of the aggregates with depth were selected using the random simulation test (RST) as a stopping rule adapted to ecological data with important variability (Guidi et al, submitted). These patterns were used as references in order to look at the links between phytoplankton size-fractions and the particulate matter size and export to the deep water. These relations were explored at many locations around the world. Using these aggregate data plus biological and physical characteristics of the water column, different processes involved in the aggregate mass or flux variations were investigated.

4.2. Material and methods

4.2.1. Particle observations

Particle size distributions have been measured between the surface and 1000 m depth throughout the oceans during the last 2 decades using three generations of the Underwater Video Profiler (UVP). The UVPs records images of particles illuminated in slabs of water whose volumes ranges from 0.20 to 10 L, where the volume depends on the UVP model used. An image can be analyzed for information about the size and shape of objects in its field of vision, which can then be used to calculate particle size distributions and abundances of large organisms as a function of depth (Gorsky et al. 2003; Gorsky et al. 2000). The detection limit has improved through time, with the minimum observed particle diameter improving from 250 down to 90 μm ; the effective maximum particle size depends on the sample volume (Jackson et al. 1997; McCave 1984). The UVP is lowered on a cable at a speed chosen to avoid overlapping regions in the images (1 m s^{-1}). The images are recorded digitally and processed by image analysis software to yield the projected area for each particle. The Equivalent Spherical Diameter (ESD) of each particle is calculated assuming that the particle projected shape is a circle. The instruments have been calibrated in a sea-water tank using natural particles of different aggregate types to determine the conversion between pixel and metric unit (Gorsky et al. 2000; Stemmann et al. 2002). Different generations of instruments have been intercalibrated and the consistency of the measurements verified (Guidi et al. 2007). These profiles have been collected using the UVP in 27 different cruises in the Pacific, Atlantic and Indian oceans and the Mediterranean Sea representing more than 1300 UVP deployments. Profiles of particulate matter size distribution have been assembled in a database (aggregates between 90 μm and 2 cm in ESD). In this study, we restricted the size range of interest to 250 μm - 1.5 mm in order to use data from older UVPs models.

4.2.2. Ancillary data

During some of the UVP deployments, temperature and salinity (TS) were measured with SeaBird CTD SBE911 and water samples were collected for pigment

analysis. We considered the data sets as being collected at the same location if they were collected within 1 day in time and 0.1° latitude and longitude in space. There were 193 profiles for which there were particle size distributions, pigment data, and TS data (Figure 21). The water characteristics have been analyzed by TS diagrams to identify water masses.

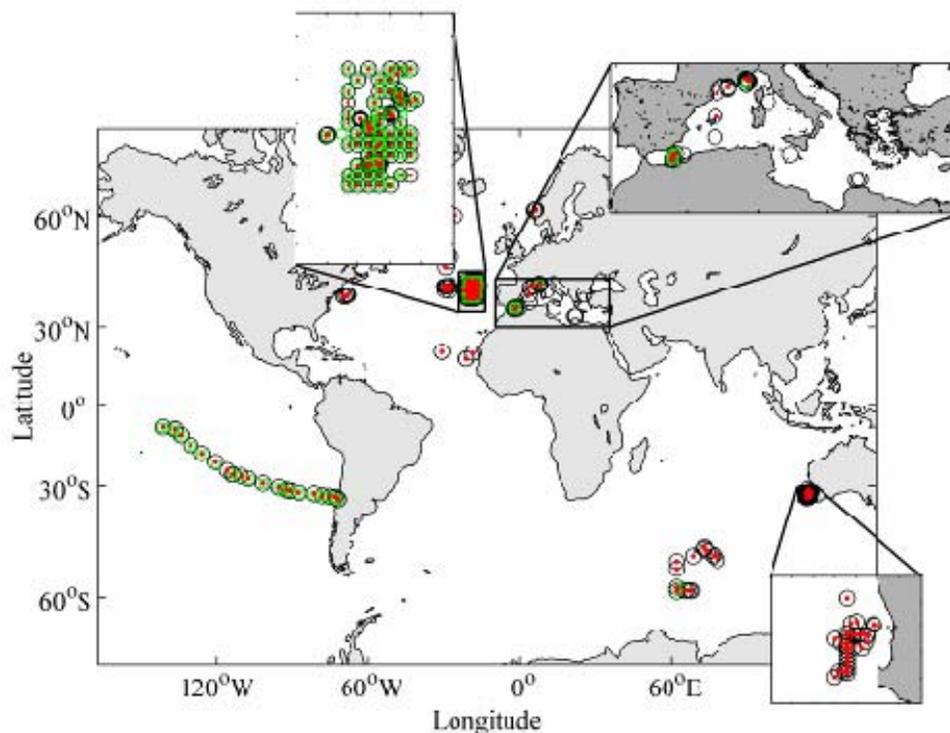


Figure 21: Samples location of UVP (black circles), CTD (red dots), and pigment profiles (green squares).

Pigment analysis was performed on water samples using HPLC techniques (Claustre et al. 2005). The results were used to determine the amount of chlorophyll *a* (Chl *a*) in three phytoplankton classes: microphytoplankton ($>20 \mu\text{m}$, fucoxanthine + peridinin), nanophytoplankton ($2\text{--}20 \mu\text{m}$, $19'$ -hexanoyloxyfucoxanthin + $19'$ -butanoyloxyfucoxanthin + alloxanthin), and picophytoplankton ($<2 \mu\text{m}$, total Chl *b* + zeaxanthin) using empirical equations (Claustre et al. 2005). The producer community has been calculated using the average pigment composition in the euphotic layer (Uitz et al. 2006).

Progressive integrations of vertical Chl *a* water column content were used to compute the depth of the euphotic layer (Z_e) through an iterative process (Morel and Berthon 1989). Chl *a* can be described as a function of Z_e approximated by two successive linear segments.

$$Z_e = 912.5 \cdot \text{Chl } a^{-0.893} \text{ for } 10 \text{ m} < Z_e < 102 \text{ m}, \quad (\text{Eq. 22})$$

$$Z_e = 426.3 \cdot \text{Chl } a^{-0.547} \text{ for } 102 \text{ m} < Z_e < 180 \text{ m}, \quad (\text{Eq. 23})$$

When Z_e becomes lower than the depth used when integrating the profile, the process is stopped. While Chl *a* corresponds to discrete data, the exact Z_e is determined by interpolating every 0.1m (Morel and Maritorena 2001).

4.2.3. *Treatment of aggregate size distribution*

The aggregate size distributions were fit to power relationships of the form $n = a d^b$, where n is differential size spectrum as a function of diameter (d) (e.g. Jackson et al. 1997). The parameters a and b are estimated using a straight line fit to the log-transformed distribution data and diameters. The exponent b is the slope of the log-transformed distribution and can be used as a proxy of this distribution (McCave 1984). The steeper the slope, the smaller the aggregates. For example a slope of -5 indicates the dominance of small aggregates in the water column whereas a slope of -3 highlights the dominance of large aggregates. The observed slope of the distribution has been calculated on all particles grouped into 5 m bins.

All vertical profiles of slopes have been smoothed by the eigenvector filtering method (EVF; Ibanez and Etienne 1992) in order to remove the noise associated with small scale vertical variability. The EVF procedure corresponds to a principal component analysis (PCA) calculated on an autocovariance matrix based on the original profile. The first and second axes extracted from PCA represent the main modes of variability. The smoothing window has been calculated for every profile according to its autocorrelation function.

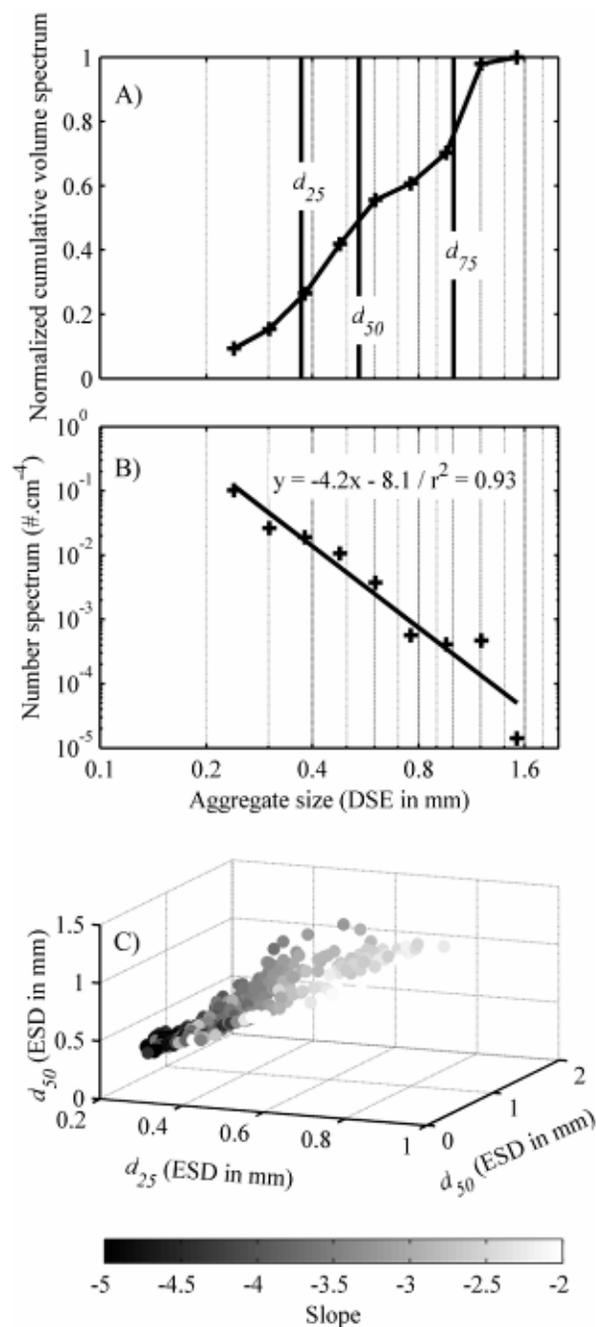


Figure 22: Comparison of different measures of the number distribution: b (slope of the number distribution), d_{25} (Equivalent spherical diameter (ESD) relative to 25% of the cumulative volume distribution), d_{50} (ESD relative to 50% of the cumulative volume distribution), d_{75} (ESD relative to 75% of the cumulative volume distribution). An example of measurements on one distribution (A and B), the 4 measurements correspond to 1 point in C). A) Cumulative volume distribution. B) Number spectrum n from which b was calculated. C) Relationship between b and d_{25} , d_{50} , and d_{75} .

Because the slope only represents the linear part of the spectrum, other parameters provide insight into its shape. For example, the integrated volume spectrum $I(d)$ is the amount of particle volume in particles smaller than d ; it can be calculated in terms of the number spectrum and the particle volume:

$$I(d) = \int_0^d n(d')V(d')dd' \quad (\text{Eq. 24})$$

It can be characterized in terms of the diameters at which $I(d)/I(\infty)$ is 0.25, 0.5, and 0.75 (d_{25} , d_{50} , and d_{75} ; Figure 22A). Because there is a lower size limit on the data, the integration is only approximate.

The particle size distribution has been used to estimate the vertical fluxes (F) of aggregate mass following the simple power relationships.

$$F = \sum_{i=0}^{\infty} n_i \cdot 109.5 \cdot d_i^{3.52} \quad (\text{Eq. 25})$$

The constants were derived by fitting sediment trap fluxes to aggregate size distributions distributed globally (Guidi et al. in revision). While the sum should be done on the whole particle size range (0 to ∞), the approximation was performed between 250 μm - 1.5 mm, the size range available for this study. A sensitivity analyses has been done in order to estimate the difference between flux estimation using size range (250 μm - 1.5 mm) and the largest size range available with last UVP model (90 μm to 2 cm). A maximum factor of 2 had been calculated between the two flux estimations. Given that global flux varies over 3 orders of magnitude we contend that difference of about a factor of 2 remains a reasonable approximation.

4.2.4. *Typology on vertical patterns of slopes*

Profiles were selected to minimize extraneous effects on particle distributions. Therefore, profiles going through different water masses, sampling a region with sea floor shallower than 1300 meters, or having surface light contamination deeper than 20 m were excluded from the classification. Samples within 20 m of the surface were removed from the analysis in order to avoid the effect of the light on the estimate. The surviving profiles will be denoted as deep water profiles (Table 11).

Table 11: Distribution of profiles within clusters for each cruise. The numbers in the C columns indicated the number of profiles that fall into the cluster.

Location	Cruise	Starting	Ending	C₁	C₂	C₃	C₄	C₅	C₆	Total
Aegean Sea	egee2	03/1998	03/1998	3	0	1	0	1	5	10
Atlantic O.	eumeli5	12/1992	12/1992	0	0	0	0	5	3	8
Atlantic O.	maine2002	09/2002	09/2002	4	0	1	0	3	1	9
Atlantic O.	mareco2002	11/2002	11/2002	9	1	5	1	8	4	28
Atlantic O.	mareco2004	06/2004	07/2004	0	0	0	0	1	0	1
Atlantic O.	nor2000	03/2000	03/2000	0	0	1	0	3	7	11
Atlantic O.	pomme111	02/2001	02/2001	0	0	0	0	0	1	1
Atlantic O.	pomme112	03/2001	03/2001	9	0	2	0	5	0	16
Atlantic O.	pomme211	03/2001	04/2001	3	0	2	0	0	1	6
Atlantic O.	pomme311	08/2001	08/2001	0	0	3	0	9	0	12
Atlantic O.	pomme312	09/2001	10/2001	1	0	4	0	0	0	5
Mediterr. Sea	almofront1L2	05/1991	05/1991	0	0	3	2	1	1	7
Mediterr. Sea	barmed	03/2003	06/2003	0	1	0	0	0	0	1
Mediterr. Sea	dyfabac	11/1995	12/1995	1	0	15	12	0	0	28
Mediterr. Sea	dynaproc	05/1995	05/1995	4	0	0	19	0	0	23
Mediterr. Sea	euromarge	06/1995	06/1995	2	0	24	12	2	0	40
Mediterr. Sea	frontal93	01/1993	12/1993	0	0	0	6	0	0	6
Mediterr. Sea	frontal94	01/1994	12/1994	1	0	2	0	0	0	3
Mediterr. Sea	frontal95	01/1995	03/1995	1	0	15	0	7	0	23
Mediterr. Sea	frontal96	02/1996	06/1996	12	0	4	0	0	0	16
Mediterr. Sea	pauline	11/1994	11/1994	0	10	0	0	0	0	10
Mediterr. Sea	picnic	03/1995	03/1995	4	1	4	0	0	2	11
Indian O.	antares3	10/1995	10/1995	2	0	4	0	9	18	33
Indian O.	keops	01/2005	02/2005	9	11	20	0	11	15	66
Indian O.	ss052006	05/2006	05/2006	0	0	1	0	0	5	6
Pacific O.	biosope	10/2004	12/2004	13	3	4	10	0	0	30
Total				78	27	115	62	65	63	410

Profiles of aggregate size distributions were partitioned by conventional clustering techniques. The Euclidean distance coefficient was computed and the flexible link for

hierarchical clustering method was applied to classify the remaining 410 of over 1300 slope profiles available in the database (Lance and Williams 1967).

The next step consists of selecting the best number of clusters. This was done using a new stopping rule, the random simulation test (RST) developed especially for ecological data with strong variability (Guidi et al. submitted). The method generates 10,000 new slope profiles (λ) with values encompassed in the variance of the original dataset. These λ are classified against real data. The distance for which one λ forms a group by itself, corresponds to the distance used for cluster selection. Finally, λ s generate a frequency distribution of a possible number of groups. Number of groups with highest frequency gives the distance that needs to be used for the groups' selection. These clusters have been used to characterize the phytoplankton community structure in the euphotic layer.

4.2.5. *Multidimensional analysis: the principal component regression*

The classical multiple regression between a dependent variable Y and p independent descriptors X (Y and X with the same number of observations: n) enables an estimation of the contribution of each X_j ($j=1,2...p$) to the variance of Y and to develop a forecasting model. However, the conditions of application (multiple normality, non autocorrelation, and non linearity between descriptors) are difficult to meet simultaneously and thus the estimation of partial correlation coefficients may be biased.

In order to avoid, at least, the collinearity of the descriptors, we applied a principal component regression (PCR), which corresponds to a multiple regression between Y and k ($k < p$) principal components of the matrix X . PCR has already been used to make meteorological forecasts (Pottier, 1991) or to reconstruct paleoclimates (Buckley et al, 2004).

Usually the selected k principal components are those explaining the highest variance. However, considering the order of the variance of the successive components does not indicate which explain most of the variance of Y (Components with low variance may present high contribution in the multiple regression model) (Jolliffe, 1986). Thus, how to retain the best k components?

Simple linear regression between Y and each component C_j ($j=1,2,\dots,p$) leads to a square correlation $r^2(YC_j)$. Since the p components C_j are orthogonal, it is easy to know the coefficient of determination R^2 of the multiple regression. Taking together the first and second component, the coefficient will be: $R^2(YC_1, C_2) = r^2(YC_1) + r^2(YC_2)$.

Ordering all the $r^2(YC_j)$ provides knowledge of the increase of the R^2 , listening their successive values from the highest to the lowest. The plot between the ordered p components and the corresponding R^2 indicates the goodness of the fit by multiple regression model. The shape of the curve shows a plateau reached with k components, where k corresponds to the optimal order of the multiple regression model (Gnanadesikan & Kettenring 1972).

The model with k components C_i ($i=1,2,\dots,k$) is :

$$\hat{Y} = \bar{Y} + Cb \quad (\text{Eq. 26})$$

where \hat{Y} are the predicted values, \bar{Y} the mean of Y , and b the vector of the k partial correlation coefficients of the multiple regression. C corresponds to the matrix of the k components, each with mean equal to zero and variance equal to their corresponding eigenvalues.

C is a linear combination of the reduced descriptors (x) and the eigenvector matrix V (with p rows and k columns) extracted from the correlation matrix between the descriptors (X) such as $C = xV$.

Hence the model can be expressed as function of original reduced descriptors (x): $\hat{Y} = \bar{Y} + xVb$ or $\hat{Y} = \bar{Y} + xh$ where $h = Vb$.

At this stage, the partial correlation coefficients (h_i) represent the influence of each descriptor on Y . The larger (h_i) the stronger is the influence of x_j on Y .

where $x_j = \frac{X_j - \bar{X}_j}{\sigma X_j}$ with \bar{X}_j the mean of X_j and, σX_j its standard deviation.

The model can be function of the original descriptors (X_j) such as:

$$\hat{Y} = H + Xd \quad (\text{Eq. 27})$$

where $d = \frac{h}{\sigma X}$ and $H = \bar{Y} - \bar{X}d$

In order to test the normality of the residuals of the model ($\varepsilon = Y - \bar{Y}$) the skewness (third central moment divided by the cube of the standard deviation) and kurtosis (fourth central moment divided by fourth power of the standard deviation) coefficients of their distribution were calculated.

We were interested in relating the properties of the euphotic layer to the vertical flux at 400 m (F_{400}), as estimated from the particle size distribution. The 7 descriptors used in this analysis were the total integrated chlorophyll *a* in the euphotic layer (B_a), the fraction of micro-, nano- and pico-phytoplankton (f_{micro} , f_{nano} , f_{pico}) and the integrated chlorophyll *a* in euphotic layer in each of the three phytoplankton size fractions (B_{micro} , B_{nano} , and B_{pico}). The independent variable is the log-transformed mass flux calculated from the of aggregates distribution at 400 m (F_{400}).

4.3. Results

4.3.1. Aggregate size distribution estimator

Table 12: Spearman correlation between 4 parameters of the aggregate size distribution (n=410), all correlation were significant.

	<i>b</i>	<i>d</i> ₂₅	<i>d</i> ₅₀	<i>d</i> ₇₅
<i>b</i>	1			
<i>d</i> ₂₅	0.8490	1		
<i>d</i> ₅₀	0.7813	0.8780	1	
<i>d</i> ₇₅	0.6082	0.7272	0.8780	1

The slope of the number spectrum has been compared to d_{25} , d_{50} and d_{75} in order to find the best estimator of the aggregate size distribution (Figure 22). The slope (b) varied between -2 and -5. The value of d_{25} , d_{50} , and d_{75} varied between 0.24 and 0.82 mm, 0.31 and 1.21 mm and 0.45 and 1.42 mm (Figure 22C). When b increases, the 3 others parameters also increase. The Spearman correlation coefficient is largest between b and d_{25} , and smallest between b and d_{75} . However, the correlation is always positive and statistically significant between all pairs of variables (Table 12).

4.3.2. *World wide aggregate size distribution with depth*

The clustering of profiles is based on the slope distribution with depth and on the absolute value of b in the mesopelagic zone. There were six different patterns identified by the process (Figure 23). These patterns included profiles from different UVP models intermingled. The slopes of the aggregate size distribution decrease with depth (from -2 to -4) for cluster 5 while they increase for cluster 4 (from -5 to -3.5). For clusters 1, 2, 3 and 6 the slopes are constant below 300 m. All clusters are characterized by an abrupt change of the slopes within the surface 300 m of the water column. The mean slope for all 410 profiles is around -4.

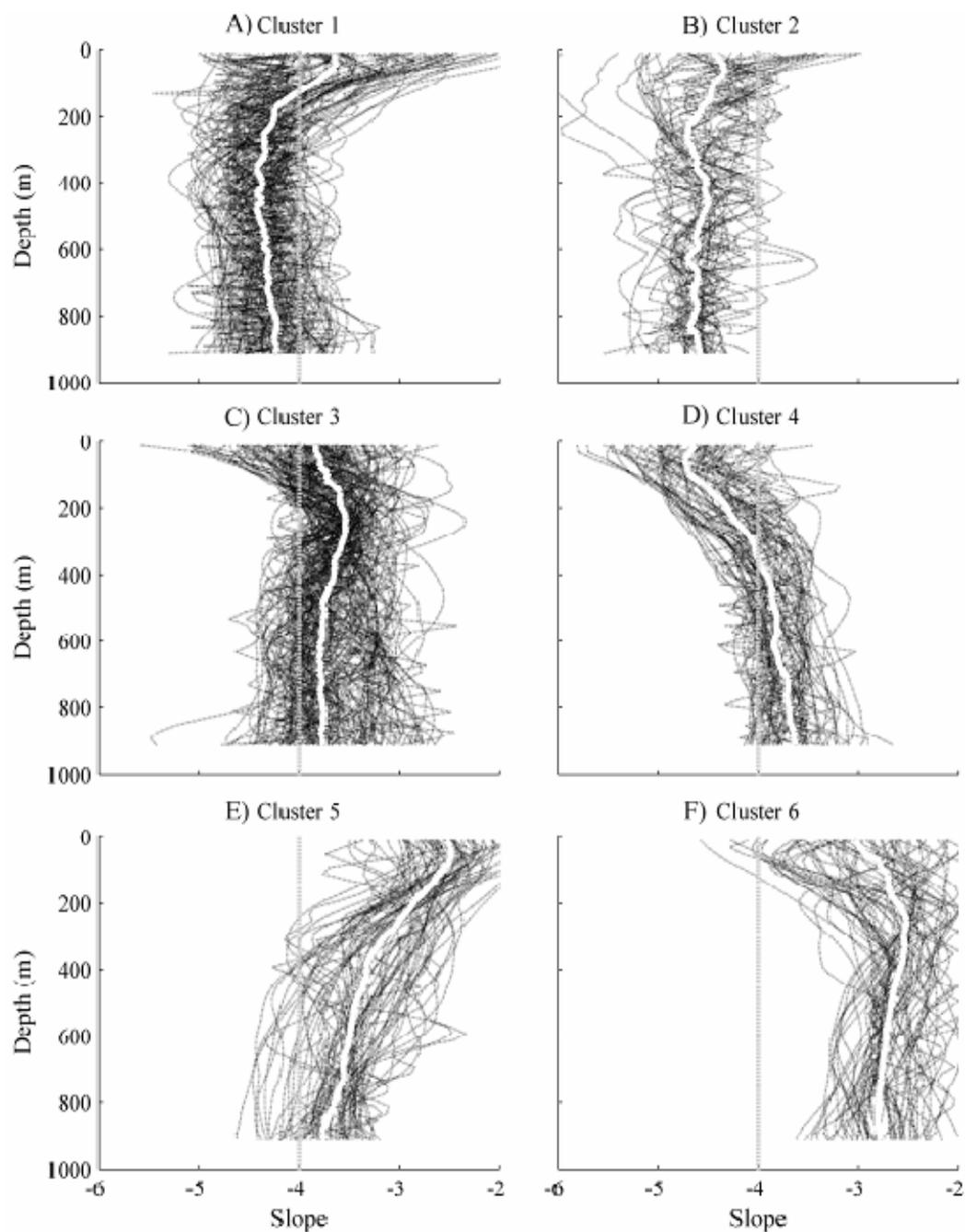


Figure 23: Slope profiles based on the particle size distribution, divided into 6 patterns. The Euclidean distance and the flexible link were used for the classification. Number of clusters were selected with the random simulation test (RST) (A to F for clusters 1 to 6).

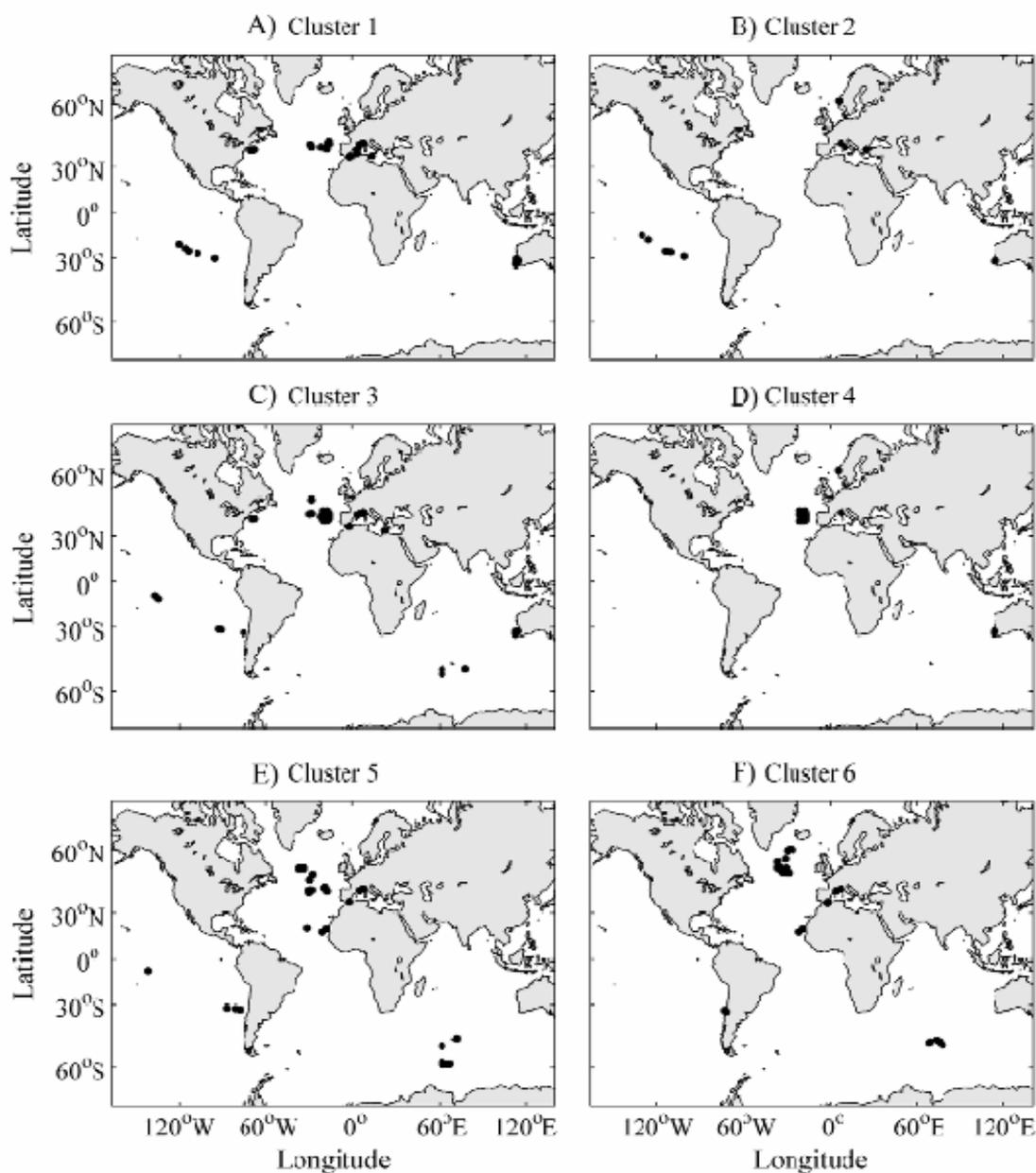


Figure 24: Location of the 6 patterns of the slope profiles based on the particle size distributions of aggregates in the water column (A to F for clusters 1 to 6).

4.3.3. Results from clustering

Clusters can be grouped by the value of the slope in the mesopelagic zone (deeper than 300 m). Profiles from clusters 1 and 2 (~29% of the profiles) have $b < -4$

and are predominantly located in low productivity waters that include the Mediterranean Sea, the Atlantic Ocean in late summer and fall, the Indian Ocean near the Australian western coast and the South Pacific Gyre (Figure 24, Table 11). The South Pacific Gyre has the distinction containing the optically clearest water ever measured in the ocean (Morel et al. 2007).

Profiles from clusters 5 and 6 (~28% of the profiles) have $b > -4$ and are located mainly in more productive waters. Profiles in cluster 6 are located in upwelling zones along the Pacific coast of Chile and along the Atlantic coast of northwest Africa (Figure 24, Table 11). Profiles from cluster 5 are located around the highly productive area of Kerguelen Plateau in the Indian Ocean, around the Marquesas and in the minimum oxygen zone off the Chilean coast in the Pacific Ocean. The remaining profiles of cluster 5 were located in the Mediterranean Sea and the Atlantic Ocean and were collected mainly during spring bloom (Figure 24, Table 11). Values of b for these clusters (5 and 6) can reach -2 in deep water.

Profiles from remaining two clusters (3 and 4) are located mainly in the North Atlantic Ocean. Profiles were collected during spring bloom conditions in dynamic water. These regions present mesoscale circulation features such as eddies and frontal zones. These structures had been shown to extend their influence deeper than 1000 m (Guidi et al. 2007). For examples eddies in the North Atlantic had bases at 3000 m (Memery et al. 2005).

4.3.4. *Near surface phytoplankton size communities*

The 6 clusters were described by their phytoplankton community relative to the pigment composition and the integrated chlorophyll a content (B_a in mg m^{-2}) in the euphotic layer. Clusters 1, 2 and 3 have very low fractions of micro-phytoplankton ($f_{\text{micro}} \sim 10\text{-}18\%$) and co-dominance of nano- and picophytoplankton ($f_{\text{nano}}, f_{\text{pico}} \sim 43\%$). $B_a < 21 \text{ mg m}^{-2}$, with the lowest value observed for cluster 2, $B_a = 15.93 \text{ mg m}^{-2} (\pm 9.49 \text{ mg m}^{-2})$. Cluster 4 is distinguished by a clear nanophytoplankton dominance, with $f_{\text{nano}} = 57\% \pm 11\%$, $f_{\text{pico}} = 23\%$ and $f_{\text{micro}} = 20\%$. Its integrated chlorophyll a content is high ($B_a = 27.74 \pm 8.14 \text{ mg m}^{-2}$). The B_a is low for cluster 5, $19.35 (\pm 6.13 \text{ mg m}^{-2})$ while

nanophytoplankton dominate ($f_{nano}=48\%$, $f_{micro}=26\%$, $f_{pico}=26\%$). Cluster 6, previously identified with profiles in productive waters, is dominated by microplankton ($f_{micro}=65\%$, $f_{nano}=16\%$ and $f_{pico}=19\%$). The highest B_a of 37.95 (± 12.71 mg m⁻²) is also found for this last group (Table 13).

Table 13: Phytoplankton size structure (% of f_{micro} , f_{nano} , f_{pico}) and integrated chlorophyll a content (B_a) in the Z_e compared to the total aggregate flux below the euphotic layer at 400 m: F_{400} .

Clusters	$f_{micro}(\%)$		$f_{nano}(\%)$		$f_{pico}(\%)$		Integrated Chl a in Z_e (mg m ⁻²)		F_{400} (mg m ⁻² d ⁻¹)	
	Mean	STD	Mean	STD	Mean	STD	Mean	STD	Mean	STD
1	18	10	46	9	36	15	20.73	8.46	42.23	79.17
2	10	3	41	9	49	10	15.83	9.49	4.25	2.16
3	14	8	45	8	41	13	18.93	6.44	27.45	46.18
4	20	10	57	11	23	11	27.74	8.14	25.94	37.16
5	26	17	48	7	26	14	19.35	6.13	57.11	57.60
6	65	19	16	12	19	18	37.95	12.71	291.94	176.34

4.3.5. Mass flux and phytoplankton community structure

Flux estimates range between 1.8 and 578 mg m⁻² d⁻¹, B_a varied between 4.80 and 55 mg m⁻². B_a and F at 400 m (F_{400}) are correlated (Spearman correlation coefficient: 0.50; $p < 0.001$). The highest mass fluxes ($F_{400} > 300$ mg m⁻² d⁻¹) were associated with profiles dominated by microphytoplankton ($f_{micro} > 60\%$; Figure 25). The lowest fluxes were associated with surface communities dominated by the picophytoplankton. Mass fluxes were intermediate when the associated phytoplankton structure was dominated by nanophytoplankton. These previous descriptive results were summarized on a ternary plot where all parameters (f_{micro} , f_{nano} , f_{pico} and F_{400}) have been displayed (Figure 26A). This representation highlights the conclusion that mass flux increases with B_a when the f_{nano} and f_{pico} decrease (Figure 25 and Figure 26A).

PCR analysis was used to highlight the relation between aggregate flux and the producers' community. The determination coefficient (r^2) does not increase significantly after the third component and p values become greater to 0.01 (Table 14). Components 1, 4 and 2 were selected for the multiple regression (Figure 27). The final model explains 68% of the aggregate flux variance at 400 m (Table 14).

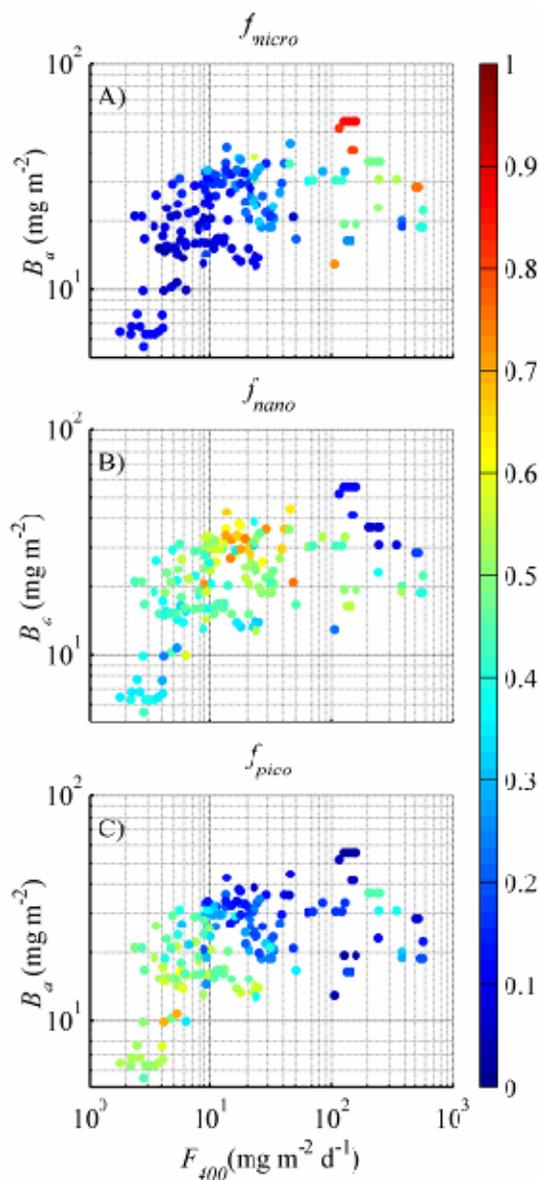


Figure 25: Phytoplankton size classes related to the estimated flux at 400 m. A) Micro-phytoplankton fraction (f_{micro}) in color: chlorophyll a integrated over Z_e (B_a) versus total flux at 400 m (F_{400}). B) Same parameters for nano-phytoplankton (f_{nano}) in color. C) Same parameters for pico-phytoplankton (f_{pico}) in color.

The first model of the logarithm of aggregate mass flux is the following function of the 3 previous selected components:

$$\text{Log}(F_{400}) = -0.48 C_1 + 1.45 C_4 + 0.19 C_2 + 2.84 \quad (\text{Eq. 28})$$

A summary of coefficients and confidence intervals are given in Table 14.

The components can be translated into reduced variables, symbolized by a straight line over the name of the variable, as follow:

$$\begin{aligned} \text{Log}(F_{400}) = & -0.98 \bar{f}_{pico} + 0.96 \bar{f}_{micro} + 0.51 \bar{B}_{pico} - 0.36 \bar{B}_{micro} \\ & -0.24 \bar{B}_a - 0.18 \bar{B}_{nano} - 0.07 \bar{f}_{nano} + 2.85. \end{aligned} \quad (\text{Eq. 29})$$

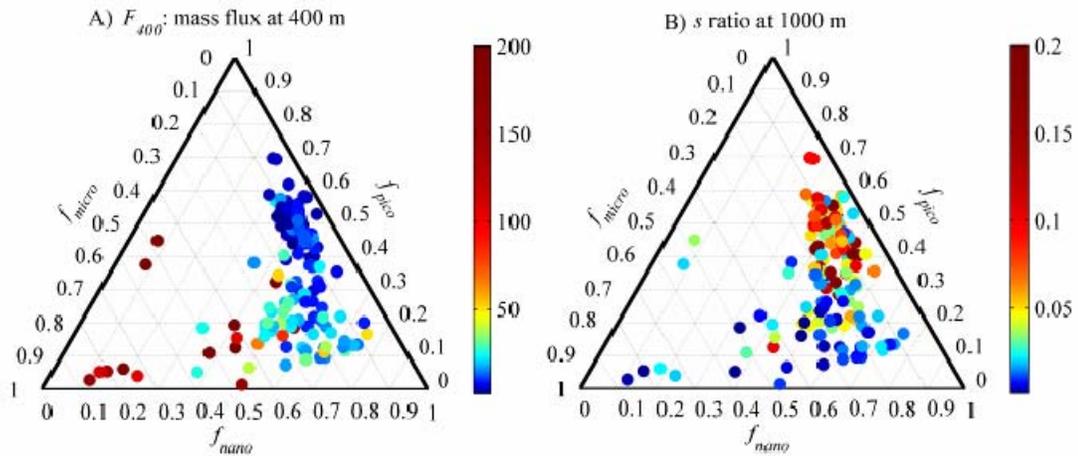


Figure 26: Flux in the mesopelagic zone. A) Ternary plot of total aggregate flux at 400 m (F_{400}) B) Ternary plot of the aggregate mass flux fraction estimated at 1000 m compared to the estimated aggregate mass flux below Z_e . Both calculation are related to the phytoplankton structure in Z_e (f_{micro} , f_{nano} , f_{pico} in fractions).

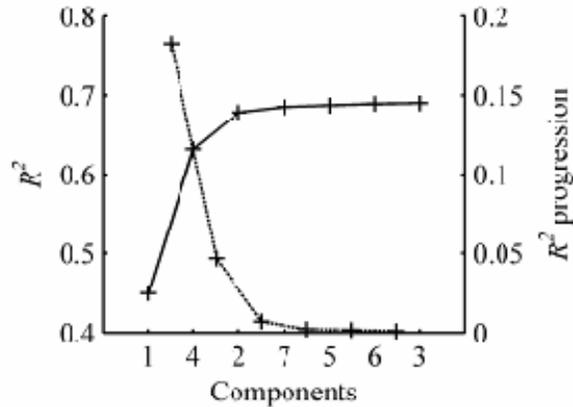


Figure 27: Selected components (C) of PCA for PCR. The solid line corresponds to the coefficient of determination R^2 of the multiple regression. The dashed line corresponds to the R^2 progression by successive component addition.

The partial correlation coefficients highlight the influence of each variable on the aggregate mass flux. It clearly appears that f_{micro} and f_{pico} are most responsible for variations in the flux at 400 m. These two variables are followed by B_{micro} and B_{pico} . The integrated Chl a content in the euphotic layer (B_a) shows up at the fifth rank. Variables with little influence on flux are B_{nano} and f_{nano} .

The last step of the PCR allows the return to the root variables. The final model is the following (Figure 28):

$$\begin{aligned} \text{Log}(F_{400}) = & -5.73 f_{pico} + 5.17 f_{micro} + 0.15 B_{pico} - 0.04 B_{micro} \quad (\text{Eq. 30}) \\ & -0.02 B_a - 0.02 B_{nano} - 0.46 f_{nano} + 3.98. \end{aligned}$$

Finally, the residues distribution has been tested against a normal distribution. The skewness equals 0.25 ($p=0.076$) and kurtosis coefficient equals 0.07 ($p=0.42$). Residues are normally distributed validating the model.

Table 14: Components from PCA of descriptors, sorted by their decreasing r^2 , correlation with the flux at 400m; r^2 values and probability (p) associated. Component selected for the PCR are in bold. Model's coefficient and their confidence interval after the multiple regression between the 7 descriptors (f_{micro} , f_{nano} , f_{pico} , B_{micro} , B_{nano} , B_{pico} , B_a) and the aggregate flux at 400m (F_{400}) summarized in the 2 last columns.

Components	Correlation with the flux (r)	r^2	Cumulative sum of r^2	p associate to r^2	Coefficient	Confidence interval	
1	-0.67	0.45	0.4492	<0.001	-0.4810	-	-
4	0.43	0.18	0.6318	<0.001	1.4485	1.1705	1.7265
2	0.22	0.04	0.6786	<0.005	0.1914	0.1188	0.2639
3	-0.08	0.007	0.6855	0.26			
5	-0.05	0.002	0.6875	0.53			
6	-0.04	0.002	0.6893	0.56			
7	-0.03	0.0009	0.6902	0.68			
intercept					2.8453	2.7366	2.9540

4.4. Discussion

4.4.1. Aggregate size estimation

The slope of the aggregate size distribution is a poor descriptor when considering mass distributions (Figure 22). However, in our case it was useful for highlighting substantial differences among profiles (Figure 23). In some cases the slope may not be an appropriate estimator of the distribution. If the total aggregate mass needs to be inferred for the size distribution, the volumetric spectrum shall be used. If not, the importance of large aggregates to the total mass could be lost (Stemmann et al, submitted).

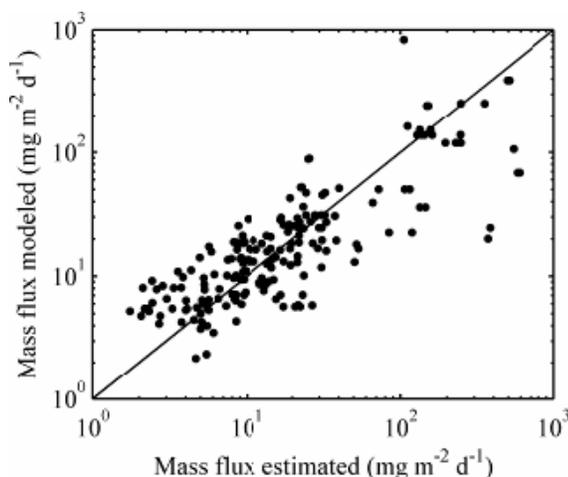


Figure 28: Flux measurement vs flux modeled by the PCR, $n=193$.

4.4.2. *Patterns characteristics: producers linked to aggregate distribution*

Previous studies reported a close relation between phytoplankton composition and large aggregate export to the deep water. Phytoplankton, especially chain-forming diatoms can form large aggregates with high settling speed (few 100 m d^{-1}) yielding a pulse of organic matter to the sea floor. These events can lead to fluffy carpets of detritic material and living organisms already observed around the world (Beaulieu 2002; Lampitt 1985). Several other authors have reported evidence of marine snow formation while micro-phytoplankton (diatoms) was abundant in the surface water (Lampitt et al. 1993a; Riebesell 1991; Sarthou et al. 2005). However, to our knowledge, the aggregate size distributions in the mesopelagic zone and the phytoplankton composition at the surface has not previously been compared at global scale principally due to a lack of data.

The clustering analyses partitioned the dataset in 6 groups. Clusters have been shown to be closely related to the producer community (Figure 25 and Table 13). Slopes of the deep aggregate size distribution were < -4 where pico- and nano-phytoplankton dominated in the euphotic layer (cluster 1 and 2). Such phytoplankton composition is usually characteristic of oligotrophic waters (Partensky et al. 1999). At the opposite, clusters 5 and 6 were characterized by $b > -4$ in the mesopelagic zone. These slopes were

associated with high surface biomass ($B_a > 37 \text{ mg m}^{-2}$ for cluster 6) with micro-phytoplankton dominance in the euphotic layer (Clusters 5 and 6). Profiles of cluster 3 and 4 were dominated by medium cell size (nano-phytoplankton). Several profiles of these clusters were carried out in oceanic water associated with mesoscale eddies and frontal zones (North Atlantic Ocean, off the western Australian coast and close to the Liguro-Provencal Current in the Mediterranean Sea). In such areas the size structure of phytoplankton may depend directly on hydrodynamical forces. In areas of upward motion mean size of phytoplankton should be bigger than in areas of downward motion, because upward motion increases the residence time of large cells in the upper layer against sinking process (Rodriguez et al. 2001).

To summarize; a relation between the aggregate size and the phytoplankton size structure seems to exist on a global scale. The mean aggregate size increases in the euphotic layer and in the mesopelagic realm when the size of producers' community increases at the surface. The phytoplankton size-fractions, through microbial or herbivore pathways, could lead to forecast the aggregate size distribution in the ocean interior (Legendre and Le Fèvre 1995).

4.4.3. Hypothetic processes leading to the observed vertical aggregates size distributions

UVPs profiles can be described by the mesopelagic slope of aggregate size distribution and the depth evolution of this slope. Hypothese about aggregate transformation processes can be inferred from these 2 parameters. There are a variety of processes which consume and redistribute matter in settling aggregates, including physical coagulation (Jackson 1990), microbial degradation (Kjørboe 2001; Ploug and Grossart 2000), zooplankton feeding (Graham et al. 2000; Jackson and Kjørboe 2004; Stemann et al. 2004a), and zooplankton fragmentation (Dilling and Alldredge 2000; Goldthwait et al. 2004). These biological processes can lead to a removal of organic carbon relative to inorganic carbon. For example, they may act to decrease the median size of the aggregate and therefore decrease the related carbon flux to the deep ocean. At the opposite end, physical processes such coagulation tend to increase the mean

aggregate size while they settle (Jackson 1990; Kiørboe et al. 1994). Break down of particle size can be observed when strong shear and turbulence occur in the water column (MacIntyre et al. 1995). Clusters 1 and 5 are clearly identified by a decrease of the medium aggregate size with depth (slope from -2 at the surface to -4 at 1000 m for cluster 5). Processes such as microbial degradation, disaggregation and zooplankton fragmentation could explain this observed change in particle size.

Even if a decrease of aggregate size with depth has been observed (clusters 1 and 5: 141 profiles), most of the profiles highlight an increase of size with depth (clusters 3, 4 and 6: 240 profiles). The aggregate size increase could be attributed to zooplankton feeding and repackaging or to physical coagulation as a combination shear and differential settling. Small differences remain between these clusters. There is a change of the speed of the size increases with depth from cluster to cluster. The medium aggregate size of cluster 4 gently increases until 600 m which is the depth where a constant slope is achieved. The observed change of slope for clusters 3 and 6 are focused in the first 300 m of the water column. This suggests that this area of the water column is the location of intense biological and physical activity that transforms the aggregate size distribution and furthermore the aggregate flux to the deep water. The same remark can be made for profiles where a decrease of the mean aggregate size with depth has been observed.

4.4.4. *Fraction of surface stock exported to the mesopelagic zone*

Bias may exist calculating the fraction of the surface aggregate stock exported to the mesopelagic zone. There is a mismatch between particles observed below Z_e and at 1000 m. These aggregates should spend around 7 days to settle from the surface to 1000 m deep assuming a mean settling speed of 150 m d^{-1} (Berelson 2002; Peterson et al. 2005). Therefore aggregates recorded at these 2 different depths are probably different.

Particle flux at 400 m normalized by the flux at the base of Z_e varied between 0.01 and 0.2 (*s ratio*; Figure 26B). These estimations were opposed to the values of deep aggregate flux related to the producers' community (Figure 26A). The *s ratio* is low when the flux is associated with waters dominated by micro-phytoplankton (<5 %).

However mesopelagic flux remains high in these regions. These observations may result from intense remineralization just below Z_e (Berelson 2001; Buesseler et al. 2007b; Hopkinson and Vallino 2005) or aggregate accumulation on the pycnocline (Azetsu-Scott and Johnson 1992; MacIntyre et al. 1995). For these waters, up to 99% of the surface accumulation disappears before reaching the mesopelagic realm. Conversely, when Z_e is dominated by the pico-phytoplankton, the flux observed at 1000 m is low but represents 20% of the flux at Z_e .

Processes at the origin of these 2 different dynamics may be different. In upwelling regions when a phytoplankton bloom occurs, zooplankton growth and grazing can be fast, decreasing efficiently the surface phytoplankton production before it sink. This match between phyto- and zoo-plankton intensifies the carbon recycling in the euphotic layer (Wassmann 1998). In oligotrophic waters such as the South Pacific gyre, aggregates are smaller than in rich waters, leading to low settling velocities. The aggregate transformation could be dominated by bacterial degradation rather than by the zooplankton feeding (Karl et al. 1988). The small size of the phytoplankton and constant remineralization pressure may prevent the accumulation of large particles in Z_e .

4.4.5. Implications for the carbon flux modeling

The fate of export production is commonly modelled by empirical uniform power law functions to describe the distribution of particulate matter across the water column (Martin et al. 1987; Suess 1980). With the exception of some syntheses (Dunne et al. 2005; Lutz et al. 2002), many quantitative biogeochemical studies use the Martin power relationship parameterizations, although they are based on data sets from a limited geographic and depth range. The rate of flux decrease with depth has been shown to vary within and between ocean basins (Buesseler et al. 2007b; Karl et al. 1996; Usbeck et al. 2003). Our study suggests that aggregate dynamics could follow at least 2 patterns. First, aggregates produced in the euphotic layers dominated by micro-phytoplankton lead to high aggregate flux in the mesopelagic zone. This flux represents only a very low fraction of the surface aggregate flux (< 5%). Conversely, oligotrophic systems dominated by pico-phytoplankton present low aggregate flux in the mesopelagic zone

however representing up to 20% of what flux estimated below Z_e . Modelers expressed the speed at which the flux decreases with depth by the remineralization length representing the rate at which flux decreased with depth. In this paper it has been shown that the estimated flux at 400 m and below can be directly related to the surface phytoplankton population. Furthermore, the fraction of the surface particle stock reaching the mesopelagic zone has been related to the same phytoplankton population. Then, systems dominated by pico- or micro-phytoplankton could be represented by different values of the remineralization length in biogeochemical models. A high remineralization length should represent a drastic decrease of the carbon flux below the Z_e while a low remineralization length should correspond to a slow decrease of the carbon flux with depth. A regional modeling approach of the carbon cycle based on the phytoplankton composition and aggregate size distribution is a direction that needs to be explored if we want to better estimate the quantitative importance of the biological pump on a global scale.

CHAPTER V

VERTICAL DISTRIBUTION OF AGGREGATES (>110 μM) AND MESOSCALE ACTIVITY IN THE NORTHEASTERN ATLANTIC: EFFECTS ON THE DEEP VERTICAL EXPORT OF SURFACE CARBON

5.1. Introduction

One of the important results of the VERTEX and JGOFS programs is the generally observed power law decrease of particle flux with depth due to midwater biological activity (Martin et al. 1987). Aggregates collected in sediment traps at 1000 m can come from a surface area hundreds of kilometers away (Siegel and Armstrong 2002; Siegel and Deuser 1997; Waniek et al. 2005). However, frequent observations of deep episodic fluxes lasting less than 1-2 weeks (Beaulieu 2002; Conte et al. 2003; Nodder and Northcote 2001) and spatial mesoscale (<100 km) variability in the flux (Beaulieu 2002) suggest that rapid biological and physical processes may be involved in the transfer of surface production to the deep ocean.

Oceanic areas where advection or convection of water masses take place are subject to mesoscale changes in biogeochemical characteristics, especially in nutrient enrichment of the upper layer (McGillicuddy and Robinson 1998; McGillicuddy et al. 1998; Zakardjian and Prieur 1998). These cause patchy distributions of phytoplankton (Martin 2003; Rodriguez et al. 2001) and zooplankton (Abraham 1998; Boucher et al. 1987; Madin et al. 2001). Moreover, upward water motions in the ageostrophic frontal circulation caused by mesoscale and sub-mesoscale physical structures result in divergence, which may reduce the sinking of large phytoplankton through upwelling, control the size structure of phytoplankton assemblages and favor the formation of patches in the upper layer (Rodriguez et al. 2001). Hence, higher concentrations of aggregates are expected in divergence zones, as was shown by Gorsky et al. (2002) in the Almería Oran frontal system. Much less is known about the horizontal and vertical transport of suspended and sinking aggregates. Suspended aggregates could be entrained

or diluted by downward convection (Backhaus et al. 2003; Wehde et al. 2001). In contrast, sinking aggregates may escape lateral dilution, and sink below the zone of primary production yielding mesoscale zones of intense aggregate fluxes. Because traditional sampling techniques (traps, in situ pumps in the mesopelagic layer) are not adapted for resolving these spatial scales, the mesoscale distribution of aggregates (Gorsky et al. 2002; Peinert and Miquel 1994) or fluxes (Gorsky et al. 2002; Peinert and Miquel 1994) has been seldom reported, and the depth extent of these features remains unknown.

During the POMME (Programme Ocean Multidisciplinaire Meso Echelle) research cruises in the Northeastern Atlantic, we used a non-destructive imaging method (Underwater Video Profiler, UVP; (Gorsky et al. 1992; Gorsky et al. 2000) to gain information on the spatial distributions of aggregates in the mesopelagic layer, and to assess the extent of particle source area in a highly dynamic field. The present paper focuses on the possible origin of aggregates and the relationship between their spatial variability and mesoscale physical features. Field sampling and mesoscale modeling simulations have shown that the POMME area contains significant mesoscale and sub-mesoscale features, such as filaments located at fronts between mesoscale eddies (Memery et al. 2005; Paci et al. 2005). In this physical context, we propose here that downward particle export in a mesoscale context is restricted to relatively small zones, challenging the idea of a wide collection area for deep sediment traps. The global implications of this process are discussed.

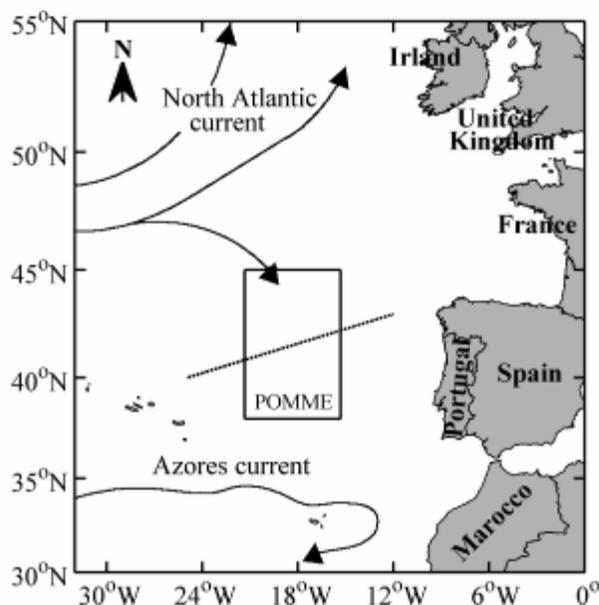


Figure 29: Study area in the Northeastern Atlantic. The dashed line is the approximate location of the zone of discontinuity of the winter mixed layer associated with subduction of mode water masses.

5.2. Materials and methods

5.2.1. Study area and sampling

The study area was located in the Northeastern Atlantic Ocean off the Iberian Peninsula and Azores Islands (39 – 45°N, 15 – 21°W; Figure 29). Three cruises were conducted between February and September 2001, corresponding to three seasons: end of winter, spring, and summer. Stations for each sampling period are shown in Figure 30. Conical sediment traps (PPS5) in time-series mode were moored over one year at 4 locations (Figure 30). Each cruise comprised two legs. Leg 1 focused on biogeochemical parameters and the description of hydrological structures from surface down to 1000 m using a vessel-mounted acoustic Doppler current profiler and intensive CTD (SBE911)/UVP casts. Leg 2 focused on selected ‘long stations’, which were sampled over 48 hours for studying various biogeochemical processes on samples collected with a CTD-rosette, floating sediment traps and in situ pump. In this paper, we will focus

mainly on the results from Leg 1 of the three cruises (Table 15). Some additional data from Leg 2 of each cruise are also presented.

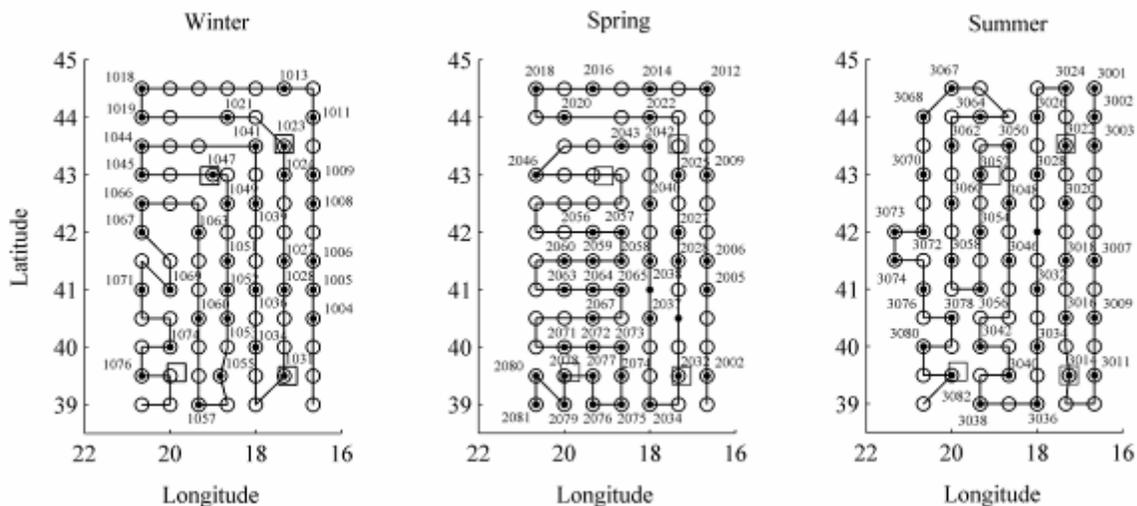


Figure 30: Sampling grid during the three POMME cruises. Locations of CTDs, shown by open circles, UVP stations by closed circles, and long stations and sediment traps by open squares.

The UVP images were analyzed and treated automatically using custom-made software. The objects in each image were identified and enumerated, and the area of each individual object was measured. The minimum size of particles efficiently measured by the UVP is $110\ \mu\text{m}$; therefore, this was the cutoff used for aggregates. The resulting data were combined with the associated CTD, fluorometer and nephelometer data. Because two types of UVP were used during the POMME cruises, we intercalibrated the two systems. For this purpose, two vertical profiles were recorded simultaneously at a station off the Bay of Villefranche (Northwestern Mediterranean Sea). We found that the two systems had similar spectra for aggregates larger than $110\ \mu\text{m}$ and smaller than $1\ \text{mm}$. To estimate the masses and fluxes of aggregates, we converted the aggregate individual sizes to mass, and the mass to flux using empirical equations given by Alldredge and Gotschalk (1988) and confirmed by (Alldredge 1998). They found that, in the epipelagic zone, the mass of aggregates is a function of the equivalent spherical diameter regardless of their origin or season of collection.

Therefore, we used the same algorithm to compute the mass and flux of each aggregate. Our estimates may be in the lower range of possible values because the algorithms we used tend to underestimate the settling speed (see Figure 2 in Stemmann et al. 2004b). Mass and flux were summed over each 5 m interval to provide total mass and flux in 5 m steps over the 0-1000 m water column and for all seasons.

Table 15: Cruises and UVP characteristic uses for all profiles.

Cruises	Dates	Profiler type	Camera	Min. size of aggregate
POMME 1	31 Jan 01 - 24 Feb 01	PVM 2c	24 mm	89 μm
POMME 2	23 Mar 01 - 13 Apr 01			
POMME 3	25 Aug 01 - 12 Sep 01	PVM 4	8 mm	200 μm
			25 mm	60 μm

Using the hydrographic data from the CTD SBE911, the mixed layer depth (MLD) was computed as the depth where water density exceeded the surface density by 0.02 kg m^{-3} (Claustre et al. 2005). Pigments were measured by high-pressure liquid chromatography using water collected from Niskin bottles mounted on the rosette. These data were used to determine the amount of chlorophyll *a* (Chl *a*) in three phytoplankton classes, according to (Claustre et al. 2005): micro- ($> 20 \mu\text{m}$, fucoxanthine + peridinin), nano- ($2\text{-}20 \mu\text{m}$, 19'-hexanoyloxyfucoxanthin + 19'-butanoyloxyfucoxanthin + alloxanthin), and picophytoplankton ($<2 \mu\text{m}$, total chlorophyll *b* + zeaxanthin). Transformation from pigments to chlorophyll was done with the empirical equations used by Claustre et al. (2005). The fluxes calculated from the UVP were compared to those measured at 400 and 1000 m in the sediment traps at four locations (Guieu et al. 2005).

To synthesize all the information on the distribution of particulate matter (mass, flux), phytoplankton, and physical data, we used horizontal, and vertical 2D maps. The

main drawback of such maps is that they mix spatial and temporal variability. One should be aware of this when examining connections between data geographically close to each other but separated in time. Since the ship followed different routes during the three cruises, the coordinates (distance, depth) in the vertical maps do not necessarily correspond to the same geographical locations.

5.3. Results

5.3.1. Hydrological context

5.3.1.1. Horizontal field

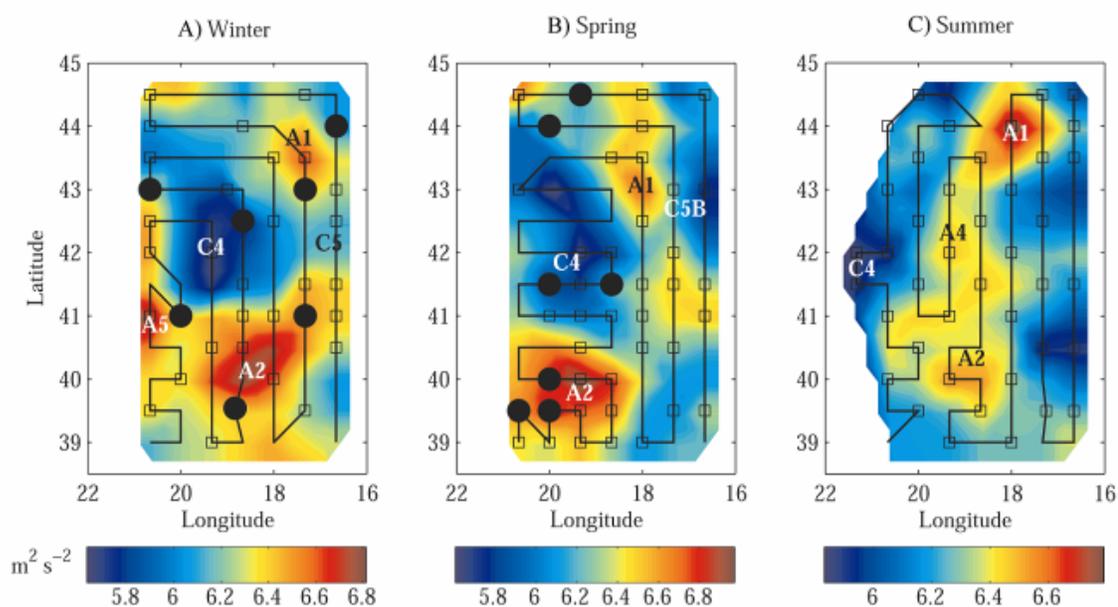


Figure 31: Geopotential anomalies at 300m calculated from hydrographic data during (A) winter, (B) spring, and (C) summer calculated from the sampling grid. The squares represent the locations of the UVP profiles. The black circles represent the positions where high stocks of aggregates were observed in the mesopelagic layer during winter and spring. These positions correspond to the locations where the 400-800 m integrated concentrations exceeded 5 times the surrounding integrated concentrations. These calculations were not performed for the summer cruise because of the lack of data deeper than 500 m.

Geopotential anomalies at 300 m calculated from hydrographic data (Figure 31) illustrate the locations and sizes of the mesoscale features encountered during our study. These geopotential anomalies have been compared with the sea surface height (SSH) and by assimilating the SSH in a model (Paci et al., 2005). The other maps do not challenge the general feature inferred from the hydrographic data. The ~ 55.5 km sampling grid only allowed the description of the largest anticyclonic (A1, A2, and A5) and cyclonic eddies (C4, and C5). Among them, some had deep roots (1000 m), and some persisted (A1, A2, and C4) during the three cruises although all the eddies presented a southwestward drift (Le Cann et al. 2005).

During winter (Figure 31A), the cold core cyclonic eddy C4 was centered at 42°N , 19°W (approximate core diameter 100 km). The western border of C4 was in contact with anticyclonic eddy A5. The eastern border of C4 was in contact with anticyclonic eddy A1 located at 43.5°N , 17.5°W . The core of eddy A1 had a diameter of approximately 50 km. The southern border of C4 was in contact with another warm core anticyclonic eddy A2. Its inner core was located near 40°N , 19°W , and had a 60 km diameter. In addition, the northern and eastern borders of anticyclonic eddy A1 were in contact with one cyclonic eddy C5, which was only partially covered by our sampling. During the spring cruise (Figure 31B), the cyclonic eddy C4 was located around 42°N , 19.5°W . High current velocities were observed along the eastern border of C4, which are presumed to be associated with the frontal zone, as was the case during winter. At 43°N , 18°W , the anticyclonic eddy A1 was observed with a 50 km core diameter. Anticyclonic eddy A2 was observed around 40°N during spring. Mesoscale activity was less intense during summer (Figure 31C) and eddies were less marked. Anticyclonic eddy A1 was located in the north-eastern part of the study area (44°N , 18°W).

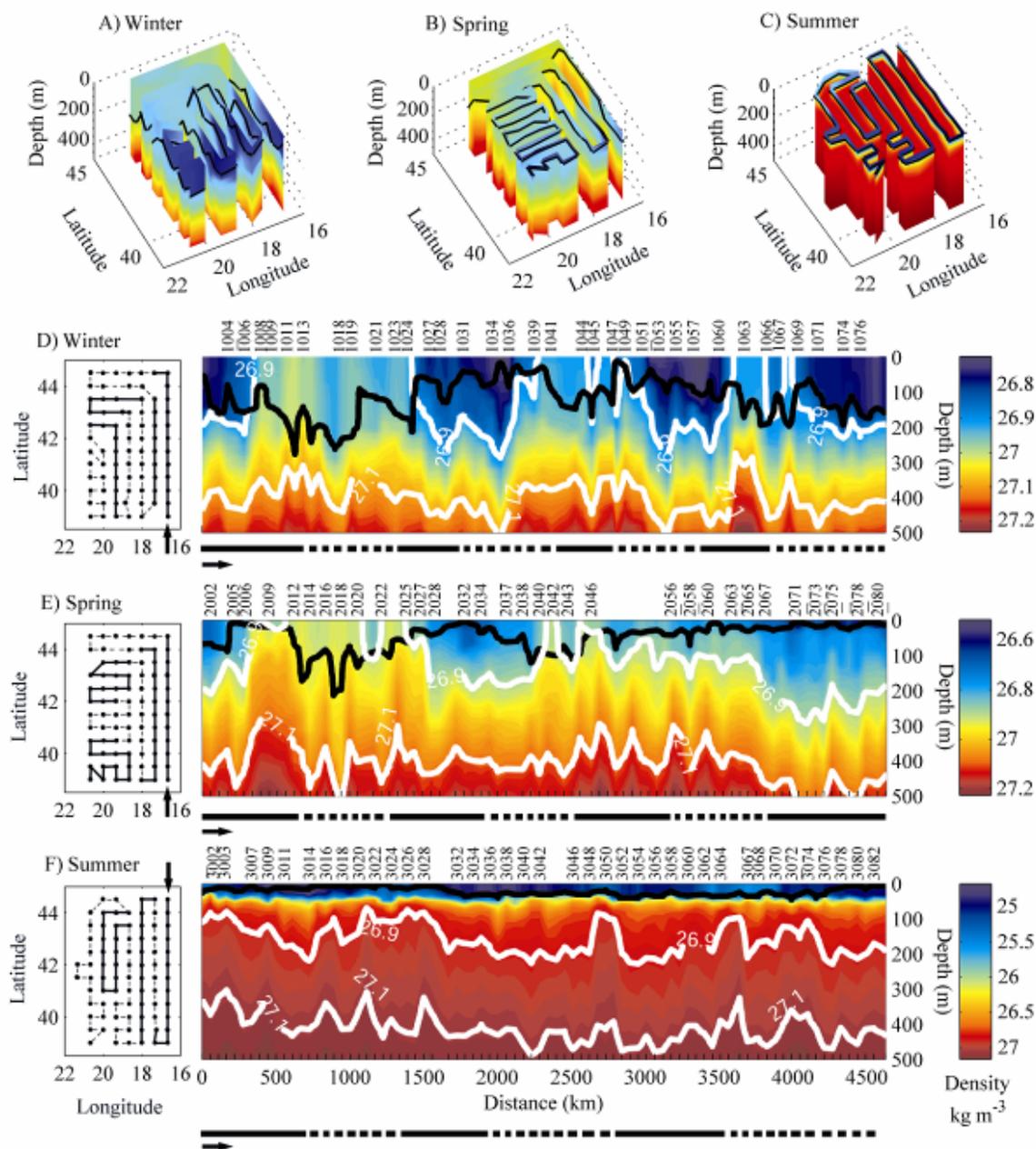


Figure 32: 3D maps of density field during (A) winter, (B) spring, and (C) summer and vertical sections of sea-water density in (D) winter, (E) spring, and (F) summer as inferred from all the CTDs. The MLD is marked by the black continuous line in both the section and 3D maps and the mode water is located between the 2 white continuous lines. The station numbers where the UVP was deployed are given above each section. The ship tracks are given on the maps on the left of each section. The continuous and dotted lines on each map are repeated under each section in order to help the reader to localize itself. The arrows point at the start of the track.

5.3.1.2. Vertical field

The frontal structure is clearly visible in the winter horizontal density field transitions from low (<26.9) to high (>26.9) density values (Figure 32A, D). The main frontal structure (between 41 and 42° N) was crossed on all the north-south transects (between stations 1006 and 1008, 1024, and 1027, 1036, and 1041, 1047, and 1051, 1060, and 1063, 1068, and 1069). During spring (Figure 32B, E), the sampling grid was modified to follow eddies, and fewer north-south transects were performed. As a consequence, the front was clearly crossed only three times (between stations 2006, and 2009, 2025, and 2028, 2040, and 2042). During summer (Figure 32C, F), the density front was more difficult to observe due to pronounced vertical stratification.

A clear seasonal variation was observed in surface density with the establishment of stratification during spring (Figure 32B, E). MLD extended deeper in the northern area during winter (143.6 ± 57 m), while in the southern area, it reached 124.1 ± 45 m (Fernandez et al. 2005). During spring, a general decrease in MLD was observed, but average values were slightly greater in the southern area (96.25 ± 40 m; Fernandez et al. 2005). The shallowest MLDs and the smallest difference between the northern and southern areas were observed during summer, where the MLD varied between 27.8 ± 9 m in the south and 28.44 ± 10 m in the north.

The mode water (defined by density > 1026.95 kg m⁻³; Memery et al. 2005), formed in the northern area of the sampling zone, was most evident during summer between 200-500 m. In winter and spring, the deep boundary was observed around 400 m while the upper limit sometimes reached the surface.

5.3.2. *Seasonal variability in the vertical profiles of aggregates*

Median vertical distribution of the calculated masses of aggregates in the study area is shown in Figure 33 for the three seasons. There was a consistent seasonal variation between periods. Within one cruise, the relative variability is low: the range of error expressed as the first and third quartile is 7 to 61 % for winter, 4 to 57 % for spring and, 1 to 55 % for summer. The vertical means were 29, 18 and 15 %. In the 0-200 m layer, aggregate masses were highest during spring (100–120 mg dry wt m⁻³) and lowest

during summer and winter (1-10 mg dry wt m⁻³). In the deeper layers, down to 1000 m, the seasonal pattern was different with concentrations higher in spring and summer and lowest in winter (for example at 800 m, 5-10 mg dry wt m⁻³ in spring, and summer, 1-5 mg dry wt m⁻³ in winter). During spring, a small midwater increase of aggregate concentration was observed between 300 and 600 m. In contrast, a clear minimum was observed between 300 and 500 m in summer.

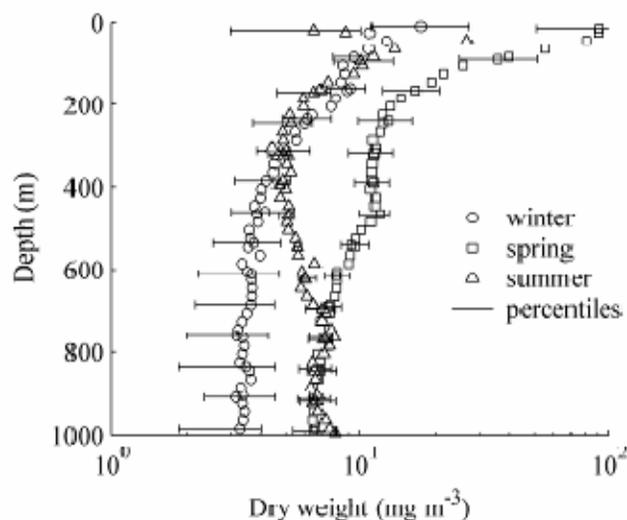


Figure 33: Median vertical profiles, and first and third quartiles, of aggregate mass during the three cruises: winter ($n=36$), spring ($n=43$) and summer ($n=41$). Note that for the summer profiles, median values deeper than 500 m were calculated using only 6 available UVP profiles.

5.3.3. Temporal and spatial changes in vertical distributions of aggregates

Spatio-temporal changes in aggregates showed high variability within cruises, although a seasonal pattern could be clearly observed (Figure 34). The highest concentrations in the water column occurred in spring, and the lowest in winter and summer. The timing of aggregate increase and removal can be determined by examining the 8 mg dry wt m⁻³ isomass. This concentration was chosen because winter deep mesopelagic aggregate concentrations never exceeded this value. Hence it may be considered as the reference pre-bloom concentration. In addition, it showed less within-cruise vertical variability than does a smaller isomass contour. If we assume that the

source of particles was located in the surface productive zone and that the average concentration of aggregates in the mesopelagic layer before the start of the productive season was $< 8 \text{ mg dry wt m}^{-3}$, then the deepening of this isomass from 149 (± 103) to 642 (± 171) m from early February (beginning of winter, Figure 34A, D) to mid-March (beginning of spring, Figure 34B, E) yields a bulk settling speed of roughly 10 m d^{-1} for aggregates $> 110 \mu\text{m}$. However, this calculation represents the settling speed of the bulk export, and should be taken with caution because aggregate mass distributions varied widely in space and time.

Surprisingly, we found that the mesopelagic layer was very heterogeneous, with zones where the concentrations of aggregates remained high as deep as 1000 m in winter (Figure 34D, stations 1011, 1024, 1028, 1044, 1055, 1069) and at least as deep as 500 m in spring (Figure 34E, 2005, 2006, 2020, 2058, 2060, 2071, and 2080) and summer (Figure 34F, stations 3002, 3020, 3048, 3074). In these zones, the concentrations of aggregates and the vertical extension of homogeneous distributions from surface to depth tended to decrease from winter to summer. In these structures, showing deep homogeneous distributions, concentrations could be up to 5 times higher than in the adjacent waters (see stations 1024, 1028, and 1049 during winter, Figure 34D). These structures were generally observed on single casts (on two occasions, they were at neighboring stations, i.e., 1044, and 1045, and 2071, 2078, and 2080), suggesting that their maximum size was on the order of 100 km. They were located below most of the strong horizontal density gradients that were crossed during the winter and spring cruises (geopotential anomalies in Figure 31; see stations 1011, 1024, 1045, 1069, 2020, 2060). However, several structures could also be observed in eddies (Figure 31; see station 2071, and 2078 in anticyclonic eddy A2).

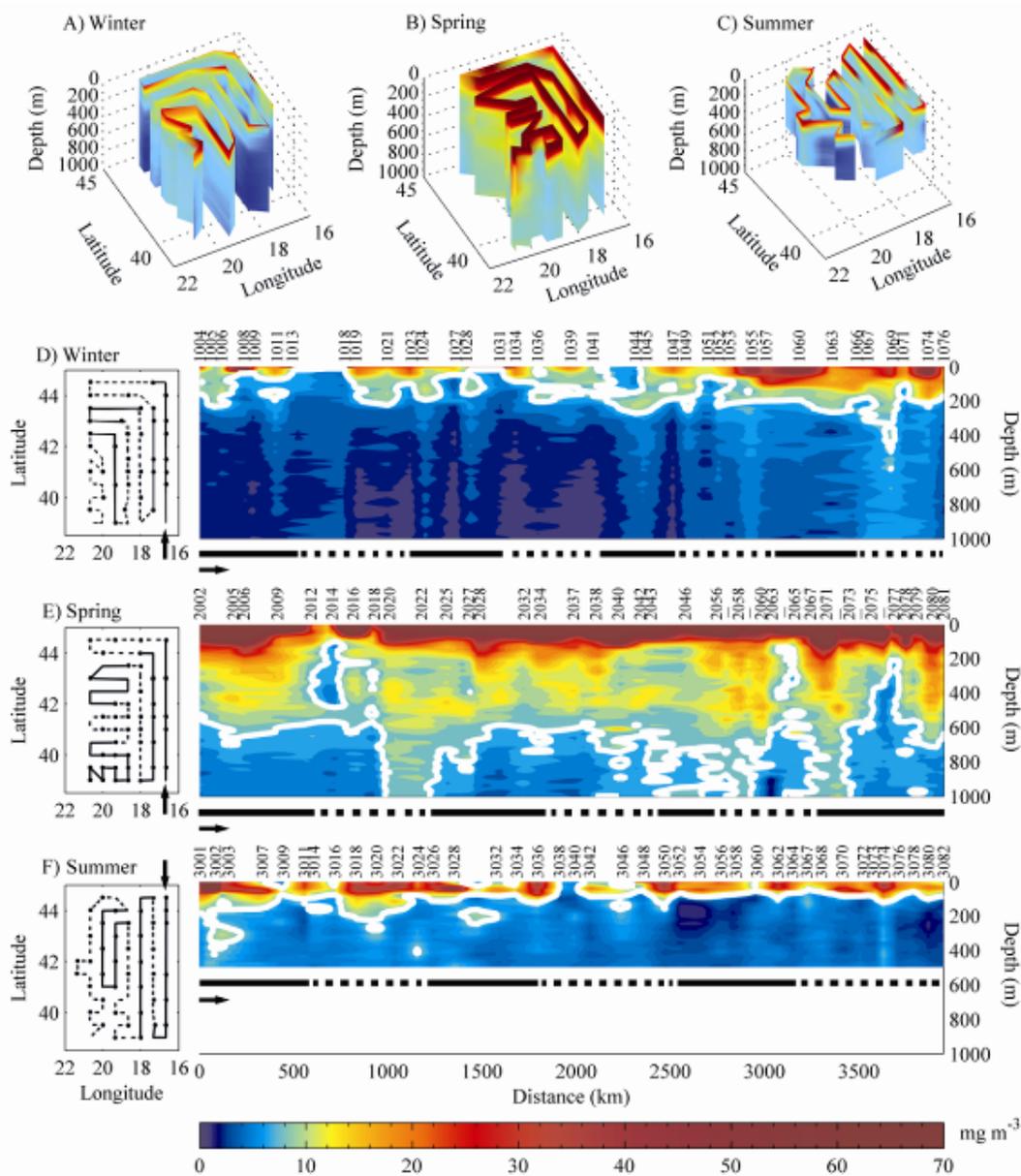


Figure 34: 3D maps of seasonal changes in the vertical distribution of aggregates in (A) winter, (B) spring, and (C) summer, and vertical sections of aggregate distribution along the ship tracks in (D) winter, (E) spring, and (F) summer, in mg dry wt m^{-3} . The station numbers where the UVP was deployed are given above each section. The color scale emphasizes variability at the lower end of the concentration range. The depth of the isomass of aggregates 8 mg m^{-3} is given by the white line. The ship tracks are given on the maps on the left of each section. The continuous and dotted lines on each map are repeated under each section in order to help the reader to localize itself. The arrows point at the start of the track.

5.3.4. Spatial distribution of phytoplankton

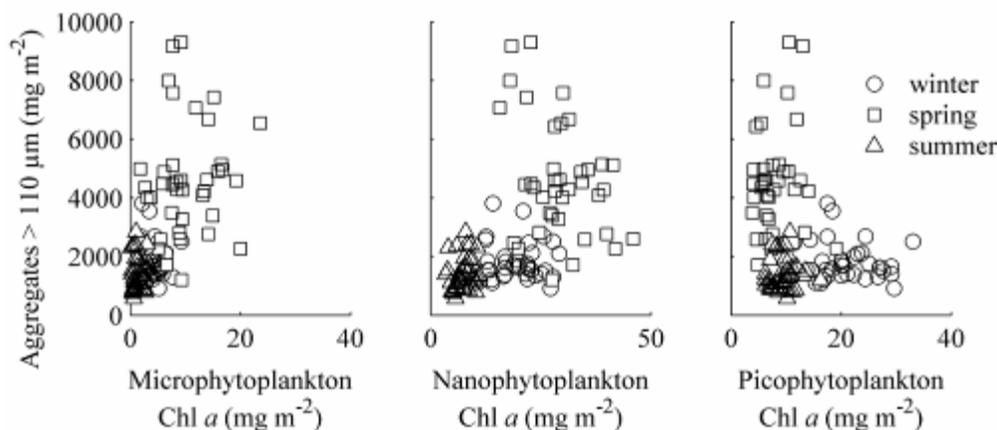


Figure 35: Vertically integrated concentrations of aggregates as a function of vertically integrated Chl *a* in three phytoplankton groups during the different cruises for the 0-200 m layer.

Vertically integrated total chlorophyll *a* (Chl *a*) for the three phytoplankton size classes were compared to the integrated mass of aggregates in the euphotic layer. For all phytoplankton and aggregate data, the lowest values were observed in summer, and the highest in spring except for picophytoplankton (Figure 35). Significant correlations between Chl *a* and aggregate concentrations were only observed during spring (Table 16). That correlation was driven by the correlation between aggregates and microphytoplankton. In summer, only the microphytoplankton were correlated with aggregates.

Table 16: Spearman correlation coefficient between integrated aggregate concentrations and integrated pigment concentrations in the 40-60 m layer.

	Winter	Spring	Summer
Total Chl <i>a</i>	0.10	0.45*	0.32
Micro-phytoplankton	0.12	0.60*	0.40*
Nano-phytoplankton	0.12	0.12	0.27
Pico-phytoplankton	0.08	0.03	0.10

* : $p < 0.01$

Spatial distributions of phytoplankton differed between seasons but mesoscale structures were constantly observed. The highest integrated concentrations (0-200 m) of Chl *a* occurred in spring ($\sim 100 \text{ mg m}^{-2}$) south of A1, and the lowest in summer in the southern part of the studied area ($< 10 \text{ mg m}^{-2}$) (Figure 36). During spring, the two anticyclonic eddies (A1 and A2) had similar and high integrated Chl *a* concentrations, but the mesopelagic aggregate concentrations were high under eddy A2 only (Figure 36B).

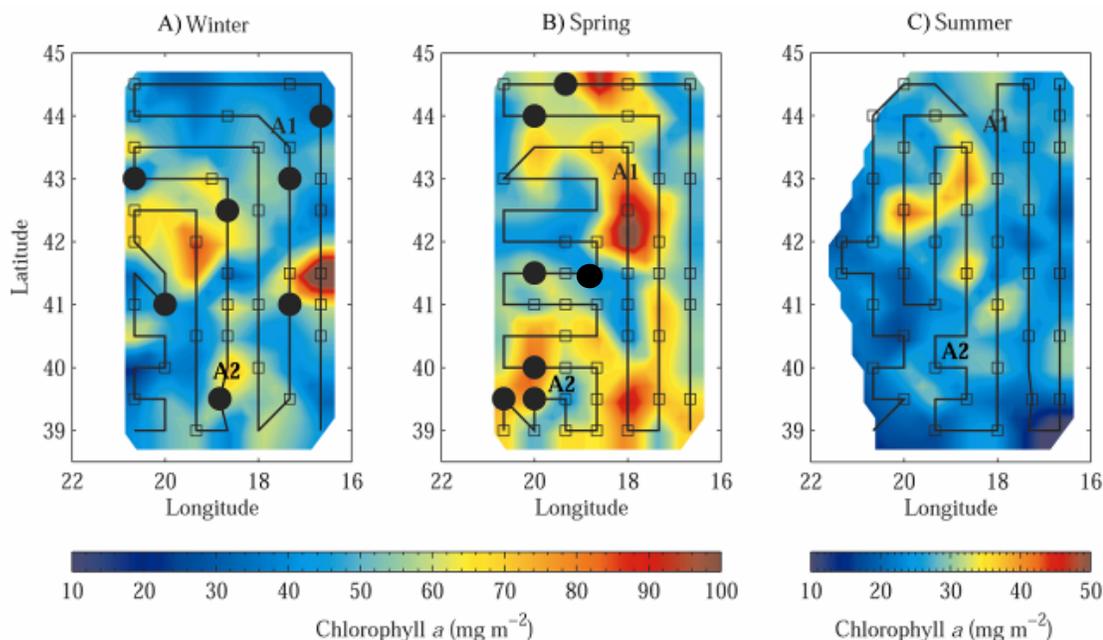


Figure 36: Integrated concentration of total Chl *a* ($\text{mg Chl } a \text{ m}^{-2}$, 0-200 m) during (A) winter, (B) spring, and (C) summer calculated from the sampling grid. Squares represent the locations of the UVP profiles. The black circles represent the positions where high stocks of aggregates were observed in the mesopelagic layer during winter and spring. These positions correspond to the locations where the 400-800 m integrated concentrations exceeded 5 times the surrounding integrated concentrations. These calculations were not performed for the summer cruise due to the lack of data deeper than 500 m.

5.3.5. UVP calculated flux and sediment traps

Sediment trap and UVP fluxes were of the same order of magnitude, especially at 400 m. However, some discrepancies occurred at 1000 m. Mass fluxes estimated from UVP data were higher in summer, and winter and lower in spring when compared to sediment trap data (Figure 37).

Sediment trap mass fluxes and UVP potential mass fluxes followed the same trends. The sediment trap fluxes increased during winter to reach maximum values during spring (April) at 400, and 1000 m with $600 \text{ mg m}^{-2} \text{ d}^{-1}$, and $620 \text{ mg m}^{-2} \text{ d}^{-1}$, respectively, after which the fluxes decreased to reach minima during late summer (September). The sediment trap data show that the flux at 400 m was highest in the

northeastern area (close to A1), and the flux at 1000 m was highest in the southwestern area (close to A2) (Figure 37).

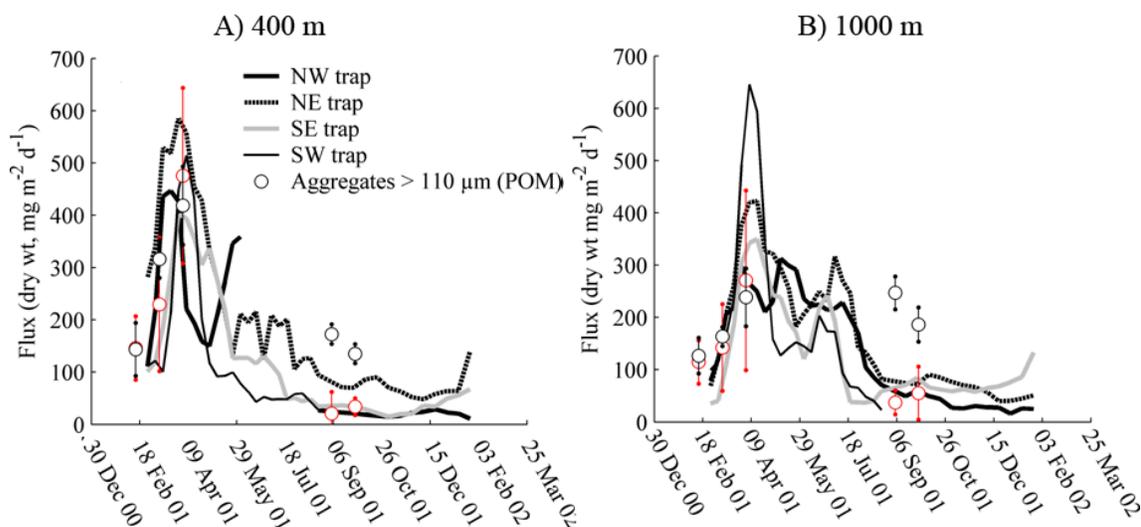


Figure 37: Figure modified from Guidi et al. (in revision). Comparison between UVP potential mass fluxes and mass fluxes from sediment traps at (A) 400 m and (B) 1000 m. Potential fluxes from UVP using Allredge and Gotschalk (1988) in black circles and using relationship presented in chapter III in red circles. The sediment traps were corrected for trapping efficiency, which was estimated to range from 20 to 50% (Guieu et al. 2005).

5.4. Discussion

Determining the sampling strategy in biogeochemical studies is difficult because the time needed to cover a large hydrographic grid with a ship (i.e., weeks) overlaps with seasonal variability and horizontal patchiness. The sampling grid of POMME achieved a compromise between small-scale structures and the mesoscale observation field. It allowed us to sample the study area on a 55.5 km grid. Due to lack of time, the UVP casts could not be performed at each station, so that the UVP sampling grid was not as tight as the CTD sampling grid (see Figure 30).

5.4.1. *Relation between aggregates and the phytoplankton community*

The median vertical distribution of aggregates mass concentrations was high throughout surface, and a quasi-exponential decrease with depth below (Figure 33). Higher mass concentrations in the upper layers compared to the deeper layers suggest that the surface was the source of aggregates while the deep ocean was the sink. In the surface zone of the ocean, the original source of small particles is phytoplankton cells. Aggregates can be formed from these initial particles either directly by physical coagulation, when cell concentrations, stickiness, and shear rates in the ambient water are high, or indirectly by secondary production (e.g., feces, gelatinous feeding webs, and molts; Alldredge and Silver 1988; Jackson 1990). Therefore, one may expect a correlation between the spatio-temporal distributions of phytoplankton and aggregates, which also may be modulated by ambient hydrodynamics and zooplankton activity. Because of the lack of a consistent zooplankton data set, we could only correlate the integrated aggregates with phytoplankton stocks.

The correlation between aggregates and total Chl *a* is mainly driven by the correlation between aggregates and microphytoplankton (Table 16). In summer, aggregate concentrations were not correlated with total Chl *a* but with the microphytoplankton. These results suggest that the amount of aggregates in the epipelagic layer depended on the size structure of primary producers. This is consistent with the common assumption that very small phytoplankton cells do not generally lead to large aggregates (e.g., Legendre and Le Fèvre 1995), the same should be true for nanophytoplankton. The absence of correlation between total Chl *a* and aggregates in summer, despite the fact that the microphytoplankton were correlated with aggregates, could have resulted from a low contribution to total Chl *a* (<10%; Claustre et al. 2005). In spring, the doubling of their contribution (20% of total Chl *a*; Claustre et al. 2005) may have triggered the formation of large aggregates.

5.4.2. *Chronology of the accumulation and disaggregation of aggregates in the mesopelagic zone*

From the deepening of the 8 mg dry wt m⁻³ isomass between February and March, we estimated a bulk settling speed of 10 m d⁻¹ for aggregates >110 µm. This average settling speed is consistent with previous works (reviewed in Stemmann et al. 2004), and is of the same order of magnitude as the estimates of Stemmann et al. (2002) obtained from the chronology of aggregate export in the North western Mediterranean Sea. However, the bulk settling speed is to be taken with caution, because it is an average over a wide range of aggregate sizes and chemical compositions, and therefore settling speeds. Furthermore, the observed mesoscale patterns in the mesopelagic distributions of aggregates suggest that the settling speed varied greatly in the study area.

During the summer cruise, there were fewer aggregates in the water column than during spring down to 700 m but not below (Figure 33). This suggests that the signature of the spring bloom (March-April) was preserved in the deep layers late in summer (August-September). There may be a fraction of aggregates that had a very low settling speed. In contrast, most aggregates had disappeared from the upper mesopelagic layer during summer. Hence, a small part of the stock of aggregates was stored for several months in the mid-mesopelagic layer before being removed. This observation is consistent with Gardner et al. (2000), who showed that, in the mesopelagic layer of the Ross Sea, there were more aggregates in the late summer-autumn period than in early spring, and that this matter may have consisted of slowly sinking aggregates that did not reach the bottom of the mesopelagic layer until late in the season.

5.4.3. *Comparisons with sediment traps*

The potential fluxes calculated from the UVP data at 400 and 1000 m are of the same order of magnitude as the estimates from sediment traps corrected for trapping efficiency at the same depths, especially in winter, and spring (Guieu et al. 2005). The sediment trap correction from 20 to 50% was obtained by comparing the Thorium-230 flux in the trap with the Thorium-230 production in the overlaying water column. Moreover, the seasonal trends of UVP and trap data were similar at the two depths

(Figure 37). The standard deviation of the UVP flux reflects spatial and temporal variability.

However, the UVP flux is much higher than the trap flux in summer at 1000 m, and to a lesser extent at 400 m. If we assume that the trap corrected fluxes are correct, the use of a constant conversion factor between aggregate size and mass may explain the overestimation by the UVP. The constant conversion factors have been defined for relatively fresh aggregates loaded with diatom skeletons (Alldredge and Gotschalk 1988), while the chemical properties of aggregates changed through time over the three cruises. Indeed from spring to summer, the carbonate and opal fraction decreased (from 70 to 60% and from 15 to 10% respectively) and the organic fraction increased (from 16 to 26%), so that the ballasting effect was probably lower in summer (Guieu et al. 2005). Therefore, similar sized aggregates must have settled more slowly in summer than in winter-spring. This effect is not taken into account in our algorithm. Other reasons for the disparity between calculated potential UVP flux and observed sediment trap flux can come from differences in the quality of the material collected or recorded by the two methods. Sediment traps collect mostly fast-sinking aggregates over 15 days, whereas the UVP measures instantaneously all aggregates and does not take into account any dissolution or fragmentation processes that could lead to lower values in sediment trap fluxes.

The use of algorithms presented in chapter III increase the fit between UVP estimated fluxes and sediment trap flux measurements especially in summer at 400 and 1000 m (Figure 37). The better estimation by the new algorithm compare to the Alldredge and Gotshalk relationship is achieved because their settling speed relationship was too flat giving a relatively greater importance to small aggregates in fluxes.

Despite all methodological biases, the similarity between the two flux estimates suggests that vertical export can be derived from vertical profiles of aggregates, providing that the conversion factors between aggregates sizes, masses and settling speeds are known. The advantage of UVP is to provide information on the spatial distribution of export on both the horizontal and vertical scales. This point is of

importance in cases of intense but geographically constrained vertical export, as suggested by our observations (Figure 34; see below).

5.4.4. *Mesoscale vertical export of aggregates*

If we assume that the source of aggregates is located in the surface productive layer, then the presence of high aggregate concentrations in the mesopelagic zone at spatial scale <100 km implies that surface production is exported to the deep ocean in a rapid and coherent manner rather than being diluted during its vertical transport (Figure 34).

The first mechanism that could explain the deep occurrence of aggregates in restricted geographical areas is the rapid settling of local surface production. Such efficient export would be enhanced in systems dominated by large phytoplankton producing aggregates with high settling speed. For example during spring, the two anticyclonic eddies A1 and A2 had equal integrated Chl *a* concentrations, but the mesopelagic aggregate concentrations were high only under the second eddy. According to Claustre et al. (2005), the taxonomic composition of phytoplankton differed at these two sites, with dominance of microphytoplankton in A2 (>50% of total Chl *a*) and nanophytoplankton in A1 (microphytoplankton <25% of total Chl *a*). It is possible that the occurrence of smaller primary producers in A1 led to an ecosystem that produced fewer of the large aggregates, and thus exported the surface production to the deep sea less efficiently compared to the ecosystem in A2. The sediment trap data support this hypothesis showing that the fluxes under A2 at 400 and 1000 m depth were similar while under A1, the flux at 1000 m depth was smaller than that at 400 m. These results suggest that the efficiency of export close to eddy A2 was higher than in the area close to eddy A1. However, mostly during winter, the mesopelagic areas with high aggregate concentrations did not always match the surface areas with high phytoplankton biomass. Hence, the direct export by settling of the high local phytoplankton production cannot account alone for the observation of high aggregate concentrations in the mesopelagic layer.

The second mechanism able to concentrate or disperse existing aggregates is horizontal and vertical circulation. Horizontal circulation around eddies may concentrate phytoplankton production in zones of converging currents, where physical and biological aggregation can take place (Martin 2003; Martin et al. 2001; Williams and Follows 1998). This mechanism could explain the high concentrations of aggregates in areas of low surface phytoplankton biomass, above stations 1024, 1069, and 2058, which were located at the edges of eddies (Figure 36). Once the aggregates were concentrated in these areas, they would settle out, or could be entrained into, the ageostrophic vertical circulation that takes place at sub- to mesoscale levels. Upward and downward velocities are generally high in the mesopelagic layer at eddy boundaries (a few tens of m d^{-1} ; Allen et al. 2001; Levy et al. 2005; Pollard and Regier 1990). Combined settling of aggregates and maximum downward convective transport can enhance the total vertical speed (up to more than 100 m d^{-1}), which could explain the export of aggregates to 1000 m in less than 10 days.

The sampling strategy of POMME was designed to investigate mesoscale features in the area. The resulting sampling grid did not allow us to fully capture the processes involved in the observed pattern of aggregate export because aggregate dynamics were controlled by a mixture of biological and physical processes that partly occurred at smaller scales.

5.4.5. Seasonal changes in mesoscale vertical export

There are very few direct observations of episodic mass fluxes triggered by the mesoscale activity of surface eddies. In the western Sargasso Sea, Conte et al. (2003) suggested that an abrupt increase in the flux at 3200 m during autumn was due to an increase in surface biological production due to the passage of a mesoscale eddy. Thus, the effects of mesoscale features on the perturbation of mixed layer dynamics are likely to vary seasonally, and may trigger episodic fluxes at times of low vertical stability. This could be one explanation for the high variability in mass flux that is commonly observed in the Sargasso Sea in the December–March period (Conte et al. 2001). For the North East Atlantic, we found that spatial variability in the mesopelagic distributions of

aggregate concentrations was lower in summer than winter (Figure 34). Since mesoscale activity and therefore downward aggregate transport was a minimum in summer (Memery et al. 2005), our data support the hypothesis that seasonal variability in aggregate export was linked to the seasonal mesoscale activity. In the Mediterranean Sea, using a multi-year time series, we also observed a link between the seasonal activity of a cross-shelf frontal system and the occurrence of spatially constrained high concentrations of aggregates in the mesopelagic layer (Stemmann et al., personal communication). It follows that temporal changes in mesoscale hydrodynamics may be of great importance for the export of surface production to the mesopelagic layer at mesoscale levels.

5.4.6. Implications for the deep export of carbon

Although the mechanisms are not as yet entirely clear, data collected in different geographic locations with the UVP suggest that 'hot spots' of vertical transport take place in frontal areas of the ocean. These 'hot spots' have been previously reported for aggregates larger than 500 μm in several frontal systems of the Mediterranean Sea (Gorsky et al. 2002) and in the Pacific equatorial system (Gorsky et al. 2003). The POMME results together with previous findings suggest that mesoscale variability in the export of surface production is a common feature in highly dynamic ocean systems.

Spatially structured downward export is different from the usual belief that the aggregates collected in sediment traps at 1000 m are advected from a surface area hundreds of kilometers away (Siegel and Armstrong 2002; Siegel and Deuser 1997; Waniek et al. 2005). In this generally held view, the spatial domain from which the collected sinking aggregates likely originated is called the "statistical funnel" (Deuser et al. 1990; Deuser et al. 1988). The funnel's intersection with the sea surface can be thought of as circumscribing the catchment area of the trap. The greater the fluctuating, or eddy, velocity field above the trap, the greater the spatial extent of the statistical funnel. For the North East Atlantic (BIOTRANS site), the catchment's area for sediment traps at 1000 m depth has been calculated, using a model that accounts for the flow fields, to range from 250 to 350 km, and from 350 to 600 km for aggregates with settling

speeds of 50 to 100 m d⁻¹ (Waniek et al. 2000). In our study, the horizontal scale of massive export is smaller than 100 km, which is much smaller than previously thought. However, as the eddies moved southwestward by approximately 50 km per month (Guieu et al., 2005), the instantaneous position of a chimney does not necessarily reflect the actual vertical transport, which can be increased by the horizontal displacement of the whole structure.

Eddies have been reported to be coherent features in the whole North Atlantic over months (Wade and Heywood 2001), and also in many other areas. Therefore, mesoscale export of aggregates may be a typical feature related to ocean hydrodynamics, which had not been directly observed until now because of the low spatial resolution of available technology, e.g., sediment traps. Results from recent observations and modeling suggest that surface submesoscale and mesoscale primary production may account for 50 % of the total production of oceanic basins (Oschlies and Garçon 1998), but very little is known about the fate of the resulting particulate matter. Our observations suggest that a large quantity of this particulate organic matter may be exported to depth in spatially limited zones where the physical conditions allow intense small-scale processes to occur. Although these profiles provide greater horizontal and vertical resolution of aggregate distributions and calculated particle fluxes than previously available, the resolution is still insufficient to quantify and explain the processes leading to such localized fluxes. Future studies and adapted sampling grids should provide insights into these potentially important features, which sediment traps can only occasionally capture.

CHAPTER VI

GENERAL CONCLUSION AND PERSPECTIVE

6.1. Main results

Sediment traps have been widely deployed the last 30 years, leading to a better understanding of the carbon cycle in the ocean. However recent research highlights weaknesses of this technology and the need for additional sensors (Buesseler et al. 2007a). Image systems such as the Underwater Video Profiler (UVP) are powerful tools to estimate spatial variability of aggregate size in the surface kilometer of the ocean. Different aggregate characteristics are directly related to particle size. Settling speed is perhaps one of the most important aggregate characteristics that is critical to carbon flux. UVPs do not provide information on aggregate chemical or biological composition. However, they can sample aggregate size distributions with high resolution in the vertical dimension.

Chapter III of this dissertation described a new approach to estimate carbon flux in the ocean interior based on aggregate size (diameter) distributions. UVPs profiles were combined with fluxes determined using sediment traps. The comparison led to an estimate of aggregate flux, aggregate fractal dimension and aggregate settling speed, all as a function of aggregate diameter. Estimating vertical fluxes using profiles of aggregate size distribution provides higher vertical export resolution than trap measurements. The use of fluxes derived from sediment trap measurements to calibrate the method assumes that the sediment trap measurements were correct and does contribute to some uncertainty about the conclusions. Improvement of sediment trap methodology (Buesseler et al. 2007a) should improve the techniques developed and applied in this chapter. Observation of carbon flux with high vertical resolution (quasi continuous profiles) can provide more precise information on the aggregate remineralization depth and rate.

Chapter IV compared aggregate size distribution in the oceans to physical and biological environment variables. Profiles of aggregate size distribution between 20 and

1000 m were found to separate into 6 characteristic groups. Strong spatial heterogeneity of aggregate size was shown to exist on a global scale. Profiles with a high proportion of large aggregates were found in productivity “rich” waters while profiles with a high proportion of small aggregates were located in productivity “poor” waters. This qualitative approach suggests a potential relationship between surface phytoplankton population and aggregate size. Using an original statistical procedure, aggregate size and mass flux in the mesopelagic layer were correlated to the nature of primary producers (micro-, nano-, picophytoplankton fractions) and to the amount of integrated chlorophyll *a* in the euphotic layer (Z_e). Vertical distributions of phytoplankton populations in the open ocean can be estimated from surface chlorophyll *a* data obtained by satellite (Uitz et al. 2006, Figure 38).

Global annual/seasonal carbon flux in the mesopelagic zone could be inferred from space knowing the relationship between flux and nature of the phytoplankton population. The JGOFS program collected sediment trap time-series all over the world and made them freely available. These data could be used to validate the model developed in the fourth chapter of this dissertation where particle distribution data are also available.

Chapter V is focused spatial variability of carbon export in the ocean. We have shown that in a mesoscale hydrodynamic region (~100 km) of the North-Eastern Atlantic some flux events were localized in small areas at rates 5 times higher than in the surrounding waters. These areas correspond to eddies and frontal structures. In another region in the North-Western Mediterranean Sea, the Ligurian Sea frontal system has been shown to influence aggregate size distribution. Smaller aggregates ($150 \mu\text{m} < \text{ESD} < 1 \text{ mm}$) were more abundant in coastal waters than in the open ocean as a result of continental input, cross-slope export, and re-suspension along the slope. The concentrations of large aggregates ($\text{ESD} > 1 \text{ mm}$) were highest in and under the frontal zone, probably as a result of physical coagulation, and/or biological transformations (Stemmann et al in press). Finally, UVP data for the western coast of Australia (unpublished data) appear to confirm the importance of mesoscale structure on aggregate

export. The eddy detected at this location seems to constrain the spatial distribution of aggregates. This chapter highlights 3 situations where mesoscale oceanic structures influence aggregate size distribution. Eddies and fronts are found commonly throughout the ocean. Carbon flux could be driven by such mesoscale (10-100 km) structures at least at regional scale.

6.2. Remaining key questions

This work points out how important the knowledge of aggregate size distribution is to identify processes about the origin of the carbon export to the deep ocean. Despite advances made by this PhD research, several questions remain.

6.2.1. *Aggregate transformation vs remineralization*

Carbon flux has been described as decreasing with depth following approximately a power relationship and this decrease is usually assumed to be constant in all oceans systems (Martin et al. 1987; Suess 1980). Only a few works suggest that oceanic regions are characterized by different rates of flux decrease (Lutz et al. 2002; Schlitzer 2002). In agreement with these 2 recent studies, we have seen that the estimates of particle flux at 1000 m normalized by the estimated flux at the base of euphotic zone (*s ratio*) varies a lot in a way that is related to the overlying phytoplankton population. Surprisingly in regions dominated by pico-phytoplankton, particle fluxes are low in the mesopelagic zone and the *s ratio* is elevated, suggesting that a high fraction of flux leaving the euphotic zone makes it to 1000 m. An other explanation could be that aggregates formation and degradation occur at the same rate through the 0-1000 m water column. In such system aggregates are usually small (<100 μm) with settling velocity close to zero. Then aggregate degradation would occur at aggregate formation depth yielding a low aggregate vertical transfer. The understanding of the underlying processes is a key to estimate the flux in these regions. In contrast, the *s ratio* is low in oceanic regions dominated by microphytoplankton, indicating that only a small fraction of the flux falling out of the euphotic zone reaches 1000 m. However, the fluxes in the intervening mesopelagic layer are higher below the microphytoplankton zones than

below the picophytoplankton zones. Within the vertical dimension, aggregates undergo several biological and physical transformations while they settle. Hence aggregates below the euphotic zone differ from aggregates observed 100s of meters deeper. What processes lead to differences observed in systems dominated by pico or micro-phytoplankton? How do transformations of particles by bacterial or zooplankton differ from those from physical coagulation? What is the relative importance of these biological and physical processes in the oceans? Some ideas were discussed in this dissertation. Future modelling studies integrated aggregate size distribution, coagulation and good knowledge of bacterial and zooplankton community structure and depth repartitioning could provide some answers. Long time series such as DYFAMED, HOT or BATS stations provide extensive set of data that could be use with these modelling approaches.

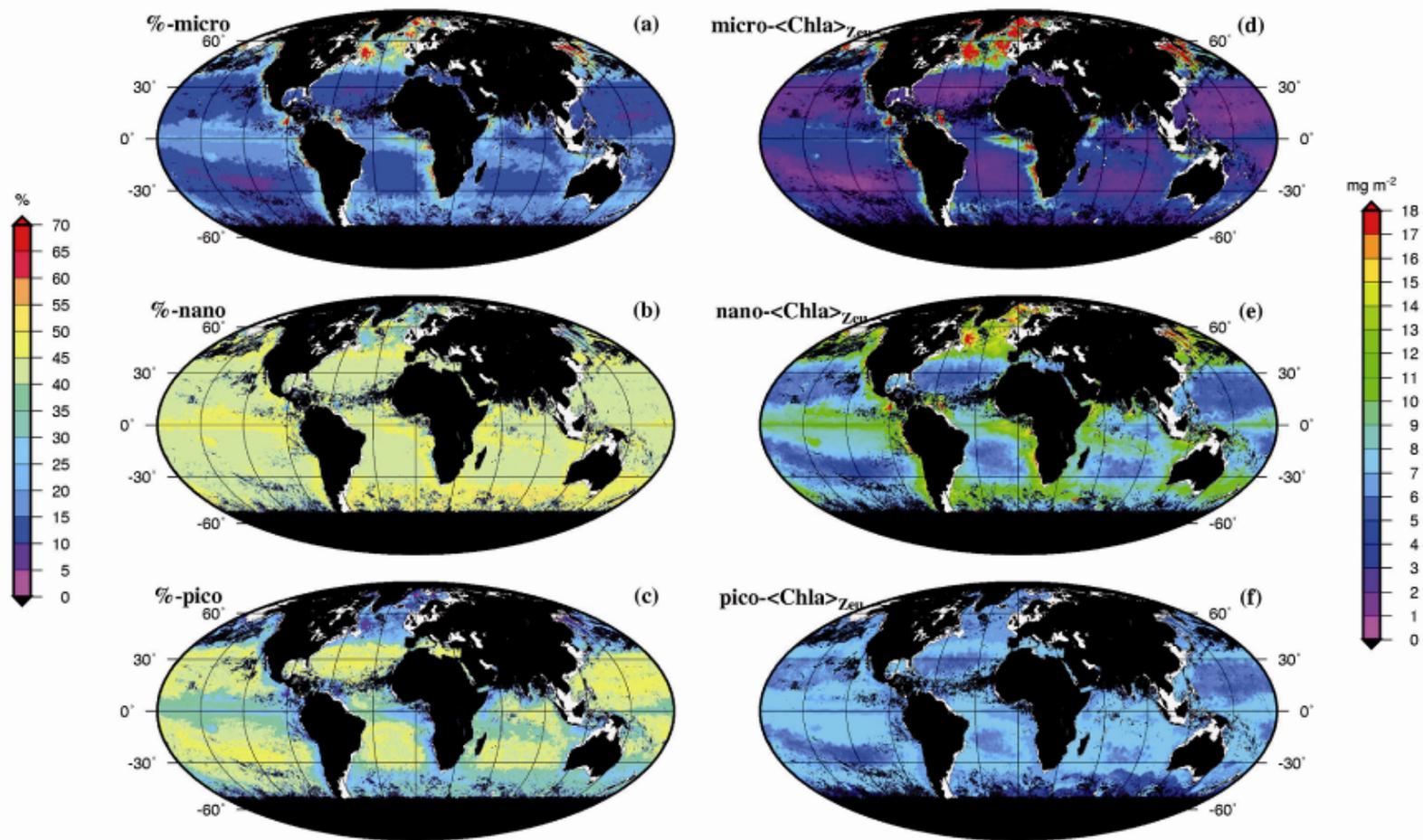


Figure 38: From Uitz et al. 2006. Phytoplankton community composition for June 2000 (SeaWiFS composite): (a–c) phytoplankton fractions (f_{micro} , f_{nano} and f_{pico} in %) within the 0–1.5 Z_e layer, and (d–f) integrated contents within the same layer (B_{micro} , B_{nano} and B_{pico} in mg m^{-2}). Coastal areas (less than 200 m deep), large lakes and inland seas are represented in white.

6.2.2. *Constant flux decrease with depth*

Several authors have observed situations where particle flux increases with depth. This increase can be measured when sediment traps are deployed in different water masses. This apparent increase of carbon flux with depth has been attributed to advection processes. Sediment trap deployment in a nepheloid layer can lead to similar observations when strong currents carry sediment from a continental slope.

Others observation reports localized increase of carbon flux without apparent advection (Karl and Knauer 1984; Nodder 1997). For these situations, a likely explanation is that the increase of carbon flux is due to the mesopelagic biological activity however leading to a mass conservation problem. Where does the carbon come from?

UVP profiles can provide aggregate flux estimates with high vertical resolution. In this dissertation, flux variations with depth have not been systematically studied. However several profiles of the database present a deep increase or a deep maximum of the particle flux. Chapter III, Figure 20, is a good example of flux increase in the mesopelagic zone at latitude 0° and 6°S around 500 m. In this REGION, THE flux increase was attributed to AN accumulation caused by oceanic circulation. What is the impact of such increase on the mesopelagic communities? These locals increase of flux could lead to intense biological activity and formation of new fresh aggregates. Future studies could be focused on these specific profiles in order to identify reasons of this deep maximum. What processes could lead to increase the carbon flux with depth? What is the impact of such increase for the mesopelagic microbial, zooplankton and fish communities? Is this phenomenon local or global? Several ways can be explore to answer these questions. Long time series with sediment trap could be use to measure mesopelagic flux increase and analyse environmental available data. However chance to identify these events are low with discrete data. Development of platforms with sediment trap coupled to UVP could provide unique valuable data extremely useful to answer to previous questions.

6.2.3. *Carbon flux and spatial heterogeneity*

Oceanic mesoscale structures, such as frontal zones and eddies, have been shown to drive the aggregate export from the euphotic to the mesopelagic zone over relatively short horizontal scales (<100 km). The Ebene cruise data from the Equatorial Pacific have been used in chapter III to highlight horizontal and vertical variation of flux related to mesoscale oceanic circulation. Previous study had described this mesoscale particle distribution driven by physics, but data were still too sparse to understand the mechanisms (Walsh et al. 1997) and to assess if it was a general pattern in the different oceans. Chapter IV was also a very good example of flux spatially constrain by oceanic circulation in the North Atlantic. In the Mediterranean Sea, the horizontal scale of flux variations is even shorter (around 10 km). Our study has shown that deep mesoscale particle distribution associated to frontal systems and eddies are commonly found in the oceans. What is the implication of these structures for fluxes at the global scale? What is the error mad by global biogeochemical models missing these mesocale flux variations? Is a regional modelling approach needed for realistic global carbon flux estimates?

Carbon flux heterogeneity may have implications for feeding by mesopelagic organisms. Carbon flux localized in a spatially limited area could enrich the deep water in fresh material produced at the surface. Deep water enrichment could generate patches of zooplankton feeding on settling particles. How does this localized export modify the deep living organism distributions? How important are these fluxes to sustain deep life?

The structured and homogenized database of aggregate size distribution and biological and physical parameters of the upper 1000 m of the water column built during my research project led to original results on the carbon export at global and regional scale. We especially have shown how useful the aggregate size distribution is to independently estimate flux (chapter III), to probe biological (chapter IV) and hydrodynamic (chapter V) processes at the origin of spatial flux variability. Aggregate size distribution seems to be a key parameter that needs to be retrieved on larger scale in the future in order to better understand the carbon cycle at global and/or regional scale.

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APPENDIX A

ARTICLE A

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Vertical distribution of aggregates (>110 μm) and mesoscale activity in the northeastern Atlantic: Effects on the deep vertical export of surface carbon

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Abstract

Spatial and temporal variability in the distribution of marine aggregates (>110 μm) was studied using underwater video profilers in an area off the Iberian Peninsula and Azores Islands dominated by mesoscale and submesoscale hydrodynamics in winter, spring, and summer 2001. In the 0–200-m layer, aggregates were most abundant in spring (100–120 mg dry weight [dry wt] m^{-3}) and lowest during summer and winter (1–10 mg dry wt m^{-3}). In the deeper layers (down to 1,000 m), the seasonal pattern was different, with concentrations highest in spring and summer, and lowest in winter (e.g., at 800 m, 5–10 mg dry wt m^{-3} in spring and summer; 1–5 mg dry wt m^{-3} in winter). The seasonal change in the abundance of aggregates in the upper 1,000 m was consistent with changes in the composition and intensity of the particulate flux recorded in sediment traps and with seasonal changes in the surface phytoplankton community. In an area dominated by eddies, surface accumulation of aggregates and export down to 1,000 m occur at mesoscale distances (<100 km). The occurrence of a rich aggregate layer may be related to mesoscale activity in water flow that drives nutrient inputs, phytoplankton production, and the formation of large aggregates. Such spatially constrained zones of massive export may be typical of frontal open-sea systems, and may have been missed by conventional sediment trap moorings, which cannot resolve export at this mesoscale level.

APPENDIX B

ARTICLE B

Particle size distribution and flux in the mesopelagic: a close relationship.

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Abstract

Large aggregates commonly named “marine snow” are difficult to collect and study because of their fragile nature but they comprise the largest fraction of vertical carbon flux in the ocean. Developments in imaging sensors and computer systems have facilitated the development of *in situ* image acquisition systems that can be used to produce profiles of aggregate size distribution and abundance. However, it is difficult to collect information on the different properties of particles, such as their composition, from *in situ* images. In this paper, we relate sediment trap data to particle size (d) distributions to estimate the vertical fluxes (F) of mass, particulate organic carbon (POC), particulate inorganic carbon (PIC) and particulate organic nitrogen (PON) using simple power relationships ($F = A \cdot d^b$). Mean aggregate fractal dimension of 2.1 and a size-dependent settling speed are determined from the flux estimations. We have used these relationships to map the distribution of mass flux along 180°W in the Equatorial Pacific. Similar mass fluxes below the euphotic zone have been reported along 150°W for the same period with conventional sediment traps, supporting the accuracy of these relationships. The high spatial resolution of sedimentation processes studied *in situ* with the Underwater Video Profiler allowed to undertake a detailed study of the role of physical processes in vertical fluxes.

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APPENDIX C

ARTICLE C

A new procedure to optimize the selection of groups in a classification tree: Applications for ecological data

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Abstract

Agglomerative cluster analyses encompass many techniques, which have been widely used in different fields of science. However in biology and ecology, the datasets are generally highly variable, which increase the difficulty to identify statistically relevant number of clusters. We developed a new algorithm, which aims to identify statistically the optimal level of partition in a classification tree using a generated random observation or variable. The Random Simulation Test (RST) is evaluated against (1) the well-known Iris dataset (Fisher 1936), (2) predetermined clustered data generated automatically by the procedure of (Milligan and Cooper 1985) and finally (3) applied on real ecological data analyzed in Beaugrand et al. (2002). The RST performed generally well on simulated data and especially when the datasets were highly variable.

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APPENDIX D

ARTICLE D

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Effects of frontal processes on marine aggregate dynamics and fluxes: An interannual study in a permanent geostrophic front (NW Mediterranean)

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Abstract

This study provides and discusses the spatial distributions of abundances and sizes of marine-snow aggregates across the Ligurian Sea frontal system. A cross-front transect was sampled 34 times between 1992 and 1996, using the Underwater Video Profiler (UVP). Atlantic Water flows parallel to the Ligurian coast in the NW Mediterranean Sea, where that current creates a quasi-permanent front that separates the central and coastal waters. The horizontal distribution of aggregates ($> 150 \mu\text{m}$ ESD, Equivalent Spherical Diameter) in the upper 1000 m shows two main features. First, the smaller aggregates ($150 \mu\text{m} < \text{ESD} < 1 \text{ mm}$) are more abundant in coastal waters, as a result of continental input, cross-slope export, and re-suspension along the slope. The layers that contain very high concentrations of small aggregates are observed from surface down to 1000 m, and extend from the continental slope to the front. Second, the concentrations of large aggregates ($\text{ESD} > 1 \text{ mm}$) are highest in and under the frontal zone, probably as a result of physical coagulation, and/or biological transformations. The seasonal intensity of large aggregate accumulations in and under the frontal structure seems to be more related to the autumn–winter increase in sub-mesoscale and mesoscale activity of the current flow than to the surface phytoplankton biomass. Interestingly, the horizontal distribution of aggregates is affected not only in the frontal zone (0–300 m depth), but also deeper down to 1000 m, probably as a consequence of rapid sinking or vertical transport. Results suggest that the settling of large aggregates under the frontal zone may limit the cross-slope transport of fine-grained particles by coagulation due to differential settling between the small particles suspended in the continental nepheloid layer and the large aggregates. This process, which takes place in sub-mesoscale zones (5–10 km wide), was also observed in one other front in the Western Mediterranean Sea. This led us to hypothesize that the impact of frontal processes on particle and aggregate dynamics might be generalized. Since fronts exist in many other coastal regions, the vertical fluxes at sub-mesoscale may have consequences for the transport of continental particles to the ocean's interior.

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Keywords: Marine-snow; Aggregates; Plankton; Vertical flux; Fronts; Mesoscale features; Mediterranean Sea

APPENDIX E

ARTICLE E

Global biogeography of fragile macrozooplankton in the upper 100-1000 m depth inferred from the Underwater Video Profiler.

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Abstract

Mesopelagic gelatinous zooplankton fauna are insufficiently known due to inapt and infrequent sampling, but may have important trophic roles. In situ imaging systems and undersea vehicles have been used to investigate their diversity, distribution and abundance. The use of different platforms, however, restricts the comparison of data from different regions. Since 2001, the Underwater Video Profiler (UVP) has been deployed during 12 cruises in six oceanic regimes (Mediterranean Sea, North Atlantic shelves, Mid-Atlantic ridge, tropical Pacific Ocean, eastern Indian Ocean, and sub-Antarctic Ocean) to determine the vertical distribution of organisms in the uppermost 1000 m. A total of 9 oceanic provinces were identified based on the hydrological properties of the water column. Twenty-one morphotypes have been recognized: sarcodines (8 groups), ctenophores (2 groups), siphonophores, medusae (5 groups), crustaceans, chaetognaths, appendicularians, salps, and fishes. The similarity in the morphotype assemblages of zooplankton was significantly higher within regions than between regions in most cases. The regions correspond to nine of the biogeochemical provinces defined by Longhurst (1998), suggesting that the spatial structuring of the mesopelagic is similar to that of the epipelagic. These results suggest that the vertical export of particles from the surface ocean can be the link between the epi- and mesopelagic zones.

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APPENDIX F

ARTICLE F

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Volume distribution for particles between 3.5 to 2000 μm in the upper 200 m region of the South Pacific Gyre

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Abstract

The French JGOFS BIOSOPE cruise crossed the South Pacific Gyre (SPG) on a transect between the Marquesas Islands and the Chilean coast on a 7500 km transect (8°S – 34°S and 8°W – 72°W). The number and volume distributions of small ($3.5 < d < 30 \mu\text{m}$) and large particles ($d > 100 \mu\text{m}$) were analysed combining two instruments, the HIAC/Royco Counter (for the small particles) and the Underwater Video Profiler (UVP, for the large particles). For the HIAC analysis, samples were collected from 12 L CTD Rosette bottles and immediately analysed on board while the UVP provided an estimate of in situ particle concentrations and size in a continuous profile. Out of 76 continuous UVP and 117 discrete HIAC vertical profiles, 25 had both sets of measurements, mostly at a site close to the Marquesas Islands (site MAR) and one in the center of the gyre (site GYR). At GYR, the particle number spectra from few μm to few mm were fit with power relationships having slopes close to -4 . At MAR, the high abundance of large objects, probably living organisms, created a shift in the full size spectra of particles such as a single slope was not appropriate. The small particle pool at both sites showed a diel pattern while the large, implying that the movement of mass toward the large particles does not take place at daily scale in the SPG area. Despite the relatively simple nature of the number spectra, the volume spectra was more variable because what were small deviations from the straight line in a log-log plot were large variations in the volume estimates. Results showed that the volume of large particles can equal the volume of the smaller particles. However the proportion of material in large particles decreased from the mesotrophic conditions at the border of the SPG to the ultra-oligotrophy of the center in the upper 200 m depth. We expect large particles to play a major role in the trophic interaction in the upper waters of the South Pacific Gyre.

VITA

Lionel Guidi was born in Monaco. His parents are Jean-François Guidi, of Roquebrune, and Martine Royale from Sospel, both towns in South France. Lionel earned a B.S. in organisms biology at the University Aix-Marseille III in 2002 spending a year at the Université du Québec à Rimouski (UQAR). Then he earned an M.S. in biological oceanography and marine environment with marine ecosystem modelling and data analyses specialization in 2004, and a Ph.D. in oceanography at Texas A&M University in 2008 and at the Université Pierre et Marie Curie in Paris in France in 2008.

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